A riparian perspective on species ecology and evolution: *Melaleuca leucadendra* (Myrtaceae)

Thesis submitted by

Caroline Chong, BSc(Hons) Adelaide

in May 2008

for the degree of Doctor of Philosophy

in the School of Marine and Tropical Biology

James Cook University

Statement of access

I, the undersigned, author of this work, understand that James Cook University will make this thesis available for use within the University Library and, via the Australian Digital Theses network, for use elsewhere.

I understand that, as an unpublished work, a thesis has significant protection under the Copyright Act and;

I do not wish to place any further restriction on access to this work.

30 June, 2008

Signature Date

Statement of sources

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

30 June, 2008

Signature Date

Statement on the contribution of others

Supervision

My principal supervisor was Associate Professor Michelle Waycott and my co-supervisors were Dr Will Edwards and Professor Richard Pearson.

Funding and in-kind support

- Australian Centre for Tropical Freshwater Research, James Cook University (ACTFR)
- Land & Water Australia
- Cooperative Research Centre for Tropical Savannas Management
- School of Marine and Tropical Biology, James Cook University (JCU)

I received an Australian Postgraduate Award, a Land & Water Australia/ACTFR Riparian Research Postgraduate Scholarship, and a CRC for Tropical Savannas Postgraduate Scholarship (Top Up).

Co-authorship

One chapter of my thesis has been published, Chapter 3. My co-authors, Will Edwards and Michelle Waycott, made contributions to the development and overall interpretation of results, as well as substantial editorial suggestions, but the work is primarily my own.

Logistic and editorial assistance

Michelle Waycott, Will Edwards and Richard Pearson, my supervisors, provided editorial comments on all sections of this thesis.

Ainsley Calladine and Michelle Waycott assisted invaluably in figure preparation and in the editorial preparation of this thesis.

Mirjam Maughan, John L. Dowe and ACTFR staff contributed assistance with GIS applications, figure preparation and field trip logistics.

Analysis facilities

MegaBACE genotyping was conducted at the Advanced Analytical Centre, Genetic Analysis Facility, JCU.

DNA sequences were conducted at the Advanced Analytical Centre, Genetic Analysis Facility, JCU and by Macrogen Inc., South Korea.

Bayesian phylogenetic data analyses were facilitated by resources at the High Performance Computing Unit, JCU and the Australian Partnership for Advanced Computing.

Acknowledgements

The production of this thesis was immensely challenging, and immensely enjoyable. I am deeply grateful for the support of the many individuals and organisations behind its evolution.

To my supervisors and supporters:

Michelle Waycott—for knowledge, patience, and extremal time and effort; for encouraging and understanding my exploration of new research concepts; for questioning me towards the broader perspectives; and especially for our shared enjoyment of research itself;

Richard Pearson—for constant support and deep perception, words of guidance and sage wit;

Will Edwards—source of inspiring insights and innovative thinking, and great encouragement.

I thank the Australian Centre for Tropical Freshwater Research, in particular John L. Dowe and George Lukacs, for introducing me to northern Australian riparian landscapes, facilitating the financial and logistical aspects of my research, and humouring my extended office lodgings.

I am very appreciative to the Cooperative Research Centre for Tropical Savannas Management and the School of Marine and Tropical Biology, James Cook University, which also provided core financial support for my research and scope of learning.

For the opportunity to learn with you and from your insights, I especially thank:

John L. Dowe, for memorable Vivaldi-filled field trips in the Upper Burdekin river catchment;

Ainsley Calladine;

Michelle Waycott and Ainsley Calladine for understanding, supporting and very kindly lodging me during the 'write-up' phases—not least in Charlottesville, Virginia, as the leaves fell;

Keith F. Walker, thoughtful mentor from afar;

And to Tom Rayner, Zoe Baker, Jodi Rowley, Karin Kassahn, Allyson Lankester, Michelle Boyle, Lauryne Grant and Adrian McMahon for sharing the postgraduate experience, some discoveries, much life, and many laughs…

Thank you.

- caroline

Abstract

This thesis investigates structure and survivorship in vegetation that inhabits disturbance-driven riparian environments. The outcomes of this thesis contribute to developing a framework to test predictions of scale-dependent variation in genetic structure and functional traits in woody species in relation to patterns of disturbance. I use as a model species *Melaleuca leucadendra* (Myrtaceae)—the paperbark tree that inhabits river systems across northern Australia. These environments are sub-humid and seasonally arid, typical of dry southern hemisphere subtropical biomes, and are among the most hydrologically variable systems on a global scale. In these river systems, the flow regime features stochastic high-energy floods and seasonal drought. The genus *Melaleuca* is a major group in the family Myrtaceae and is dominant in riparian habitats. *Melaleuca* displays diverse phenotypes and unclear taxonomic boundaries. I aim to improve our understanding of how members of this genus persist and the influence of the environment on genetic processes within this lineage. This will contribute to a broader understanding of the interaction between plant ecological strategies and drivers of evolutionary change, with special relevance to questions related to species persistence in disturbance-driven ecosystems.

I demonstrated high capacity for stem resprouting in *Melaleuca leucadendra* throughout the seedling life stage and strong spatial aggregation of stems relating to clonal genotypic structure in the mature life stage. These results agree with the theory that resprouting, as a clonal growth mechanism, confers advantages for survival against physical disturbance. It also demonstrates that environmental pressures can influence above-ground spatial genetic structure of ramets through increased spatial aggregation of stems. In *M. leucadendra* and *Eucalyptus camaldulensis*, two conspicuous species that occupy niches with elevated hydrological stress, the physiological capacity to resprout is independent of seed size and relative growth rate, is acquired very early in ontogeny and is maintained during seedling growth. Thus conventional explanations for resprouting as a resource-constrained trait do not account for this pattern. Resprouting more plausibly reflects a biological solution for generalised physiological tolerance across individual life spans. Spatial genetic analyses conducted on adult-stage *M. leucadendra* provided evidence of selection for resprouting. The probability of detecting clonal ramets was far greater at three mainstream locations than at a headwater location differentiated by hydrological energy. Clonality was detected in 42 genotypes (30% of mainstream samples) in the range 0.12–17 m, corresponding to clumps of stems within groves. In contrast, there was no evidence that clonal growth extends genetic structure beyond 20 m, or at any scale at the headwater location (all 90 genotypes unique).

Data from these studies support clonal growth as a principal mechanism defining survival and dominance in river environments subject to unpredictable and severe

fluvial disturbance. In addition, non-clonal dispersal via the river system appears to constrain population connectivity. No relationship was detected between spatial proximity and genetic relatedness among individuals within sampled populations (here 600 m channel lengths) whereas a pool of common genotypes was detected over distances greater than 100 km in the river system. In addition, mainstream and headwater locations are differentiated by an order of magnitude difference in disturbance as assessed using stream-power distributions and flood extreme event analysis. These stream types (mainstream and headwater) feature strong population structure and genetic differentiation mechanisms with low probabilities of allelic exchange. This suggests a process hierarchy whereby (i) resprouting in response to disturbance promotes individual survival (i.e. clonality); (ii) fluvial action, including floods and channel re-structuring, causes stochastic changes in demography and genetic connectivity; (iii) periods of genetic and fluvial connectivity result in admixture among mainstream locations forming a common genotype pool; (iv) selection occurs for phenotypic tolerance to variable environmental stresses enabling niche persistence.

In this thesis I have demonstrated that a hierarchy of scales is a useful construct to examine organismal life-history strategies. Valuable insights may be gained from extension beyond conventional concepts of biological units as individuals, populations and species. *Melaleuca leucadendra*, the focus of this thesis, represents an example of how individuals, populations and species are interlinked by genetic exchange. In addition, feed-back with abiotic processes such as natural disturbance provides both a driver of, and a barrier to, evolutionary change (speciation). The phenotypic variability observed in this group across all levels represents both an expression of (selection for adaptability) and a solution to (environmental stochasticity) evolutionary drivers acting at different spatial and temporal scales. This warrants further investigation in the context of the poorly-studied arid and sub-humid Australian flora. Adaptability in phenotypic and evolutionary responses may be common in taxonomic groups that do not exhibit rapid radiations under variable environmental conditions.

Table of contents

List of tables

List of figures

Chapter 1—Introduction

This thesis explores survival strategies in riverine vegetation and the implications for species structure and evolution. Rivers and riverine environments present substantial challenges to the recruitment and survival of plants, especially in systems that are prone to unpredictable floods and droughts. These environments therefore present an opportunity to investigate the interlinked processes of ecology, genetics, population biology and species evolution in potentially extreme conditions where traits should be highly adaptive. I have adopted an hierarchical framework, including spatially explicit studies of genetic structure at individual, population and species levels. Hierarchical frameworks offer great potential for studying biological phenomena such as growth, survival and dispersal in plant species because our understanding of these processes, which form continuous distributions in the life history of a plant, depends upon our scales of interpretation. Biological concepts are based on phenotypic and/or genetic differentiation at scales that may not well describe the role of environmental processes in adaptability. Understanding of these processes informs the debate on what constitutes a population or a species, a primary question pertaining to research in ecological theory, genetics, functional biology, cladistics and conservation biology. Interaction among demographic, genetic and abiotic environmental processes is important to interpret plant ecology and evolution because these interactions continuously shape the probabilities of establishment, persistence and gene flow, driving the distributions of genetic and functional diversity (Diaz and Cabido, 2001).

In this thesis, I utilise molecular population genetic, phylogenetic and experimental approaches to infer the processes that shape phenotypic traits and genetic structure. Understanding the interaction between biotic and abiotic mechanisms that may select for alternative life histories requires assessment of them at spatial and temporal scales ranging from individuals to ecosystems (Levin, 1992; Dale, 1999; Legendre et al., 2002; Lichstein et al., 2002). Riverine landscapes exemplify the concept of open, non-equilibrium ecological systems because of the operation of multi-scale interactions between physical and biological phenomena (Malanson, 1993; Tabacchi et al., 1998; Ward et al., 2002). River systems reflect a distinctive mix of both terrestrial and aquatic landscape elements, including vegetation systems, surface waters, and geomorphic features such as channel networks. Fluvial processes including flooding, erosion, transport and deposition dynamically link these elements longitudinally, laterally and vertically (Malanson, 1993), which combine to generate complex habitat dynamics.

For riverine vegetation, fluvial action acts as a physical means of dispersal as well as an agent of disturbance and landscape change. For example, stream flow can disperse plant propagules and promote gene flow. Fluvial disturbance may also impact directly on genotypic variation (McLellan et al., 1997). Floods damage, scour, inundate, bury, uproot, or transport plant vegetative parts as well as propagules, causing changes in the

demographic structure of existing populations as well as altering gene frequencies within them. Moreover, disturbance due to fluvial action may act as a selective agent on life-history attributes such as clonal growth, leading to a multi-stemmed habit (Barsoum, 2002; Rood et al., 2003). Clonal growth has two benefits for plants experiencing unpredictable fluvial disturbance. First, it increases structural tolerance to scouring and flood impact, promoting individual survival. Second, resprouting ability that exists as a prerequisite for clonality allows for rapid re-establishment of above-ground biomass following disturbance, promoting individual competitive ability and longevity (Peterson and Jones, 1997).

Stream flow variation and predictability interact with species' life histories, in particular reproductive strategies (Puckridge et al., 1998). Although models of the functioning of riparian vegetation imply an understanding of the linkage between biological processes and fluvial processes, the multiple scales across which they interact are not well resolved. Thus, current understanding required to fully interpret demographic structure in riparian vegetation is lacking. For example, the Flood Pulse Concept (FPC) (Junk et al., 1989), which describes seasonal processes in large tropical rivers, implies that regular flood pulses exert strong influence on patterns of recruitment that structure species demography. However, the FPC was based on systems with predictable flood events, and did not adequately acknowledge that channel connectivity and floods can vary extensively even within river systems (Puckridge et al., 1998). In semi-arid systems, riverine habitat represents a mosaic of interactions among spatial elements, vegetation and physical states that change recurrently as a function of highly variable climatic and fluvial activity. These factors dictate that germination, establishment, survival and dispersal events in riparian vegetation follow highly unpredictable distributions.

To develop hypotheses about ecological patterns and processes such as dispersal and survival and the evolutionary implications of them, spatially explicit genetic information can be utilised (Ouborg et al., 1999; Ennos, 2001; Silvertown, 2001). Importantly, data obtained from molecular markers can be used to identify the spatial architecture and distribution of genetic individuals which may be cryptic in species exhibiting clonal growth forms (Suzuki et al., 2004). Molecular techniques offer greater utility than field excavations to discriminate between offspring derived from vegetative or sexual regenerative events, and to quantify the spatial influences of clonal growth on genetic variability. Genetic tools thus provide potential insight into the demographic and evolutionary implications of growth traits; that is, effects on overall species' fitness.

Genotypic information also allows estimates of genetic structure and connectivity in dynamic or fragmented landscapes, and the relative contributions of pollen and seed to effective gene flow (Nathan, 2006). For example, Bacles *et al*. (2006) used seedling and parent microsatellite genotype data to assess the spatial distribution of seed-mediated gene dispersal in *Fraxinus excelsior* (common ash, Oleaceae) across a fragmented forest

landscape. Up to 53% of realised seed-mediated gene flow occurred from outside the 900 ha study region, suggesting that long-distance seed dispersal events help maintain genetic connectivity and that long-distance gene flow events may occur across tens of kilometres (Bacles et al., 2006). This implies that large dispersal events—that is, events at the outer tails of dispersal distributions—can have a disproportionate influence on shaping genetic structuring in excess of that predicted from estimates of the mean spatial or temporal trends derived from the events distributions. In such cases it is likely to be the outer extreme of the dispersal distribution that influences gene flow and the probability of colonising new habitats. However, conventional modelling and empirical approaches rarely accommodate the distribution tails of ecological phenomena when inferring demographic structure and processes (Katz et al., 2005).

In large Australian river systems the disturbance regime, that features seasonal aridity interspersed with episodic channel-changing floods, may determine the fitness value of phenotypic strategies. Within this environment, *Melaleuca* species (the paperbarks) are ecological specialists. Indeed, the genus is dominant in disturbance-driven ecotones throughout many biogeographic regions in Australia. The genus also displays extreme phenotypic variability (Specht, 1990; Fielding et al., 1997), for example, *Melaleuca* occupies diverse habitats, from open heath in semi-arid south-western zones where they typically occur as low shrubs, to woodland riparian systems in the northern dry tropics where a large tree habit predominates (Barlow, 1988; Wrigley and Fagg, 1993; Craven and Lepschi, 1999). The diverse conditions in which the genus is found display various environmental pressures, including fire, drought and flood (Crandall et al., 2000; Ackerly and Cornwell, 2007).

This study focuses on the 'broad-leaved' *M. leucadendra* species complex, which includes taxa that have a large-tree habit and are sympatric in semi-arid to sub-humid seasonally inundated riparian habitats (Craven and Lepschi, 1999). Taxonomic resolution between putative taxa (species) is poor, but it is unknown whether this represents a lack of informative data or inadequate species resolution. Therefore, *Melaleuca* occupying natural river environments provides a potentially ideal system to study the interactions between biophysical processes and processes of gene flow that could determine survivorship and genetic differentiation.

The taxon *M. leucadendra* (L.) L. is considered to represent the ancestral generic state of the *M. leucadendra* group (Barlow, 1988). It is mono-dominant in high-disturbance river channels in northern Australian semi-arid systems (Figure 1.1). It is tolerant of the characteristic conditions of these environments, such as extreme fluvial disturbance, physical scouring and submersion as well as periods of prolonged drought. *Melaleuca leucadendra* also displays distinctive phenotypic characters, such as a capability for clonal growth via resprouting, which suggests that resprouting is a mechanism for persistence under selective conditions (Table 1.1). Moreover, the unpredictable nature of floods in these environments means that gene transfer (either via seed or propagule

transport) is highly stochastic. Mechanisms for survival and genetic variability might both be expected to reflect the influence of fluvial processes, but may also, themselves, influence the physical properties of river dynamics (Tabacchi et al., 1998; Ward et al., 2002). For example, the persistent multi-branched stem and root systems of mature trees are a structural element of the river bed that facilitates alluvial deposits during floods (Fielding et al., 1997; Fielding and Alexander, 2001). The feed-back between biological structure, habitat structure, stream flow, sediment transport and deposition enhances the role of *Melaleuca leucadendra* as keystone in the riparian ecosystem.

New analytical pathways that incorporate probabilistic methods are needed to integrate genetic and ecological concepts of plant populations and species (Silvertown and Antonovics, 2001; Manel et al., 2003). Examining genetic connectivity at the intra-species level is important because genetic exchange within and among populations acts as a mechanism for trait heritability (Whitham, 2003). Gene flow among interacting populations maintains ecologically important phenotypes that could promote species-level persistence and evolution, and shape species' niche occupancy. In turn, the spatio-temporal distribution of genetic connectivity could be expected to reflect the fluvial disturbance regime, which may vary at the within-river scale.

Thesis structure

In this thesis, I investigate plant phenotypic responses and genetic structure in the riparian vegetation of a disturbance-driven river system. I use as a model taxon *Melaleuca leucadendra* in the Burdekin River catchment, north-eastern Australia (Figure 1.2). This catchment spans approximately 400,000 km^2, includes semi-arid to sub-humid climatic zones, and features extreme and multi-scale stream flow variations. *Melaleuca leucadendra* is dominant in the Burdekin River system, while the *M. leucadendra* group occurs across all riparian environments in northern Australia, demonstrating its success in these disturbance-driven systems. Thus the study of this taxon in the riverine environment is a useful system in which to investigate the interplay between biological and abiotic processes.

I utilise experimental methods to assess riparian survival life histories (resprouting) in a cross-species context. I then apply spatially explicit analyses of genotypic structure in riverine *Melaleuca* as a mechanistic basis to examine the spatial, genetic and evolutionary implications of resprouting. I develop an events-based conceptual approach to assess spatial genetic structure in relation to within-river fluvial disturbance regimes, because individual fluvial events represent the relevant scale at which to expect interactions with survivorship and shifts in both landscape and genetic connectivity. I investigate population-level genetic structure and connectivity using probabilistic methods assuming non-equilibrium states of genetic exchange. I use this hierarchy to interpret the ecological genetic processes underlying phylogenetic relationships among taxa at population and species levels.

First, I present a review of the fluvial environment driving habitat disequilibria, and the ecological and evolutionary implications of disturbance for plant life histories (Chapter 2).

Second, I address my research questions, as follows:

(i) What relationships exist among functional traits for survival, growth attributes and seed size? I use experimental techniques to quantify the relationships among these factors (Chapter 3). Differences in growth strategies and survivorship potentially reflect, and help explain, species-level differences in niche occupancy and life histories.

(ii) What evidence exists for spatial genetic structure among individuals as a function of a clonal growth strategy? The ecological neighbourhood defines the area within which individual plants and their genes potentially interact through the processes of growth, regeneration and dispersal. I first use events-based hydrological modelling to define the temporal and spatial scales of variation in flood distributions within the study river system. I then use genetic tools (multilocus genotypes based on 8 polymorphic microsatellite loci) to quantify spatial architecture and genotypic relatedness among above-ground stems. This approach is important, because these factors are those expected to interact with fluvial regime, thus linking scales of observation, analysis and inference on demographic structure at the level of the population and higher (Chapter 4).

(iii) At what scales do spatial genetic structuring and contemporary patterns of gene flow operate in a disturbance-driven river system? I implement Bayesian clustering methods to infer population structure on the basis of microsatellite marker based allelic identity and estimate contemporary gene flow accounting for genetic drift-dispersal disequilibrium. I use this information to evaluate the spatial and temporal patterns of genetic structure and connectivity in the study system in relation to dynamic fluvial processes (Chapter 5).

(iv) What evidence exists for phenotypic and genetic connectivity among *Melaleuca* taxa at the level of species? I implement a nested taxon sampling strategy at population and species levels to investigate the phylogenetic basis of reticulate evolutionary patterns and phenotypic diversity among *Melaleuca* species. I use information on scale-dependent ecological and genetic structure derived from this thesis (chapters 3 to 5) to generate hypotheses about the processes driving population and species-level life-histories and evolutionary signatures (Chapter 6).

Finally, I synthesise my research findings developed from this thesis in the context of the fluvial processes explored in chapters 1 and 2. On the basis of these findings, I propose pathways to integrate process-based concepts of environmental disturbance and spatial genetic structure to contribute to plant ecological research (Chapter 7).

Tables and figures

Table 1.1. Summary of clonal growth mechanisms in *Melaleuca leucadendra* recorded from field observations in this research and following terminology of Lacey and Johnston (1990) and Jenik (1994) for woody plants.

Loss of apical dominance: unspecialised mainstem bases	Epicormic growth: vertical growth from epicormic shoots of fallen mainstem
	
Epicormic growth: branch layering	Root suckering
	
Epicormic growth: vertical shoot growth from lateral branches	Stem resprouting
	

Figure 1.1. Characteristic riverine habit (a) and woody capsules (b) of *Melaleuca leucadendra* in the Upper Burdekin River catchment, north-east Queensland, Australia.

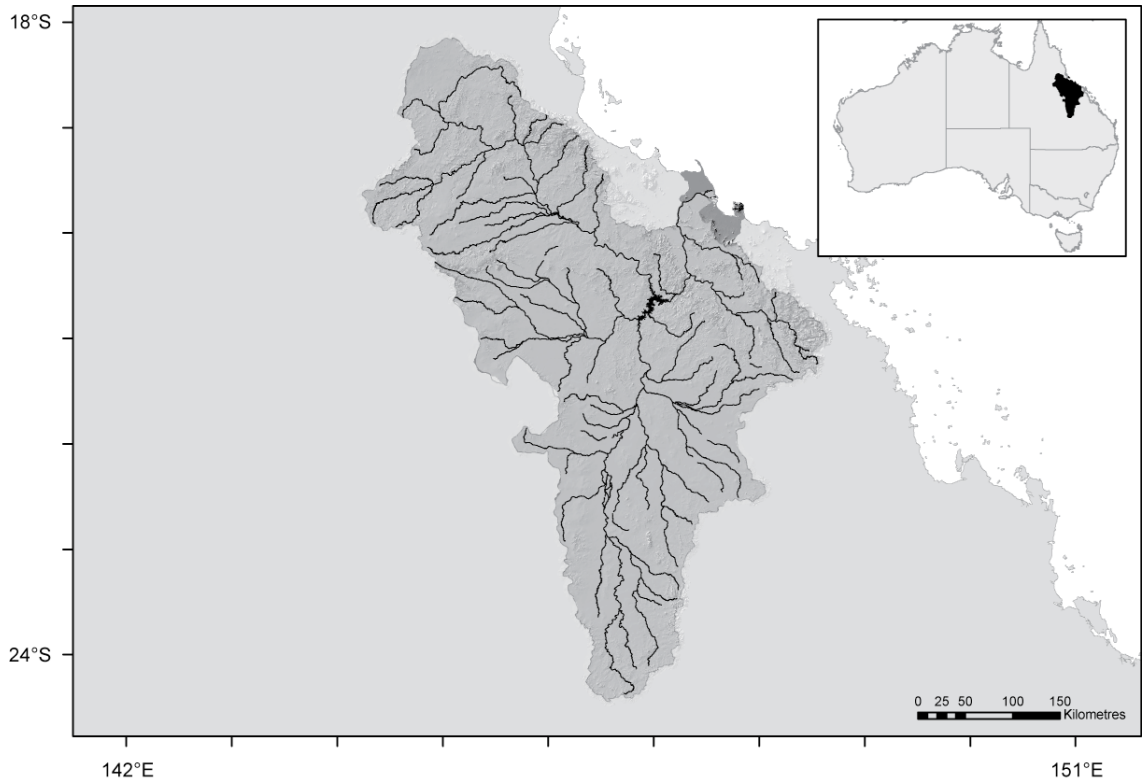


Figure 1.2. Geographic location of research study region: the Upper Burdekin River catchment, north-east Australia.

Chapter 2—Survivorship and evolution in riparian vegetation

This chapter reviews current concepts of the fluvial processes and biophysical characteristics that dictate landscape structure, connectivity and change in riverine environments. The focus of this review is to characterise, from the perspective of plant life history, the fluvial regime of large semi-arid river systems and the potential interplay disturbance enforces between survivorship, gene flow and evolution in riverine vegetation. I synthesise current knowledge about riparian woody plant life histories using *Melaleuca leucadendra* as a case study and evaluate existing ecological theories about survival and dispersal traits and population genetic structure in river systems. This provides the contextual argument and basis for the empirical studies presented in the following chapters of this thesis. I propose that process stochasticity plays a fundamental role in defining complex biological and phylogenetic structure as evidenced in *M. leucadendra*.

Semi-arid Australian riparian systems: the physical context

Large river systems in humid, seasonally arid regions are challenging environments for plant growth and survival. In these systems, monsoonal and seasonal rainfall patterns generate extreme fluvial variability across intra-annual to centennial scales (Fielding and Alexander, 1996; Pringle, 2000). Episodic high-energy, short-duration floods cause sediment mobilisation and severe channel scouring, causing frequent changes in habitat structure (Alexander et al., 1999b). In turn, habitat availability for seed bank development, germination and establishment processes are constrained by seasonal drought conditions which may last up to nine months in any year (Fielding et al., 1997; Pettit and Froend, 2001b). As a function of these climatic drivers, habitat structure differs between locations within river systems and between successive flood events, indicating the need to investigate local-to-regional-scale implications of this variability on riverine vegetation function.

Large semi-arid river systems such as the Cooper, Diamantina and Burdekin River catchments in Australia are among the most fluvially variable on a global scale. For example, comparison of 52 major world river systems based on a suite of 11 measures of hydrological variability has demonstrated greatest sum variability in Australian and South African river signatures compared to all others (Figure 2.1; Puckridge et al., 1998). An outstanding challenge of Australian riparian research is to interpret the role of this variability in the temporal setting of the plant lifespan, and this requires knowledge of the population dynamics of long-lived perennial woody species. Tree species occupying semi-arid riverine habitats are subject to continuous landscape change. In this environment, allocation of meristematic and metabolic activity to functions that promote stress tolerance as well as colonisation potential should be expected. This is because these environments exert strong selection for life-history traits

that confer fitness benefits throughout the lifetime (Iwasa, 2000; Jakalaniemi et al., 2004), and the nature of the environment should exert strong selection for these life-history traits.

Contemporary perspectives on the ecology of riparian vegetation have developed mainly from studies of northern hemisphere systems that are dictated by successional landscape dynamics. There has been a persistent bias in this regard; for example, more than 80% of the research articles published between 1971 and 2006 in the leading journal *Freshwater Biology* were conducted in northern hemisphere temperate and boreal systems (Hildrew and Townsend, 2007). These systems typically focus on transitional forests that exist in environments that feature decadel- to centennial-scale major disturbance events. Thus vegetation studies from northern hemisphere regions are predicated upon successional landscape dynamics at these temporal scales. Pioneer riparian vegetation in the northern hemisphere is predominated by members of the family Salicaceae (e.g., willows and cottonwoods). Riparian Salicaceae typically are tolerant of fluvial action but are susceptible to drought (Karrenberg et al., 2002). These life-history characteristics generate species-level niche partitions demonstrated by discrete occurrences of species along elevation gradients (Rood et al., 1998; Karrenberg et al., 2002; Ward et al., 2002). In turn, large rare fluvial disturbance events, typically 1-in-100-year floods, are thought to promote periods of niche overlap between species by causing shifts in vegetation community structure and seral stage (Ward et al., 2002). Explanations for riparian life histories therefore emphasise the deterministic effects rather than stochastic effects of disturbance on demographic processes.

Successional models of ecological process in northern hemisphere riparian forests are arguably inapplicable to semi-arid systems that feature unpredictable shifts in habitat, channel and bedform structure caused by fluvial action. Floods in large semi-arid Australian river systems are typically frequent (1-in-8 year recurrence interval), short-duration, and one to three orders of magnitude greater discharge energy than in northern hemisphere river systems (cf. Pickett and Ostfeld, 1995; Callicott, 2002; Winfield and Hughes, 2002). Moreover, woody species dominate sub-tropical southern hemisphere riparian systems and are typically long lived. Long genet lifespan and tolerance to diverse hydrological extremes suggest strong continual selection for mechanisms promoting survival. Thus the evolutionary outcome of unpredictable environmental conditions in plant species, reflected in the distributions of genotypic and phenotypic variation, is likely to differ from the characteristics displayed by their northern latitudinal counterparts.

Hughes (1997) notes that in early successional riparian species such as the Salicaceae, the flux between seedling establishment and vegetative reproduction strategies vary between species, in different areas of the floodplain and in flood years of differing flood disturbance, including seasonal variations in the rooting ability of cuttings (Hughes, 1997). Importantly, species that exhibit a flexible range of reproductive strategies, that

may well reflect their evolution in highly disturbed and mobile environments, hold a wide range of regeneration niches and are less contingent on particular flood years for sustained recruitment. Thus the wide range of reproductive strategies exhibited within a species provides insight into their life-history, but may also reflect highly complex and dynamic interactions between evolutionary response, hydrology and fluvial geormorphology.

Evidence for biological "bet-hedging", associated with higher long-term survival in an unpredictably changing environment, is expected with greater environmental variance—that is, risk (Venable, 1997). Flood-driven riverine systems are a useful system to investigate evolution in plant species under environmental fluctuations that have variable distributions. Phenotypic variability may evolve as a bet-hedging strategy in plant species (Sasaki and Ellner, 1995). The phenotype distribution for a given genotype could be continuous where the probability of extreme fluctuations in the distribution of selection for an optimum phenotype is high (Sasaki and Ellner, 1995). Reiterative clonal growth, as a product of resprouting in response to disturbance, is one potential scenario of selection for bet-hedging strategies. Resprouting promotes indefinite individual lifespan, fast recovery of reproductive activity and thus strong generational overlap (Pan and Price, 2002), providing a mechanism for maintained opportunities for genetic variance under fluctuating selection intensities.

New research approaches are required to adequately model the stochastic rather than the deterministic effects of disturbance regime on species ecology and evolution. Identifying functional trait distributions and quantifying their implications for species survivorship at both seedling and mature life stages is important because trait advantages could co-vary with changes in functional priorities across an organism's life. This approach will allow insight into the value of traits in setting both (i) the regeneration niche, which concerns factors that influence the probability of juveniles recruiting successfully in different environmental settings, and (ii) the persistence niche, which deals with factors that influence the probability of an established adult plant maintaining its space in a community without seedling recruitment (Bond and Midgely, 2003). These two characteristics may operate together to shape the evolution of species' life histories.

Riparian life histories: implications of survival strategies on species ecology and evolution

Trees of the *Melaleuca leucadendra* species group are prominent as mono-specific groves in flood-exposed river channels and wetlands in north-eastern Australia (Barlow, 1988; Specht, 1990; Fielding et al., 1997). *Melaleuca* displays a range of morphological and physiological traits thought to promote survivorship under recurrent environmental perturbations. For example, *Melaleuca* species are physiologically tolerant to waterlogging and high salinity, and are mechanically resilient to the potentially

damaging effects of wind, fire, and floods (Table 2.1). Moreover, *Melaleuca* species display ready production of resprouts in the face of the loss of above-ground biomass. Strong resprouting ability suggests that the phenotype portfolio of riverine *Melaleuca* reflects adaptive strategies for persistence. Juvenile and mature life stages both adopt a flow-parallel multi-stemmed structure that confers resistance against the mechanical torque experienced during floods ("flood-training": Everitt, 1968). In turn, this grove structure damps flow velocity and promotes sediment accumulation, generating new alluvial landforms. Therefore, vegetative sprouting acts as a mechanism that generates persistent effects on fluvial processes at the ecosystem scale (Fielding et al., 1997; Ward et al., 2002).

Tolerance mechanisms such as growth structure suggest that species' phenotypes may produce short- and long-term fitness benefits through individual genet survival. Phenotypic selection for distinct modular architectures can affect spatial and genetic structure beyond the genet scale by interacting with population evolutionary processes such as cross-generational mating and among-deme gene flow (Fischer and van Kluenen, 2002; Karrenberg et al., 2002). For example, differential success among genotypes within populations may constrain the extent of adaptive changes in the population gene pool. However, selective filters such as fluvial disturbance are stochastic, so population- and species-level persistence and the processes that may contribute to evolutionary change are temporally unpredictable.

Clonally produced ramets in woody plants may (i) remain physiologically integrated as resprouts (Bellingham and Sparrow, 2000) or (ii) become dispersed as potential regenerative fragments (Barsoum, 2002; Rood et al., 2003). This re-growth mechanism increases the probability of genet persistence because the likelihood of mortality is spread among multiple spatial units (ramets) over the plant life time. Thus, clonal growth in woody plants is a mechanism that could influence the rate and directionality of selection for distinct phenotypes and genotypes because of its effects on spatial genetic structure and microevolutionary processes including gene flow (Charpentier, 2001; Barsoum, 2002; Pan and Price, 2002; Eckert et al., 2003). However, in contrast to recruitment from seeds, vegetative mechanisms, such as clonal growth, have been overlooked in operative classifications of plant functional systems (Bond and Midgley, 2001; Bond and Midgley, 2003) and as a component of plant fitness (Pan and Price, 2002). Only recently has resprouting been recognised as an important plant functional trait that might shape population regeneration, persistence, and demographic processes (Lavorel and Garnier, 2002; Cornelissen et al., 2003).

Recent assessment of resprouting ability across a broad range of woody plants suggests that resprouting ability is disproportionately over-represented among particular taxa and is most often associated with resource-poor or disturbance-driven habitats, including riparian zones (Peterson and Jones, 1997; Bond and Midgley, 2001; Bond and Midgley, 2003). For example, vegetative resprouting is conspicuous in the life histories of several

riparian tree taxa including Salicaceae (*Salix* spp.), Fagaceae (*Quercus* spp.), and Betulaceae (*Betula* spp.) in the northern hemisphere (Peterson and Jones, 1997; Karrenberg et al., 2002), and in the southern hemisphere Myrtaceae (*Eucalyptus* and *Melaleuca* species) (Lacey and Johnston, 1990).

Regional analyses have shown that sprouting is a widespread and evolutionarily labile phenomenon within and between life forms, habitats, life stages and phylogenetic clades (Bond and Midgley, 2003; Vesk, 2006). However, the macro-evolutionary implications of resprouting—that is, its impacts on species evolution and persistence—have not been explored. For example, if disturbance selects for the expression of resprouting as suggested, differences in disturbance intensity and/or predictability might generate differences in resprouting intensity which should be revealed through individual-scale spatial genotypic identification. Quantifying the distribution of genotypes and phenotypes among individuals and populations may thus allow inferences as to the importance of the resprouting trait to species persistence, as well as to mechanisms of gene movement that can determine the gene pools within which selective effects operate.

Vital processes such as mating, dispersal and vegetative growth are increasingly being perceived as spatially contagious phenomena. These processes can all influence demographic conditions, biological interactions and genetic relatedness among neighbours, to generate scale-dependent ("autocorrelated") spatial patterns (Borcard et al., 1992; Legendre, 1993; Dale, 1999; Lichstein et al., 2002). The paradigm of spatial autocorrelation implies that the observed value of a variable of interest at any one locality can be predicted, at least partly, by the values at neighbouring points (Legendre, 1993). Clonality is a prime example of a biological mechanism that generates spatially dependent genotypic structure. Multiple above-ground stems arising from a single genet will clearly be genetically identical. This phenomenon may obscure any ability to identify individuals in natural populations and infer the spatial and temporal scales at which they interact (McLellan et al., 1997; Barsoum, 2002; Eckert et al., 2003) unless combined with genetic studies. Traditional demographic models typically assume that adult individuals have determinate spatial identities at population, species and community levels (Legendre and Fortin, 1989; Borcard et al., 1992; Pfenninger, 2002). Clonal growth, however, has implications for ecological sampling and analysis because it generates cryptic spatial structure and potentially reiterative changes to plant size, introduces a broad upper tail to the probability distribution of mortality, and generates large variances in the spatial and temporal distributions of reproductively active stems arising from the same individual. These factors reduce the predictability of survivorship and create inter-generational demographic structure.

Landscape ecology offers a useful conceptual framework in which to investigate the spatial scales at which biological responses and abiotic environmental processes co-vary to influence genetic structure. Traditional concepts of plant population dynamics model

vegetation as a spatial mosaic of patches, corridors and matrices cycling through temporal phases of succession, rather than as an arrangement of points within the landscape (Remmert, 1991; Hansson et al., 1995; Tischendorf and Fahrig, 2000; Pearson, 2002). Investigating spatial and genetic structure as a function of scale, however, is potentially more useful than interpretations based on *a priori* spatial units such as patches, especially for species that occur in riverine systems. This is because biological responses to stochastic environmental conditions can generate fine-scale and dynamic spatial and genetic structuring not accounted for in conventional mosaic-cycle models of plant spatial ecology.

Gene movement in river systems is typically a function of stream flow (Malanson, 1993). For example, hydrochory is defined as propagule dispersal by water. In river landscapes, hydrochory is thought to facilitate long-distance dispersal, that is, gene movement across distances far exceeding those predicted from mean spatial trends in species' dispersal distributions (Nilsson et al., 1991; Williamson et al., 1999; Campbell et al., 2002; Merritt and Wohl, 2002). Hydrochory acts as a key variable in contemporary metapopulation models and in investigations of species' colonisation potential (e.g. Cain et al., 2000; Tero et al., 2003). Therefore, with stochastic stream flow, complex patterns of genetic connectivity between populations could be expected.

The spatial and genetic distributions of riverine plant species may be shaped by multiple factors, including pollination system and the balance between seed and vegetative regeneration strategies as well as between seed and pollen movement (Wolff et al. 1997; Prentis and Mather 2007; Nathan 2008). Environmental features including altitude and landscape structure such as habitat discontinuties can also strongly influence the structure and rate of evolutionary flux among populations of a riverine species (e.g. Prentis and Mather 2008). Variable flow conditions also contribute to a highly mobile and changing environment within the time-scale of plant reproductive cycles. Prentis and Mather (2007) showed that significant genetic differentiation occurred in seedlings of the stream lily *Helmholtzia glaberrima* between micro-drainages whereas altitudinal gradient had neglible influence on spatial genetic structure, indicating that opportunities for seed dispersal were constrained by hydrographic networks even at a local (100s of metres) scale. However, rare large seed dispersal events were predicted to have contributed important impact on population genetic structure (Prentis and Mather 2007). Genetic distinction between populations detected at all spatial scales suggests that strong non-equilibrium conditions, rather than landscape features, have shaped patterns of genetic diversity and differentiation in this riparian species (Prentis and Mather 2008). Evidence for strong genetic differentiation at the population and sub-population level combined with gene flow between geographically distinct areas has also been detected in *Alkannia orientalis* in the Sinnai Desert of Egypt (Wolff et al., 1997). Genetic similarities between two of four sampled subpopulations from two narrow wadis and an interconnecting plain may reflect that pollen flow could shape the genetic

subdivision of populations, while extensive gene flow between subpoplation could be facilitated by seed transport in periodic flash floods (Wolff et al., 1997).

Long-distance dispersal clearly can have profound consequences on population genetic structure and patterns of genetic connectivity (e.g. Cain et al., 2000). This is because propagules derived either from clonal fragments or sexual reproduction can travel substantial distances (kilometres) on flood waters or debris (Nilsson et al., 1991; Pettit and Froend, 2001a). Widespread dispersal or high connectivity between sites generate continuous gene flow, large and ephemeral gene pools, and multi-directional gradients in genetic relatedness (Kudoh and Whigham, 2001; Lundqvist and Andersson, 2001). For example, Tero et al. (2003) examined dispersal in *Silene tatartica* (Caryophyllaceae) by sampling 210 individuals from seven locations within a 25 km reach of the Oulankajoki River in northern Finland and north-western Russia. AFLP markers and assignment tests were used to identify long-distance dispersal events. Tero *et al*. (2003) found no supporting evidence for differences in genetic diversity within locations. This pattern represents a 'classic' metapopulation structure governed by genetic drift, suggesting that diverse sources of migrating individuals could contribute to gene pool dynamics in this short-lived (5–7 years) perennial (Tero et al., 2003).

Evidence for unidirectional gene flow in river systems is equivocal (Rousset, 1997; Arens et al., 1998; Imbert and Lefèvre, 2003). For example, genetic structuring in remnant *Populus nigra* (Salicaceae) in the Drone River, a flood-prone temperate river system in south-eastern France, did not reflect asymmetry in genetic diversity from upstream to downstream locations as might be expected under single direction (downstream) seed dispersal (Imbert and Lefèvre, 2003). Limited seed dispersal, pollen-dominated gene flow, and historical habitat fragmentation could explain Imbert and Lefèvre's results because these processes constrain the probability of finding evidence for long-distance gene movement via seeds. However, insight into gene movement in river systems also requires investigation of the temporal and spatial interfaces at which fluvial and genetic processes interact. In the same river system, Barsoum (2002) demonstrated differential spatial distributions and higher probabilities of survivorship in asexual recruits in *P. nigra* and *Salix alba*. These differences were associated with differences in the ability of clonal saplings to tolerate damage from high current velocities and scouring by coarse depositional sediments. This implies that dispersal and flood resilience in clonally-derived offspring could increase species' regeneration capacity across climatic and hydrological gradients, creating ongoing feed-back among physical disturbance processes, species function and evolution.

Classical population genetic theory assumes the existence of an equilibrium state between genetic drift and gene-flow processes (Hutchison and Templeton, 1999; Ouborg et al., 1999). These models are potentially inadequate to explain the processes underlying gene flow patterns in natural populations in riverine taxa, because fluvial action typically violates this key assumption of demographic equilibrium. Thus, river

environments are a prime example where *a priori* inference on the mechanisms driving population and species structure can be problematic.

To fully incorporate the stochasticity of high energy river systems with plant phenotypic expression and genetic basis, these features must be mechanistically linked. Events-based modelling provides for this link by producing estimates for the probability that individuals will experience physical stresses exceeding biological tolerance; that is, the likelihood and severity of the statistically extreme events (Katz et al., 2005). Such an approach links both habitat and phenotype with genetic structure. For example, geomorphologically effective floods are defined by energy thresholds expected to cause particle movement leading to alluvial and bedrock erosion (Costa and O'Connor, 1995). This is a useful approach to estimate the mechanistic forces required to impose changes in channel structure due to fluvial entrainment, and can indicate the frequency and severity of changes in the habitat structure available for riverine vegetation (Cellot et al., 1998). In addition, quantifying biological thresholds that will result in demographic change can be linked to stream dynamics. The biological threshold approach will require the use of physical proxies to plant survival, such as the capacity to withstand soil drought or shear stress, to allow mechanistic tests of variation in species' relative and absolute biological tolerance levels and quantify the effects on demography and evolution.

The benefit of bringing together information on phenotypic and genotypic distributions and environmental factors will be to develop an integrated understanding of the relationships between these potentially linked processes and responses. Identifying plant strategy dimensions (such as disturbance tolerance) which represent the combined biological solution of multiple traits are difficult to quantify and compare among habitats. One possible strategy to identify species-level trait variation is to evaluate interrelations among measurable traits using regression-based modelling techniques (Westoby, 2006). However, explanations for species trait covariances as ecologically adaptive solutions may appear decoupled over the entire life span despite their potential adaptive value. This is due to the over-arching influence of abiotic factors such as disturbance on survivorship and evolutionary response (Ackerly and Cornwell, 2007; Rees and Venable, 2007). Process-based measures such as sum exceedance values (SEVs) may more precisely define the relative overlap among taxa in niche space relative to species' physiological tolerance thresholds because the SEV approach quantifies tolerance against a measure of long-term temporal variation in the disturbance regime. For example, Silvertown et al. (1999) found that species within two temperate grasslands segregated along niche axes of soil drought and aeration tolerance, implying that fine-scale hydrological thresholds generate community structure. Silvertown et al. (1999) used SEVs to represent the frequency and magnitude at which *in situ* environmental conditions exceed biological thresholds of each species, which explained temporal variation in environmental conditions at a scale relevant to the physiological tolerances, and thus distributions, of plants (Silvertown et al., 1999).

The SEV approach may be useful to predict biological responses to, and the persistent effects of, environmental stress on genotypic and phenotypic distributions. For example, clonal growth mechanisms such as resprouting have direct effects on survivorship, potentially driving an evolutionary response to selection for the resprouting phenotype (Pan and Price, 2002). In turn, the relative fitness benefits of the resprouting trait might be expected to depend on the physical processes shaping the disturbance regime, including type, likelihood and intensity, as well as point processes such as microsite shear stress, that influence the probability of survival. For example, differential survivorship associated with differences in flood disturbance and plant life stage generated temporal shifts in genotypic variation and the balance between asexual and sexual regeneration strategies in natural populations of riparian *Populus nigra* (Barsoum, 2002; Barsoum et al., 2004). If a particular phenotype has adaptive value, population-level allelic response to among-individual selection for the suite of traits underlying that phenotype should be expected, indicating potential influence on process evolution. Constructing a hierarchical phylogenetic framework will help to identify the evolutionary pathways by which differences in adaptive trait expression could lead to differences in ecological and genetic relatedness among populations and species. For example, phenotypes vary with differences in the frequency and magnitude of environmental perturbations. Differences in growth form can change the probabilities of successive recruitment events. The dynamic links between disturbance and demographic processes suggest that incorporating modelling, genetic and experimental ecology approaches could help quantify and understand the interplay between species ecology and evolution in riparian systems. This is the approach taken in this thesis.

Tables and Figures

Table 2.1. Phenotypic traits commonly displayed in *Melaleuca* and classified as ecologically adaptive.

Phenotypic characteristic	Species	Location	References
Sexual reproduction			
Seed phenology			
Canopy seed bank	*M. quinquenervia*	Florida	Hofstetter (1988), Turner et al. (1998); Pettit and Froend (2001a)
	M. rhaphiophylla	Blackwood R., WA	
Timing of seed fall coincident with end of rainy/flood season	*M. leucadendra*	Ord R., WA	Pettit et al. (2001), Pettit and Froend (2001a)
Germination			
Floating seeds	*M. leucadendra*	Ord R., WA	Pettit and Froend (2001a)
Submersed seeds	*M. quinquenervia*	Florida	Lockhart (1996)
Vegetative reproduction			
Capacity to resprout			
Epicormic buds	*M. quinquenervia*	South Florida	Van et al.(2000)
Coppicing	*M. quinquenervia*	South Florida	Stocker (1999)
	M. armillaris	Atherton Tablelands, QLD	Sun and Dickinson (1997)
	M. linariifolia		
Root suckering	*M. linariifolia*	Southern Australia; poorly drained coastal areas	Lacey and Johnston (1990)
Lignotubers	*M. leucadendra*	Blackwood R. and Ord R., WA	Pettit and Froend (2001a)
	M. fluviatilis		
Rhizome shoots	*M. cajuputi*	Narathiwat, south Thailand	Miwa et al. (2001)
	M. ericifolia	Coomonderry Swamp, NSW	de Jong (2000)

continued…

Table 2.1. continued…

Phenotypic characteristic	*Species*	Location	References
Morphology/physiology			
Reclined trunk habit	*M. "argentea"*	Upper Burdekin R., N QLD	Fielding et al.(1997)
Multiple-stemmed form	*M. "argentea"*		Ibid.
	M. quiquenervia	Florida	Hofstetter (1988)
Thick, spongy bark	*M. fluviatilis*		Ibid.
	M. quinquenervia		
Production of extensive root network	*M. "argentea"*		Fielding et al.(1997)
Grouping of mature trees in linear, flow-parallel groves	*M. "argentea"*		Ibid.
Adventitious roots	*M. "argentea"*		Ibid.
	M. quinquenervia	Lake Okeechobee, Florida	Lockhart et al. (1999)
	M. ericifolia	Coomonderry Swamp, NSW	Lockhart (1996)
	M. linariifolia		de Jong (2000)
Aquatic heterophylly	*M. quinquenervia*	Glades County, Florida	Lockhart (1996)
Rapid early growth	*M. "argentea"*	Upper Burdekin R., QLD	Fielding et al. (1997)
	M. armillaris	Atherton Tablelands, QLD	Sun and Dickinson (1997)
	M. linariifolia		
Resilience to wind	*M. armillaris*;	Atherton Tablelands, QLD	Ibid.
	M. linariifolia		
Resilience to mechanistic flood stress	*M. leucadendra*	Ord R., WA	Pettit and Froend (2001a)
	M. "argentea"	Upper Burdekin R., QLD	
Physiologic flood tolerance	*M. cajuputi*	Narathiwat Province, Thailand/ University of Tokyo, Japan	Yamanoshita et al (2005)
Resilience to fire	*M. cajuputi*	Narathiwat, south Thailand	Turner et al (1998); Miwa et al. (2001)
Tolerance of rabbit grazing	*M. halmaturorum*	Coorong National Park, SA	Cooke (1987)
High tolerance of anaerobic and/or saline conditions	*M .leucadendra*	Australia	van der Moezel and Bell (1987; 1990), Sun and Dickinson (1995), Saintilan and Wilton (2001), Niknam and McComb (2000), Ladiges and Foord (1981), Dunn et al. (1994), Bell (1999)
	Melaleuca spp.		
Capacity for high soil water extraction rate	*M. stypheliodes* SM	Royal Park, Melbourne, VIC	Misra and Sands (1992; 1993)

Chapter 3—Differences in resprouting ability in four riparian woody species

Published as:

Caroline Chong, Will Edwards and Michelle Waycott (2007) Differences in resprouting ability are not related to seed size or seedling growth in four riparian woody species. *Journal of Ecology*, **95:** 840–850

Abstract

Resprouting is a key plant attribute facilitating persistence in disturbance-prone environments. Resprouting ability in seedlings may depend on both developmental ontogeny and seed size. However, the relationships between these factors are not well explored, especially for woody species with comparatively small seeds and epigeal germination.

We investigated resprouting capacity in seedlings from four sub-tropical, riparian, Myrtaceous tree species—*Melaleuca leucadendra*, *Asteromyrtus symphyocarpa*, *Eucalyptus camaldulensis* var. *obtusa* and *Tristaniopsis laurina*—displaying these characteristics. We recorded resprouting in response to simulated disturbance as a function of seed mass and developmental age (5–150 days post emergence) and examined the acquisition of resprouting ability in relation to growth and biomass allocation patterns.

Patterns of resprouting were distinct among species, but the acquisition of resprouting ability was not determined by seed mass. The 'small' seeded *M. leucadendra* and the 'intermediate' seeded *E. camaldulensis* showed unexpectedly high shoot resprouting vigour from cotyledon stage (70% resprouting at 5 days post emergence), as well as greatest ongoing allocation to root mass and lateral root development. In contrast, in *A. symphyocarpa* (another species with 'intermediate' seed mass) and *T. laurina* (a 'large' seeded species) resprouting rates during early development were much lower (< 10%), although there was a trend toward increasing resprouting ability with age in *A. symphyocarpa* (> 150 days). Resprouting capacity was also independent of seedling size and relative growth rate.

Our results indicate the size-dependency of resprouting capacity varies considerably among these species. This suggests physiological and morphological species traits other than those directly related to reserve size or relative growth rate may convey survivorship in river environments.

Our findings show that resprouting capacity was not related to seed size and seedling growth patterns in these four species. This is different to evidence from comparative studies undertaken in fire-prone and other temperate environments. A broader survey of

seedling resprouting ability including more species is required to determine the generality of our findings in riparian species.

Introduction

Resprouting is a critical trait for plants exposed to disturbances that cause the loss of most above-ground material (Bond and Midgley, 2001; Del Tredici, 2001; Cornelissen et al., 2003). Under such conditions, resprouting is competitively advantageous, because it provides the opportunity for new shoots to rapidly occupy opened areas (Whelan, 1995; Vieira and Scariot, 2006) as well as allowing faster return to reproduction (Whelan, 1995; Peterson and Jones, 1997; Bond and Midgley, 2003).

In adult plants, resprouting capacity is often associated with allocation to root biomass, below-ground storage organs and/or larger non-structural carbohydrate (i.e. starch) reserves (Canadell and Lopez-Soria, 1998; Landhausser and Lieffers, 2002 but see Sakai & Sakai 1998). A similar relationship may also be expected for seedlings, since any selective advantage of carbon storage in adults should also be expected during the first season of plant development when resource demands for establishment are highest (e.g. Howe and Smallwood, 1982; Schwilk and Ackerly, 2005). Indeed, the amount of metabolisable reserves in a developing seedling is considered a key factor influencing the probability of establishment under generalised environmental hazards (Westoby et al., 1996; Muller et al., 2000; Walters and Reich, 2000). If seedling reserve size promotes the ability to meet the physiological demands of development as well as stress tolerance (Saverimuttu and Westoby, 1996; Boege and Marquis, 2005), then species differences in resprouting capacity during deployment should reflect maternally-provisioned reserves as a function of seed size and/or seedling morphology (Armstrong and Westoby, 1993; Kitajima and Fenner, 2000; Green and Juniper, 2004; but see Moles and Westoby, 2006). Nearly all previous studies of resprouting ability in seedlings have focused on species that display hypogeal germination strategies. In these species, storage cotyledons remain in or on the soil, and disturbance generally removes the growing shoot without removing reserves (e.g. Harms and Dalling, 1997). Because these species retain maternally-provisioned resources, they also constitute the group in which resprouting might be expected (Lehtilä, 1999; Kitajima and Fenner, 2000; Edwards and Gadek, 2002). Only one study has examined resprouting ability at the earliest seedling stage in species with epigeal germination (Armstrong and Westoby, 1993), even though these species may be subject to similar selective effects of disturbance as hypogeal species (e.g. Paz, 2003). Understanding resprouting in seedlings from epigeal germinating species is very important, since, in contrast to hypogeal germinating species, resprouting capacity will rely on allocation strategies indirect of maternal provisioning (Lehtilä, 1999; Stowe et al., 2000).

Physiological rates of activity (as well as stored reserves) may drive resprouting response, and vary due to changing functional priorities as a plant develops (Weiner,

2004; Boege and Marquis, 2005; Lamb and Cahill, 2006). If resprouting in seedlings has similar functional value as it has in adult plants, then species differences in resprouting behaviour as seedlings might also be expected to reflect patterns of allocation to root and shoot growth associated with resprouting in adults (Schwilk and Ackerly, 2005). In seedlings, allocation to root and shoot differs between species on the basis of seed mass (Westoby et al., 1992; Westoby et al., 1996), although seed mass might be secondarily related to resprouting, via the association between seed mass and relative growth rate (RGR; Wright and Westoby, 2000; Aronne and De Micco, 2004). Low RGR is associated with structural stability and below-ground resource storage (Westoby et al., 1992; Schwilk and Ackerly, 2005) whereas rapid RGR is associated with fast turnover of above-ground plant parts supporting photosynthesis (Verdaguer and Ojeda, 2002; Gurvich et al., 2005). Thus low RGR (associated with large seed size) might be expected to confer initial resprouting ability in seedlings.

Evidence for the ecological roles and evolutionary maintenance of resprouting in woody plants draws overwhelmingly from fire-prone and/or temperate ecosystems and adult plants (Bond and Midgley, 2001; Pausas et al., 2004; Vesk et al., 2004; Vesk and Westoby, 2004). Surprisingly few field or greenhouse studies have examined resprouting in systems where the main agent of disturbance is not fire, although resprouting as a mechanism for persistence should be expected in any environment prone to inescapable damage (Gom and Rood, 1999b; Paciorek et al., 2000; Spiller and Agrawal, 2003).

Flood-prone river environments provide a unique framework for investigating resprouting. First, they represent high-stress areas where the main agent of disturbance is not fire. In sub-tropical dryland rivers in Australia, climatic and fluvial processes drive multiple agents of stress and disturbance including high-force floods and submergence, seasonal aridity, variable soil resource availability, and sediment scouring and burial (Fielding et al., 1997; Puckridge et al., 1998; Pettit and Froend, 2001b). Second, the dominant tree species in these environments tend to be small-seeded epigeal germinators, ideal to examine relationships between growth traits and resprouting in seedlings that lack large cotyledonary reserves.

In this study, we use a greenhouse experiment with simulated disturbance to evaluate the interactions between maternal investment (seed size) and seedling development on resprouting capacity in four tree species from riparian areas in northern Australia. Specifically, we test whether differences in the acquisition and extent of resprouting ability reflect differences between species in these primary developmental attributes of seedlings.

Materials and methods

Study species

We chose four plant species from high-discharge riparian ecosystems in northern Australia. All species selected were from the family Myrtaceae because this family is one of the most numerically dominant in these areas. Species were selected that 1) represented unique genera from distinct tribes within the Myrtaceae (Wilson et al., 2005); 2) primarily occurred in riparian habitat; 3) had geographical distributions that were sympatric for part of their total range extents; 4) were similar in growth form (trees); and 5) the range of seed sizes across species encompassed at least two orders of magnitude (Table 3.1). The four species were: *Melaleuca leucadendra* (L.) L., *Asteromyrtus symphyocarpa* (F. Muell.) Craven, *Eucalyptus camaldulensis* var. *obtusa* Blakely, and *Tristaniopsis laurina* (Sm.) Peter G. Wilson & J.T. Waterh. Resprouting has been previously documented in mature trees in the genera *Melaleuca*, *Eucalyptus* and *Tristaniopsis*, although there is no available evidence of resprouting behaviour in early seedlings of any of the species used here.

Seeds from each species were obtained from commercial seed suppliers (Australian Tree Seed Centre, Australian Commonwealth Scientific and Industrial Research Organisation, ACT; Nindethana Seed Company, WA; Australia) and thus were collected from multiple parent populations. For *M. leucadendra*, we collected additional seed from reproductively mature individuals at Keelbottom Creek, Upper Burdekin River catchment, Queensland, Australia. Seeds of each species from different locations were pooled. We are confident all seeds represent the same ecological taxa because, in all cases, seed suppliers provided unambiguous taxonomic and geographic identifications, although we acknowledge intra-generic relationships in the Myrtaceae are subject to ongoing study (e.g. Craven and Lepschi, 1999; Sytsma et al., 2004; Wilson et al., 2005).

Seed size

Seed size was quantified as total dry seed mass. Characteristic of their genera, *E. camaldulensis* and *M. leucadendra* seeds were not winged, whereas *T. laurina* and *A. symphyocarpa* had winged structures that may not contribute directly to seed reserve mass (cf. Leishman and Westoby, 1994). We report total seed masses for winged and non-winged species because subsequent analysis for a subset of seeds showed that removal of the winged structures had no effect on seed mass class assignations.

Seed mass was determined via random sampling of seeds drawn from four seed lots. For species with seed mass less than 1 mg (*M. leucadendra, E. camaldulensis* and *A. symphyocarpa*) an estimate of mean seed mass was calculated from 10 groups of 10 seeds. For *T. laurina* individual seeds were large enough that resolution of the balance allowed for mass determination in individual seeds. In this case we determined mean seed mass from a sample of 50 individual seeds.

Growth conditions

Plants were grown in seedling tubes filled with a 6:3:2 steam sterilised sand/peat/perlite mix containing macronutrients (Yuruga Nursery Pty Ltd and Greening Australia Townsville, Queensland, Australia; Staypak super native tubes, *c*. 70 x 70 x 160 mm). The germination substrate was brought to moisture capacity before sowing. A capillary-driven watering system was used to maintain plants based on success in pilot growth trials (the 'bog method', Wrigley and Fagg, 1993).

Plants were maintained in a greenhouse (School of Marine and Tropical Biology, James Cook University, Townsville, Australia). Periodic measurements of ambient temperature indicated a diurnal temperature range of *c*. 18–33°C, conditions typical to regional records for the season (Bureau of Meteorology 2006). Measurements of incident light indicated ranges supportive of plant growth, although considerably lower than outside conditions (e.g., average photon flux density 403 mol s^{-1} m^{-2}, 60–80% shade; LI-COR photometer model LI-189).

Experimental design: allocation to seedling tubes

Two hundred seedling tubes were randomly allocated to each of five PVC watering trays (each 1200 x 1200 x 150 mm). Within each watering tray, ten blocks of 20 seedling tubes were placed in plastic seedling frames (in total, 1000 seedling tubes; 250 tubes per species). To overcome potential germination failure, 8–20 seeds were sown in each tube. Seeds were covered with a fine layer of steam-sterilised sand and moistened with a fine spray mist. We scored emergence as radicle protrusion to full expansion of both cotyledons from the seed coat. Where necessary, seedlings were subsequently thinned to two individuals per tube at 8–10 days post emergence to minimise potential intra-specific competitive effects. Nevertheless, seedlings did not establish in every tube; thus replication was less than 250 in two species (*A. symphyocarpa* and *T. laurina*).

Experimental design: allocation to clipping and biomass experiments

For each species, the 250 seedlings were randomly allocated to three groups: 1) Clipping experiment (n = 120); 2) Biomass estimation experiment (n = 120); and 3) Control (n = 10). Within the Clipping and Biomass estimation groups seedlings were further randomly allocated into one of six treatments (see below). Where we had a total of 120 seedlings available for each species in each experimental group, sample sizes for treatments within groups were 20 (*M. leucadendra* and *E. camaldulensis*). Because *A. symphyocarpa* and *T. laurina* were represented by only 200 and 224 seedlings, respectively, replication of individuals in each clipping treatment and in each harvest was 15 (*A. symphyocarpa*) and 17 (*T. laurina*).

Experimental protocol: clipping

To examine resprouting ability with respect to seedling age we randomly assigned seedlings to six clipping treatments. The timing of the clipping treatments was five, 10, 15, 25, 40 and 60 days following full expansion of the cotyledons. Clipping involved the removal of all stem and leaf material 5 mm above substrata level using surgical scissors. Resprouting and survival were monitored daily for 15 days post clipping and every 2–3 days thereafter. For clipped individuals, we recorded initiation of resprouting response as the first visible formation of a shoot bud. For final assessment of resprouting response (new shoot formation versus seedling death) we checked all paired seedlings for survival three months after clipping.

Experimental protocol: biomass quantification

To examine the relationship between resprouting response and seedling growth patterns, we characterised plant biomass in randomly selected seedlings for each species at the time of each clipping treatment. Plants harvested for biomass quantification were independent of those assigned to clipping treatments.

We recorded leaf developmental stage (cotyledon persistence and number of expanded foliar leaves), fresh shoot lengths (hypocotyl and epicotyl), fresh total root length, and numbers of lateral roots a) arising from the root base ('basal lateral roots'), and b) in total. Individual plants were extracted from the sandy substrate and separated into cotyledon/leaf, shoot and root parts. All soil was removed with the aid of a fine brush under running water. Dry masses (65°C, 48 h) of roots, shoot and leaves of each plant were measured. Root, shoot and leaf mass fractions (RMF, SMF, LMF respectively) were calculated as component mass/total plant dry mass (Wilsey and Polley, 2006). Relative growth rates (RGR; mg mg^{-1} day^{-1}) for the period 5–25 days after emergence were estimated as the slopes of Model I regression of ln total plant dry mass against days elapsed.

Data analyses

Differences in emergence rate among species

Species differences in mean emergence time were evaluated using ANOVA. We utilised the Monte Carlo Markov Chain (MCMC) algorithm and uninformative priors in WinBUGS v.2.10 (Spiegelhalter et al., 2005), incorporating *M. leucadendra* as the reference class. A normal distribution was assumed for the species fixed effect. Within-species variances were modelled as belonging to gamma distributions with $r = \mu = 0.001$. Preliminary model selection analyses using the Deviance Information Criterion (DIC) indicated this single-factor model to be most parsimonious. We generated 100 000 samples from the model posterior distribution, discarding the initial 10 000 samples as a burn-in, for each of three independent Markov chains (thus, total sample size was 300 000 samples from the three chains). The mean and standard deviation of

the model coefficients, and the 2.5th and 97.5th percentiles of the posterior distribution (i.e. the Bayesian 95% credible interval: Johnson, 1999; Parris, 2006) were calculated.

Differences in resprouting ability among species

Bayesian logistic modelling using uninformative priors was used to identify the effects of species, seedling age (as a surrogate for developmental stage) and the interaction between these factors on resprouting ability (i.e. proportion of seedlings that survive clipping). To evaluate the *a priori* hypothesis that seedling resprouting ability is a function of seed size, species' resprouting capacity was investigated relative to the reference class *M. leucadendra*, the smallest-seeded species. We considered this modelling approach appropriate because a binomial response was predicted in the data: that is, individuals either resprouted or died. The continuous explanatory variable (age) was standardised (standardised value = $(x_{age} - \text{mean } x_{age})/sd_{age}$) to improve sampling efficiency and help reduce autocorrelation between successive MCMC samples. Preliminary model selection analyses using the DIC and parameter posterior probabilities identified this model to best fit the data, compared to an alternative parameterisation accounting for a species random effect. Hence, for this data set, total variance associated with regression of resprouting ability on age appears to be estimated validly by variation due to differences in probability with age among species. Again, we used 300 000 samples from the model posterior distribution (100 000 samples from each of three independent Markov chains, discarding the initial 10 000 samples as a burn-in) to estimate model parameters.

Differences in growth patterns among species

We began by performing discriminant function analysis (DFA) to evaluate species differences in growth characteristics in a multivariate context (JMPIN v.4.0.3, SAS Institute Inc.). DFA accounts for group structuring by generating linear combinations of variables that maximise between-group to within-group variance (Quinn and Keough, 2004).We evaluated nine growth variables via DFA: RMF, SMF, and LMF; number of leaves; total shoot length (TSL); total and specific root length (TRL, SRL); and number and frequency of lateral roots.

A key interest in this study was to determine whether resprouting ability among species differed on the basis of differences in seed size and seedling growth variables. Because allocation to root biomass was a strong indicator of species growth trends in preliminary DCA, we investigated relationships between root investment variables and resprouting among species via standardised major axis analyses ((S)MATR; Wright et al., 2001; Falster et al., 2003; Warton et al., 2006).

Relationships between resprouting ability, seed size and growth patterns among species

To examine relationships between growth parameters and resprouting ability on the bases of species and seed mass, we compared species identity (ranked in order of increasing seed mass) with species growth traits (ranked in order of increasing

magnitude), for the following parameters: RGR, specific root length, lateral root investment, total root biomass and resprouting ability.

Assessment of growth rate, biomass ratios and allometric trends focussed on data for seedling growth up to 25 days. This was because growth tube length became limiting for some individual seedlings after 25 days, potentially altering growth/allocation patterns.

Data were natural log or arcsine (ratios) transformed where appropriate prior to all analyses.

Results

Differences in seed mass among species

Species mean seed masses spanned two orders of magnitude. Mean *M. leucadendra* seed size (0.07 mg) was less than 25% that of *A. symphyocarpa* and *E. camaldulensis*, and less than 5% that of *T. laurina* (Table 3.1). We ranked species based on mean seed mass as 'small' (*M. leucadendra*), 'intermediate' (*A. symphyocarpa* and *E. camaldulensis*) and 'large' (*T. laurina*).

Differences in emergence rate among species

Germination was rapid across all species (5–8 days). Time to emergence was greater among *T. laurina* and *A. symphyocarpa* seedlings compared to *E. camaldulensis* and *M. leucadendra*, although overall, differences in time to emergence among species were less than five days (i.e. relative to *M. leucadendra*, *E. camaldulensis* mean emergence time + 0.05 days, 95% CI: -0.06 to 0.16; *A. symphyocarpa* +2.54 days, 95% CI: 2.44 to 2.64; *T. laurina* +4.09 days, 95% CI: 3.99 to 4.19; Table 3.2). Within a species, variability in time to emergence was lowest in *M. leucadendra* and highest in *A. symphyocarpa* (Table 3.2).

Differences in growth traits among species

As anticipated, total plant mass at five days post emergence was tightly correlated with seed mass ($y = 0.116 + 0.95x$, $r^2 > 0.99$, $p = 0.0007$). At this developmental stage, epigeal cotyledons constituted total leaf mass and represented a large component of total mass allocation in all seedlings (cotyledon mass fraction 0.58, 0.75, 0.63 and 0.68 in *M. leucadendra*, *A. symphyocarpa*, *E. camaldulensis* and *T. laurina* respectively; Table 3.3). Shoot architecture varied among species at cotyledon stage (specific hypocotyl length 157.10, 92.32, 128.00, and 37.66 mm mg^{-1} dry shoot mass in *M. leucadendra*, *A. symphyocarpa*, *E. camaldulensis* and *T. laurina* respectively; Table 3.3). By 25 days seedling development, the largest-seeded *T. laurina* showed proportionately lowest total mass accrual. Relative growth rate was distinct between all

four species (RGR 5–25 days: *T. laurina* < *M. leucadendra* < *A. symphyocarpa* < *E. camaldulensis*; Table 3.4).

Compared at 25 days post emergence, shoot height differed among species (mean total shoot length 8.66 mm, 23.77 mm, 61.29 mm, and 21.59 mm in *M. leucadendra*, *A. symphyocarpa*, *E. camaldulensis* and *T. laurina* respectively) whereas allometric trends in leaf development were similar (all seedlings 3–4 true leaves; data not shown).

Discriminant function analysis indicated strong separation of species measured at 25 days (first discriminant function, eigenvalue = 40.98, explained variance = 98.8%; MANOVA, Pillai trace = 1.877, $F_{27, 186} = 11.514$, $p < 0.0001$). In large part, the separation was due to differences between species on the basis of below-ground plant parts, and relative allocation to root biomass was identified as a strong indicator of growth trends among species. For example, root mass fraction, lateral root frequency, lateral root investment and specific root length contributed most to discriminant functions 1 and 2, whereas number of leaves and shoot and leaf mass fractions contributed least. Because of this we only report bivariate relationships between root biomass variables across species via SMA analyses (below). Growth tray (i.e. blocked position of plant in greenhouse) had no effect on species development (multi-response permutation procedure, A = -0.024, p = 0.953).

Differences in root characteristics among species

At 25 days post emergence, seedlings in all species allocated resources to root mass relative to total plant mass at a similar rate ((S)MATR statistic = 1.491, p = 0.703; common slope estimate = 1.18, 95%CI: 0.97 to 1.45). Among species, mass accrual was lowest in *A. symphyocarpa* and *M. leucadendra* and highest in *E. camaldulensis*. Significant shifts in elevation in both the 5–25 day and 25 day data sets (*post hoc* pair wise comparisons, $p < 0.05$) indicated that *M. leucadendra* showed greatest investment in root mass when compared at the same absolute plant mass (all pairwise contrasts, $p < 0.0001$) (Figure 3.1).

Differences in resprouting among species

Despite the assumed severity of the clipping treatment, seedlings of *M. leucadendra* and *E. camaldulensis* showed high resprouting success, even at very early seedling ages. For example, at five days post-emergence, recovery from clipping was 70% in both species, and we observed initiation of new shoots from multiple stem epicormic buds, typically 7–12 days after clipping. In contrast, there was minimal resprouting in *T. laurina* and *A. symphyocarpa* in 5–60 day old plants (in total, 3 of 102 and 3 of 90 individuals of each species resprouted, respectively). The failure of clipped seedlings to survive was not due to factors other than the clipping treatment since the unclipped paired controls in all four species experienced 0% mortality across the experiment.

Logistic modelling provided strong support for an important effect of species on resprouting ability. In particular, resprouting ability over 150 days growth was predicted to be substantially lower in *A. symphyocarpa* and *T. laurina* than in *M. leucadendra* (*A. symphyocarpa* mean -4.49, 95% CI: -5.82 to -3.40; *T. laurina* mean -7.13, 95% CI: -11.67 to -4.59; Table 3.5). In comparison, evidence in support of differential resprouting ability in *E. camaldulensis* relative to *M. leucadendra* was less strong, and positive (*E. camaldulensis* mean 1.64, 95% CI: 0.49 to 3.09; Table 3.5), but at 25 days resprouting ability in *M. leucadendra* and *E. camaldulensis* was similar. Evidence in support of the effect of age alone on resprouting ability was equivocal, with the 95% credible interval encompassing 1 (Table 3.5), whereas the species-age interaction had positive effects on resprouting ability in *A. symphyocarpa* and *E. camaldulensis* relative to *M. leucadendra* (*A. symphyocarpa* mean 1.68, 95% CI: 0.97 to 2.42; *E. camaldulensis* mean 2.74, 95% CI: 0.99 to 4.90).

Relationships between resprouting ability, seed size and growth traits among species

Species' relative resprouting capacity was consistent with general species trends in root mass investment (i.e. root mass fraction). The two species demonstrating high resprouting ability throughout early growth (*M. leucadendra* and *E. camaldulensis*) also showed intermediate to highest investment in root biomass relative to absolute plant mass, although we found no evidence that this investment was associated with development of a lignotuber at 25 days growth. There was no evidence for relationships between resprouting capacity and species ranked in order of seed mass, relative growth rate or absolute seedling size (Table 3.6).

Discussion

Relationships between riparian seedling resprouting ability and reserve size

Differences between species in seedling resprouting ability have previously been correlated to larger seed and seedling size. This suggests that the amount of stored reserves is a principal mechanism promoting survival during early plant development (Westoby et al., 1992; Garwood, 1996; Kitajima and Fenner, 2000). If resprouting was related solely to seed mass, then it should be most prevalent and acquired at earlier stages of development in seedlings from species with greatest seed mass. This was not the case in our study. Rather, we found that resprouting was acquired earliest in seedlings of *M. leucadendra* and *E. camaldulensis*, and these species had small and intermediate seed masses. Moreover, survival rates in seedlings of these species were high even after clipping at five days post emergence. At this stage, only epigeal cotyledons had developed, and plant functioning was most probably still reliant on seed-derived reserves (e.g. Kitajima, 1996; Boege and Marquis, 2005). Seedlings from *A. symphyocarpa*, however, showed minimal survival under clipping. This was also the case in seedlings from the larger-seeded *T. laurina*, despite mean seed mass in this

species being more than three times that of *E. camaldulensis*, and 20 times that of *M. leucadendra*.

Furthermore, survival or resprouting were not related to absolute seedling size. Resprouting was lowest in *T. laurina*, although absolute seedling size in this species was substantially larger than in *M. leucadendra* and *E. camaldulensis*, both strong resprouters. One potential explanation is that species differences in resprouting at deployment stage may arise due to differences in allocation to metabolic activity in stem meristem regions (Boege and Marquis, 2005). The finding of significant epicormic resprouting in *M. leucadendra* and *E. camaldulensis* indicates cotyledonary bud primordia are abundant and activated early in these species (cf. Pascual et al., 2002; Verdaguer and Ojeda, 2002), which, in turn, may enable seedlings to rapidly recover photosynthetic function even at very small plant body sizes.

Furthermore, our results suggest that considerable variation exists in species' programmes of functional development from cotyledon stage that may not be simply determined by RGR, or the interplay between seed size and RGR (Vuorisalo and Mutikainen, 1999; Muller et al., 2000; Boege and Marquis, 2005). We found no evidence that resprouting during seedling development was a simple function of RGR, nor of plant size at seed, seedling or mature life stages, and thus no support for the predicted 'cost' of resprouting ability to growth potential that may arise due to the inverse relationship between growth rate and size of stored reserves (Pate et al., 1990; Gurvich et al., 2005; Pratt et al., 2005 but see Schwilk & Ackerly 2005). Although *M. leucadendra* and *E. camaldulensis* (both strong resprouters) showed intermediate to highest root allocation, we found no evidence that this was due to investment associated with development of a lignotuber during early growth. One potential explanation for the finding that resprouting capacity was not related to RGR or seedling reserve size might be that species differ in their rates of physiological efficiency (cf. Walters and Reich, 2000; van Eck et al., 2004). For example, seedlings of *M. leucadendra* showed high shoot resprouting capacity in addition to greatest ongoing allocation to root biomass, indicating metabolic activity in both shoot and root modular regions is high (e.g. Vuorisalo and Mutikainen, 1999). Efficient resource assimilation and translocation could have functional value during early development (Garwood, 1996), because physiological efficiency can provide a mechanism allowing resprouting and recovery from damage and stress (Mulligan and Patrick, 1985; Sakai and Sakai, 1998; Reekie, 1999; Iwasa, 2000) despite small absolute biomass or reserve size. Explicit tests of this proposal are required. For instance, the relative contribution of resource assimilation rate to species differences in seedling functioning could be examined by comparing species' growth and resprouting patterns as functions of photosynthetic rate per unit cotyledon and leaf nitrogen (Kitajima, 1996; Wright and Westoby, 2000). Nevertheless, our results implicate more than one solution to the requirements of early acquired

resprouting ability. Seedlings of *M. leucadendra* and *E. camaldulensis* showed distinct allocation patterns, despite having similar resprouting capacities.

The roles of resprouting as a functional plant attribute

Our results also indicate that species differ in the acquisition of resprouting capacity during early seedling development. In support of this contention, an *ad hoc* clipping treatment at 150 days (four leaf pairs) revealed resprouting ability in *A. symphyocarpa* (12 of 15 individuals) but not in *T. laurina* (0 of 17 individuals), whereas the responses of *M. leucadendra* and *E. camaldulensis* were maintained across developmental stages. Thus, seedling resprouting ability is not well predicted by either plant size or age in *M leucadendra* and *E. camaldulensis* (cf. Muller et al., 2000; Weiner, 2004), but appears cued by increasing developmental stage in *A. symphyocarpa*. To some extent this must also be true for *T. laurina*, since resprouting has been shown in saplings and adult plants (e.g. Melick, 1990a). However, it was not developed at 150 days post emergence in our study. This is consistent with resprouting response being a widely variable phenomenon among species within disturbance type, growth form, and size-stages (Vesk, 2006).

Plants that exist in environments that impose inescapable, recurrent disturbances causing large biomass loss should experience strong selective pressure for maintaining resprouting ability throughout their lifetime (Vesk, 2006). Resprouting has been shown in many mature-stage Myrtaceae, including members of all four genera studied here (e.g. Conde et al., 1981; Lacey and Johnston, 1990; Melick, 1990b; Melick, 1990a; Miwa et al., 2001; Tierney, 2004). By demonstrating that resprouting ability is acquired by cotyledonary stage in two ecologically conspicuous riparian epigeal taxa (*M. leucadendra* and *E. camaldulensis*) and, to a lesser extent, within the first year in another two riparian species (*A. symphyocarpa* and *T. laurina*), we provide support for the general proposition that resprouting is a generalised response to disturbance at the seedling stage as well as in adult plants (Bellingham and Sparrow, 2000; Bond and Midgley, 2001; Bond and Midgley, 2003; Vesk and Westoby, 2004).

An essential complementary consideration is that processes conferring resprouting ability may be advantageous for alternate functions, including nutrient and space acquisition (Jackson et al., 1999; Iyer et al., 2003), stress tolerance and structural stability (Melick, 1990a; Mensforth and Walker, 1996; Davies and Giblin-Davis, 2004; Pratt et al., 2005) and growth (Fielding et al., 1997; Gurvich et al., 2005), all of which may exert strong selective influence. Indeed, early seedling establishment will depend on the contributions of multiple plant parts (e.g., seed reserves, cotyledons and leaves as well as roots and shoots) to multiple functions (photosynthesis and reserve storage as well as nutrient uptake, anchorage and stability; Garwood, 1996). Arguably, it is unlikely that disturbance acts as a sole selective pressure governing resprouting ability.

More plausibly, resprouting reflects a suite of characteristics that confer benefit in the face of numerous environmental constraints and hazards.

Conclusions

This study demonstrates that *M. leucadendra* and *E. camaldulensis* show high resprouting ability from early seedling developmental stages, which is not a function of resource provisioning via large seed size, nor relative growth rate. Our results also indicate considerable between-species variation in seedling resprouting capacity, suggesting physiological and morphological traits other than those related to reserve size or relative growth rate alone may also contribute to resprouting and survivorship in river environments (Malanson, 1993; Fielding and Alexander, 2001). High allocation to meristematic activity might best explain resprouting, which may be selected on the basis of advantages it conveys for other life-history requirements such as establishment, structural stability and resource acquisition (e.g. Melick, 1990a; Noland et al., 1997; Jackson et al., 1999; Abernethy and Rutherfurd, 2001). This may explain why we were unable to demonstrate an association between resprouting ability and either seed size or RGR predicted from previous studies from fire-prone temperate areas. Studies of seedling resprouting ability that include larger numbers of species from riparian systems will be required before generalisations should be attempted.

Acknowledgements

We warmly thank Richard Pearson and Michelle Ensbey for useful discussion of statistical analyses, and Allyson Lankester, Chris Gardiner and Ainsley Calladine for logistic support. Peter Bellingham and two anonymous reviewers provided very helpful advice that greatly improved the manuscript. Supported by the Australian Centre for Tropical Freshwater Research, the Cooperative Research Centre for Tropical Savannas Management and an Australian Postgraduate Award to CC.

Tables and figures

Table 3.1. Summary description of species, distribution, habit, seed form and mean total seed mass (mg) for taxa used in this study; four riparian woody tree species from distinct Myrtaceous genera were used. Extra-Australian distribution localities: PNG = Papua New Guinea, IND = Indonesia; Australian localities: QLD = Queensland, NT = Northern Territory, WA = Western Australia, NSW = New South Wales, VIC = Victoria. Localities in italics correspond to localities of seed lots used.

Code	Species	Distribution	Habitat	Habit	Seed winged	Seed and cotyledon form	Seed mass (mg) (% s.e.)
MEL	*Melaleuca leucadendra sensu lato*	*PNG*, IND, *QLD*, *NT*, WA	Watercourses; lagoons	Tree to 30 m	No	Seed narrowly obovoid/oblong; cot. obvolute	0.07 (4.36)
AST	*Asteromyrtus symphyocarpa* (F. Muell.) Craven	*PNG*, *NT*, *QLD*	Watercourses; *Melaleuca* woodlands; monsoon rainforest; coastal sand plains	Shrub or tree to 17 m	Yes	Seed obovoid, wing well developed at seed apex; cot. plano-convex	0.31 (3.05)
EUC	*Eucalyptus camaldulensis* var. *obtusa* Blakely	*QLD*, *NT*, WA	Watercourses	Tree to > 30 m	No	Seed round/obovoid; cot. obovate	0.41 (2.45)
TRIST	*Tristaniopsis laurina* (Sm.) Peter G. Wilson & J.T. Waterh.	*QLD*, NSW, VIC	Watercourses; temperate rainforest	Tree to 30 m	Yes	Seed contained in a samara; cot. obvolute	1.60 (2.37)

Table 3.2. Coefficients (mean, standard deviation, and 2.5th and 97.5th percentiles) of the explanatory variables (tspec = time in days to emergence from radicle protrusion to full cotyledon expansion within species; σ^2 = variance within species) included in the best-fit ANOVA model, for mean time from germination to full emergence among species. Values of species coefficients represent terms relative to the reference class tspec = MEL. Refer to Table 3.1 for species codes.

Variable	Mean	SD	2.5%	97.5%
$tspec_{MEL}$	3.542	0.038	3.467	3.616
$tspec_{AST}$	+ 2.536	0.051	2.436	2.636
$tspec_{EUC}$	+ 0.050	0.056	-0.059	0.159
$tspec_{TRIST}$	+ 4.091	0.051	3.991	4.191
σ^2_{MEL}	2.930	0.268	2.428	3.478
σ^2_{AST}	4.848	0.512	3.897	5.901
σ^2_{EUC}	2.542	0.232	2.106	3.017
σ^2_{TRIST}	4.280	0.424	3.490	5.149

Table 3.3. Summary of seedling growth characteristics for four Myrtaceous riparian woody tree species grown under greenhouse conditions. Data values refer to cotyledon stage (5 days post emergence) or seedling stage (25 days post emergence) as indicated. Values represent means of back-transformed data from arcsin square root (cotyledon mass fraction, root mass fraction) and ln (specific hypocotyl length, specific root length) transformations; other values as indicated. Refer to Table 3.1 for species codes.

	Species			
	MEL	AST	EUC	TRIST
Cotyledon stage				
Cotyledon mass fraction at 5 days (proportion total dry plant mass)	0.58	0.75	0.63	0.68
Specific hypocotyl length at 5 days (mm mg^{-1} dry shoot mass)	157.10	92.32	128.00	37.66
Seedling stage				
Root mass fraction (proportion total dry plant mass)	0.21	0.11	0.18	0.17
Specific root length (mm mg^{-1} dry root mass)	146.20	67.10	35.20	61.30
Lateral root frequency (mean no. laterals mm^{-1} root)	0.58	0.33	0.26	0.23
Lateral root investment (mean no. laterals mg^{-1} dry root mass)	84.80	21.90	9.30	14.70
Total root length (mean *(s.e.)*)	28.00 *(1.65)*	69.10 *(9.17)*	226.70 *(9.33)*	76.40 *(6.89)*
Number of lateral roots (median *(range)*)	15 *(10–22)*	21 *(11–24)*	59 *(32–103)*	19 *(3–43)*
Number of basal lateral roots (median *(range)*)	2 *(0–6)*	1 *(0–3)*	0 *(0–3)*	0 *(0)*

Table 3.4. Comparison of species relative growth rate (RGR) calculated from ln(total plant mass, mg) and ln(time post-emergence, days) for t = 5 to 25 days post emergence. Values are results of SMA analyses for individuals of each species. Lower and upper β represent 95% confidence intervals for the estimated SMA slopes. There were significant differences among all species slopes (SMA common slope test, P = 0.001; pairwise comparisons, P < 0.0001). Also shown are Model 1 slopes (RGR, mg $mg^{-1}d^{-1}$) for comparative purposes. Refer to Table 3.1 for species codes

Species	n	r^2	P	SMA slope	Lower β	Upper β	Model I slope
MEL	35	0.84	< 0.0001	1.47	1.27	1.69	1.34
EUC	65	0.92	< 0.0001	3.13	2.91	3.37	3.00
AST	50	0.90	< 0.0001	2.15	1.96	2.35	2.03
TRIST	68	0.83	< 0.0001	0.98	0.89	1.09	0.90

Table 3.5. Coefficients (mean, standard deviation, and 2.5th and 97.5th percentiles) of the constant and explanatory variables ($spec_X$ = species x, age = time to emergence, interaction) included in the best-fit logistic regression model, for seedling resprouting response to a single clipping treatment at seven age harvests (5, 10, 15, 25, 40, 60, 150 days post emergence). Clipping treatment comprised removal of all plant material 5 mm above substrata. Response to clip was binary; plants either resprouted or died. All observed resprouts were from stem epicormic regions. Values of species and interaction coefficients ($spec_X$, $spec*age_X$) represent terms relative to the reference class spec = MEL. Refer to Table 3.1 for species codes

Variable	Mean	SD	2.5%	97.5%
constant	1.364	0.220	0.946	1.810
$spec_{AST}$	-4.492	0.619	-5.825	-3.402
$spec_{EUC}$	1.645	0.660	0.494	3.086
$spec_{TRIST}$	-7.126	1.849	-11.670	-4.598
age	-0.159	0.219	-0.572	0.291
$spec*age_{AST}$	1.680	0.370	0.975	2.427
$spec*age_{EUC}$	2.742	0.999	0.989	4.900
$spec*age_{TRIST}$	-3.597	2.601	-9.849	0.011

Table 3.6. Summary of relationships between seedling resprouting ability and growth parameters among species at 25 days post emergence. For each parameter, species codes are listed in order of increasing magnitude of the measured parameter. Superscripts represent species groups that are significantly different (for resprouting ability and RGR, refer to statistical analyses in Table 3.5 and Table 3.4; for seed mass, total biomass and root mass fraction, groups represent results of SMA analyses: all pairwise contrasts, $P < 0.01$). Refer to Table 3.1 for species codes

Order	Resprouting ability	Seed mass	RGR	Total biomass	Root mass fraction
Lowest	TRIST [1]	MEL[1]	TRIST[1]	MEL[1]	AST[1]
	AST [2]	AST[2]	MEL[2]	AST[2]	TRIST[2]
	EUC [3]	EUC[2]	AST[3]	TRIST[3]	EUC[2]
Greatest	MEL [3]	TRIST[3]	EUC[4]	EUC[4]	MEL[3]

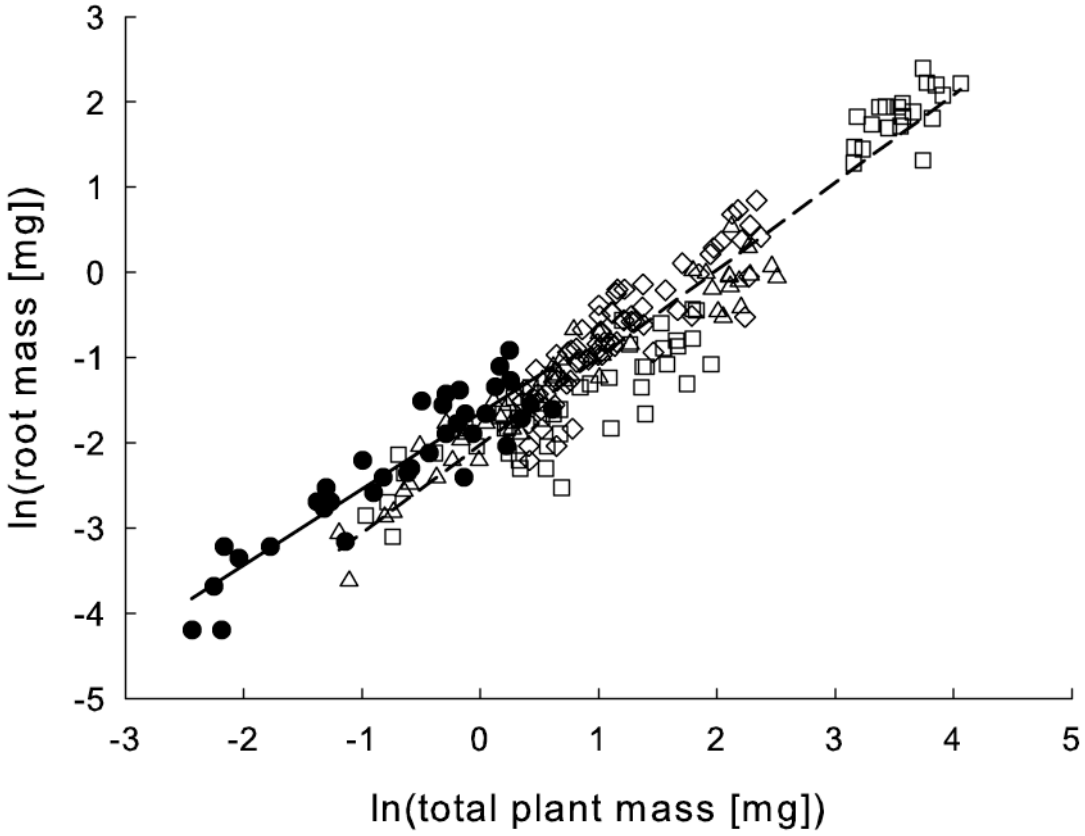


Figure 3.1. The relationship between log total plant mass and log root mass among seedlings within four tree species from sub-tropical, riparian northern Australia. Values represent the results of SMA analyses across individual plants at 25 days post emergence. Slopes were homogeneous across species ($p = 0.703$, common slope of 1.18 (0.97, 1.45)). There was a significant elevation shift between *M. leucadendra* and other species: log root mass at a given log total plant mass was greatest for *M. leucadendra* (see text for details). Lines represent the linear regression of individual values for *M. leucadendra* (solid line) and for the three other species combined (dashed line). Closed circle = *M. leucadendra*, open triangle = *A. symphyocarpa*, open square = *E. camaldulensis* var. *obtusa*, open diamond = *T. laurina*.

Chapter 4—Clonality and disturbance in riverine *Melaleuca leucadendra* (L.) L.

Introduction

Contemporary niche theory suggests that disturbance is a key filter determining within-habitat (α-level) structure in plant communities, driving variation in survival traits and niche occupancy among species (Silvertown et al., 1999; Pierce et al., 2007). Climate-driven disturbances, such as episodic floods, impose recurrent stress on plants at both landscape and local scales (Tabacchi et al., 1998; Gutschick and BassiriRad, 2003). In such environments, niche dominance might be expected to reflect variance among co-occurring taxa in their abilities to persist under localised stress regimes. Under high-intensity disturbance regimes that cause recurrent damage and removal of above-ground biomass, resprouting confers direct survival benefits to woody plants because the probability of genet mortality is spread over multiple ramets in time as well as space (Pan and Price, 2002). Resprouting individuals can also quickly re-establish above-ground biomass and reproductive function, promoting persistence (Peterson and Jones, 1997). Indeed, intense disturbances, such as fires resulting in stem-kill, appear to be strongly associated with the probability of sprouting ability across species and vegetation types (Vesk and Westoby, 2004). In turn, the fitness effects of resprouting are expected to feed back with the combined selective effects of sexual reproduction and dispersal (Peterson and Jones, 1997; Silvertown, 2001; Pan and Price, 2002) and the disturbance regime (Bond and Midgley, 2001; Vesk, 2006) to influence the size, density and genetic diversity of above-ground stems within plant populations. For example, in river systems, the intensity and predictability of floods could be expected to determine the availability of moist sites needed for seedling regeneration (Deiller et al., 2001; Goodson et al., 2001), the likelihood of long-distance dispersal of seed by water (Kubitzki and Ziburski, 1994; Nathan, 2006), and the likelihood that a developing plant will survive a given flood event (Fielding et al., 1997). Prolific resprouting in response to flood disturbance can lead to large clone size, associated with high ramet density and low diversity among genotypes. Douhovnikoff et al. (2005) showed that prolific clonal growth in *Salix exigua* (Salicaceae) in two North American river systems, characterised by clones as large as 325 m^2, was associated with a reduced disturbance regime and greater recolonisation ability, as well as reduced genetic diversity. Despite this, the relationship between plant genetic processes, plant spatial structure and disturbance regimes remains virtually unexplored outside of herbaceous and temperate communities (Silvertown et al., 1999; Ackerly and Cornwell, 2007), making it difficult to generalise between community and ecosystem types about the relationship between disturbance and selection for regeneration strategies.

In this study I apply ecological genetic methods to address multiple spatial scales of relationships between disturbance and survivorship in *M. leucadendra* in the Burdekin

River catchment of north Queensland, Australia. The Burdekin River catchment is one of the most hydrologically and geomorphologically variable in Australia and the world (Puckridge et al., 1998) and thus offers an ideal opportunity to investigate the interaction between individual plant traits and disturbance processes in establishing population genetic structure. A primary methodological challenge in studying growth, survival and dispersal in riverine vegetation is defining the scales at which disturbance processes and biological processes interact. Large semi-arid river systems feature highly unpredictable, yet frequent (1-in-8-year recurrence interval), short-duration, high-magnitude floods. These individual events impose high-impact shear stresses causing geomorphologic changes as well as changes in demographic structure due to damage, uprooting and mortality (Fielding et al., 1997; Alexander et al., 1999a). Resprouting and long lifespan are common traits of species occupying these environments, and resprouting is expressed in numerically dominant species such as the paperbark tree *Melaleuca leucadendra* (L.) L. (Myrtaceae) (Fielding and Alexander, 2001; Chong et al., 2007). Stem resprouting in riverine *M. leucadendra* has been suggested to create diagnostic channel features such as alluvial bars, which in turn persist *in situ* as the preserved remains of trees (Fielding et al., 1997). This series of processes suggests that *M. leucadendra* may represent an autogenic engineer via actively mediating local environmental conditions (e.g. Jones et al., 1994; Hastings et al., 2007). In turn, the probability distribution of large fluvial disturbance events, that is, the distribution of events at the upper tail, could be expected to represent a biologically relevant scale to interpret variation in survival responses that is likely to dictate genotypic structure in this species.

The statistical theory of extremes remains under-utilised in ecology despite that ecological stresses, typically derived from climate-driven extreme events, play an important role in population and community dynamics (Gaines and Denny, 1993; Gutschick and BassiriRad, 2003; Katz et al., 2005). For instance, exceedance of temperature, drought, or force parameters beyond biological tolerance thresholds can exert critical influence on survivorship and recruitment (Lloret et al., 2005), and in turn shape species' habitat and geographical range limits (Silvertown et al., 1999; Chaves et al., 2003; Silvertown et al., 2006). For plants, the spatial and temporal scales of disturbance processes imposing severe physical stress play a driving role in ecological and genetic interactions from individual to ecosystem levels (Karrenberg et al., 2002; Pausas et al., 2004). Understanding the effects of physical disturbance on plant functioning and life history across locations and disturbance types requires an understanding of the probability that individuals will experience physical stresses exceeding biological tolerance: that is, the likelihood and severity of the statistically extreme events (Katz et al., 2005). The statistical theory of extremes, based on the Generalised Extreme Value (GEV) family of distributions (Coles and Tawn, 1996; Behrens et al., 2004), provides appropriate methods to examine the distribution of ecological variables that typically possess a heavy-tailed distribution. Examples of these

variables are severe fire and flood disturbance events that require scaling (i.e., power law) parameterisation (Moritz, 1997; Katz et al., 2002). The direct applications of extreme value theory feature extensively in evaluating climate-driven phenomena including hydrology (stream flow), but few examples define ecologically relevant processes such as long distance dispersal events.

I assessed the scales at which clonal growth influences genetic diversity by determining the distribution of genetic individuals at a range of distances within sites, and comparing these distributions between sites that differed in disturbance regime. I predict that if stem resprouting is a mechanism for survival and species persistence, the extent to which resprouting generates clonal growth structure should reflect the likelihood and intensity of disturbance events. Specifically I ask: i) what is the spatial distribution and prevalence of clonal growth in *M. leucadendra*? ii) how do differences in flood disturbance regime relate to clonal growth? and iii) what role could clonal growth play in maintaining genetic structure and promoting survival in this species?

Materials and methods

Study system and study species

Study sites were located in the Upper Burdekin River catchment in north-east Queensland, Australia (catchment area *c*. 60 000 km^2) (Figure 4.1). The Burdekin River catchment is a dry tropics river system that exhibits seasonal drought and high-magnitude, short-duration flood events that exceed 10 000 m^3s^{-1} (Fielding et al., 1997). In the Burdekin River system and many other similar northern Australian rivers, *Melaleuca leucadendra* occurs as an open woodland forest in mono-dominant stands in the lower channels (Specht, 1990). Diverse resprouting strategies in this species exist, and include a multi-stemmed growth habit, stem layering, coppicing and root suckering as well resprouting from partly buried stems. Thus, the above-ground spatial distribution of stems (ramets) may not accurately reflect the spatial distribution of genetically unique individuals (genets). To assess the relationship between above-ground stem identity and genetic identity, a genotypic identity approach was adopted. This approach assessed the spatial structure of individuals within ecological neighbourhoods to quantify cryptic population structure.

Sampling strategy

To characterise the spatial genetic structure of individuals based on multilocus microsatellite genotypes in *M. leucadendra*, four sites, each separated by more than 40 km, were sampled within one low-flow season (June–December 2004). Three sites, Greenvale (GRE), Blue Range (BLU) and Big Bend (BIG), were located along a 150 km reach of the primary river tributary (Figure 4.1). The fourth site, Upper Keelbottom Creek (KB), was a headwater tributary (Figure 4.1). At all four locations, above-ground stem structure comprised stands of closely spaced mature stems (typically 5–20 m in length)

along both sides of the river bed. Individual stems in each stand were predominantly less than 20 m in height and generally inclined greater than 40° in the direction of stream flow. At KB, one additional stand (approximately 150 m) on the western river bank occurred in which above-ground stems were typically >20 m tall.

At each site, ten stands, each comprising five or more mature stems >15 cm diameter, were haphazardly selected along both sides of the channel. Within each stand, the diameter class and relative position of each stem was mapped with respect to the spatial coordinates of the most upstream ramet in each stand (Garmin eTrex™). The spatial locations of all ramets were subsequently standardised in UTM units using ArcView 9 (Environmental Systems Research Institute, Inc.). At KB, all 61 mature stems of the stand on the western bank were also mapped. The linear distances between individual sampled ramets ranged from 0.1–587 m within sites, and 42–147 km among sites. Samples for genetic analyses were collected by excising 1–2 fully expanded leaves from each ramet within each stand. Leaf samples were labelled and immediately stored on silica gel in airtight containers to facilitate rapid desiccation for preservation and transport to laboratory for genotypic analysis.

Genotypic analysis

Total nuclear DNA was extracted using the QIAGEN DNeasy Plant Mini Kit™ (QIAGEN, Valencia, CA), including the optional centrifugation step to remove excess precipitates. Prior to PCR amplification of samples, secondary contaminants were reduced via a silica-plate cleanup protocol (Elphinstone et al., 2003) and the integrity of extracted DNA for each sample was assessed visually via agarose gel electrophoresis and quantified by spectrophotometric analysis using a NanoDrop® ND-1000 (NanoDrop Technologies, Wilmington, DE). Candidate microsatellite loci from *M. alternifolia* (previously demonstrated to have cross-species amplification capability: Rossetto et al., 1999a) were optimised for 15 candidate loci using *M. leucadendra*. A subset of 8 loci was selected to screen across all samples. Loci were amplified using QIAGEN and Bioline DNA polymerase reagents with 5'-fluorescent tagged primers on a MJ Research DNA Engine Tetrad 2 Thermocycler (Bio-Rad Laboratories, Hercules, CA). DNA amplification of each locus followed a protocol where an initial 10 cycles of amplification included reduction of annealing temperature by 1°C per cycle for 10–15 cycles from 60°C and then followed by a further 20 cycles at the lowest temperature. Amplification products were analysed by fluorescent-dye detection on a MegaBACE 1000 (GE Healthcare) at the James Cook University Genetic Analysis Facility, Townsville, Australia and individual genotypes scored using the Genetic Profiler Suite v. 2.2 module Fragment Profiler (GE Healthcare).

Statistical analysis

Genet identification

Estimation of the likelihood that detected replicate multilocus genotypes (MLGs) arise as a consequence of vegetative as opposed to sexual propagation is critical to confident assignment of individuals as clones, and several different approaches have been advocated (Parks and Werth, 1993; Reusch et al., 2000; Arnaud-Haond et al., 2005). Here, I used standard methods implemented in GeneCap v.1.2.1 (Parks and Werth, 1993; Wilberg and Dreher, 2004). Matching genotype probabilities were generated by pairwise comparison of each allele of each sample with all others on the bases of the dataset, the missing data and the chance probability of a sibling match, thereby accounting for potential bias due to duplicate genotypes of matching individuals.

Characterisation of spatial genetic structure

Spatial autocorrelation analyses to characterise fine-scale spatial genetic structure (SGS) were performed on both the full data set, maintaining all repetitions of MLGs, and a data set using a single representation of each MLG (hereafter, ramet- and genet-level analyses respectively). For genet-level analyses in the case of repeated MLGs, I selected the spatial location of the largest diameter ramet as the most biologically plausible representation of genet spatial origin and this was used in subsequent analyses. I also estimated the clonal sub-range at each sampling site. The clonal sub-range provides a useful measure of spatial genetic structure due to clonality and defines the point where the autocorrelation function considering all ramets, and the one excluding clonality but retaining all ramet spatial information, intersect. This represents the spatial scale of autocorrelation as a function of ramet location - that is, the spatial range in which clonal structure influences SGS (Calderón et al., 2007).

Genetic co-ancestry between pairs of individuals was estimated using the kinship coefficient F_{ij} described in Loiselle *et al*. (1995) and implemented in SPAGEDI 1.2, including alleles from all individuals (Hardy and Vekemans, 1999; Hardy and Vekemans, 2002; Vekemans and Hardy, 2004). Average relatedness coefficients were estimated for F_1=0–2 m and the distance categories: 2–4, 4–6, 6–8, 8–10, 10–15, 15–30, 30–45, 45–60, 60–75, 75–100, and then in successive intervals to the maximal distance recorded at each sampling site. To visualise SGS, average F_{ij} values were plotted against the logarithm of distance and regressed on $ln(d_{ij})$ to obtain the regression slope b. To test for SGS under the null hypothesis that F_{ij} (pairwise genetic relatedness) and d_{ij} (pairwise geographic distance) were uncorrelated, the spatial positions of the individuals were permuted 10000 times and confidence intervals obtained from jack-knifing over loci (Vekemans and Hardy, 2004; Hardy et al., 2006). SGS intensity was quantified by $Sp = -b/(F_1 - 1)$, where F_1 represents the average kinship coefficient between adjacent, neighbouring individuals (Fenster et al., 2003; Vekemans and Hardy, 2004) and using b calculated over 210 m for each site.

Characterisation of population genetic structure

Evidence for population structure without prior inference of spatial origin was investigated because of the expectation that stochastic disturbance contributes to an highly heterogeneous distribution of clonal or closely related individuals within this riparian system (Dale, 1999; Barsoum, 2002). Bayesian model-based clustering methods implemented in STRUCTURE v. 2.1 (Pritchard et al., 2000) were used to probabilistically assign individuals to clusters with distinctive allele frequencies, independent of prior information of spatial identity or assumed Hardy-Weinberg equilibrium (cf. Corander et al., 2003; Guillot et al., 2005). 'True' genetic cluster number (K) estimates were conducted using a minimum of one to a maximum of eight values for K, and 20 runs for each K-value. Following preliminary parameter analyses I used a hierarchical approach to analyse each proposed cluster until no further subdivisions were evident. For individual cluster analyses I set K=1 to twice the number of indicated subdivisions. For all analyses I used the admixture model, allowing for uncorrelated allele frequencies between clusters. Runs were performed using a burn-in of 6×10^5 followed by 1.2×10^6 iterations. Convergence and mixing behaviour at successive values of K were evaluated by inspecting time-series plots of the individual parameters. Optimal clustering solutions (K genetic populations) were evaluated by examining the probability of individual assignments based on credible intervals and calculating the second order rate of change of the likelihood function with respect to K (Evanno et al., 2005).

Characterisation of local-scale fluvial signature

Local-scale catchment disturbance distributions were characterised and used to evaluate evidence for differences in fluvial signatures among sampling localities. An events-based approach was applied because this represents a biologically relevant hypothesis to expect impact on plant survivorship (Fielding and Alexander, 2001). Defining and predicting hydrogeomorphic events that have persistent effects on ecology and evolution requires arbitrary selection of an absolute threshold value, or high percentile of the distribution, to identify the frequency and intensity at which events occur and exceed biological tolerance levels (Silvertown et al., 1999; Katz et al., 2005). In river environments, assigning absolute value scales based on local demographic structure could resolve scales of effects on survivorship relatively coarsely, due to extreme variance in the spatial and temporal signatures of disturbance and genetic structure, gene flow and interactions among the biological units of interest, whether individuals, demes, populations or species. Within an interdisciplinary research framework, integrating events-based disturbance models based on hydrological flow data with genetic methods may help to inform scales of genetic relatedness and variability. This offers one potentially valuable approach to quantify the scale-dependent relationships between ecological and physical processes influencing riparian vegetation function.

In this context, I conducted extreme event analysis based on maximum likelihood and Bayesian methods to generate return level plots and examine the signatures of flood disturbance. Data evaluation was based on daily discharge records representing 33 contiguous flow years (June 1973 to 2006) at four locations corresponding to the closest available active gauging stations to my sampling sites (Figure 4.1). These gauging locations were selected as representative of the different flood regimes that occur at mainstream and headwater locations within the upper Burdekin catchment, based on previous flood duration analyses (Figure 4.2). For each location, specific stream power distributions for the three largest flow events were plotted (cf. Costa and O'Connor, 1995). These distributions were derived from characterisation of the channel features (cross-sectional profiles; Figure 4.3a–d) and flow history (hydrographs; Figure 4.4a–d) at each location. Extreme event analysis, using maximum likelihood descriptive diagnostics and Bayesian methods (Gilleland et al., 2004; Stephenson and Ribatet, 2006), was then conducted to characterise local catchment flood distributions and return levels.

First, maximum likelihood descriptive diagnostics were applied to estimate threshold and prior parameters because expert opinion was not available to elicit prior quantile estimates. Specifically, I evaluated the mean excess plot and applied multiple model fitting procedures as implemented in the extRemes v1.55 R package to assess the relative stability of parameter estimates and effects on model posterior likelihood across a range of threshold values (Behrens et al., 2004; Gilleland et al., 2004; Stephenson and Tawn, 2004) (Figure 4.5a–b). Second, the optimal maximum likelihood parameterisations were used as prior and threshold information in the Bayesian R package evdbayes v1.0.6 (Stephenson and Ribatet, 2006). Catchment return level plots were generated using the point process and MCMC procedures implemented in evdbayes (three chains, run length n=600 000; burn-in period b=20 000; thinning interval k=5). The GEV distribution has had conventional applications to fit data representing block maxima, such as annual maximum values. The peaks over threshold (POT), or point process approach, is an alternative construction of a mixture model incorporating exceedance thresholds. This approach allows use of more information (observations) about the upper tail of the distribution to estimate unknown parameters (Behrens et al., 2004; Katz et al., 2005). This parameterisation is consistent with a Poisson process for the occurrence of exceedances of a high threshold and the Generalised Pareto Distribution for excesses over this threshold (Gilleland et al., 2004). A positive value for the shape parameter of the POT distribution, $\xi > 0$, suggests that the distribution is heavy-tailed: that is, decreases at a relatively slow rate and shows high variance from the standard normal distribution.

Model diagnostic procedures included evaluation of chain behaviour from parameter time series plots and used the Gelman & Rubin (1992) diagnostic. All computations were performed in R v 2.5.0 (R Development Core Team, 2007).

Results

Allele characteristics, genotypic richness and clonal growth

Across the eight microsatellite loci used, 4–37 distinct alleles per locus were detected. Allele size ranged from *c*. 85–356 and median expected heterozygosity was 0.900 across loci (Table 4.1).

I found strong evidence for spatially localised clonal propagation at all three mainstream sampling sites. At each mainstream site, replicate multilocus genotypes (MLGs) were detected within multiple tree stands 5–30 m in length (Table 4.2). For all replicate MLGs, the estimated probability of encountering an identical genotype derived from sexual reproduction, rather than clonal growth, was low (less than 4% probability of any combination of ramets) whereas all pairwise genotype match probabilities were highly significant ($p<0.001$, $\alpha=0.01$), indicating strong support for clonal assignments. In total, 42 replicated genotypes were identified, representing groups of 2 to 5 clonal stems. Overall, 30% of samples from the mainstream catchments shared genotypes among more than one stem (Table 4.2). In contrast, no replicate MLGs were detected among samples from the headwater catchment KB ($n=90$, Table 4.2). Furthermore, each genotype from this site differed by more than two alleles from all others, confirming that genotypes represented genetic individuals. Genotypic richness - the proportion of samples at each site identified as unique genotypes - was high across sites and independent of sample size (clonal richness 0.74, 0.62 and 0.77; Simpson's diversity index 0.988, 0.978 and 0.981 at GRE, BLU and BIG respectively, Table 4.2). At KB, the headwater site, clonal richness was 1.00, because all samples corresponded to unique genotypes.

Clonal growth and spatial genotypic structure

The clonal sub-range represents the distance range beyond which clonality has negligible effects on genetic structure (Figure 4.6a–c). At the mainstream site BLU, the clonal sub-range was greater (10–15 m, Figure 4.6b) than at GRE or BIG (both 4–6 m, Figure 4.6a,c). However, for all sites the probability of clonal identity, estimated as the proportion of pairs within the corresponding distance class that include ramets with the same genotype, declined with increasing distance to $p<0.056$ at the respective clonal sub-ranges and $p<0.001$ beyond 35 m. At site GRE the maximal probability of clonal identity at the shortest distance class (0–2 m) was considerably lower ($p=0.190$) than at BLU and BIG (both $p=0.417$) whereas the maximal pairwise distance between replicate ramets was greatest (16.81 m, 15.48 m and 10.18 m at GRE, BLU and BIG respectively; Table 4.2). These differences correspond to differences in the relationship between the ramet-level (Figure 4.6a–c) and genet-level (Figure 4.6d–g) correlograms within the clonal sub-range, relative to the 95% confidence envelope indicating non-random spatial pattern. Among genets, the average kinship coefficient indicating spatial genetic aggregation was significantly positive at the first three distance classes for site

GRE ($F_{(2m)}$=0.205, $F_{(4m)}$=0.161, both P<0.001; $F_{(6m)}$=0.063, p= 0.020, Figure 4.2d) but not for sites BLU ($F_{(2m)}$=0.079; p=0.052), BIG ($F_{(2m)}$=-0.025; p= 0.753) or KB ($F_{(2m)}$=0.002; p=0.081) (Figure 4.2e–g). Across all sites, however, overlap between the ramet and genet spatial neighbourhoods was high (minimum pairwise distance between unique genets <1 m; Table 4.2, Figure 4.6), reflecting spatially aggregated stem structure characteristic of *M. leucadendra*.

The intra-individual kinship coefficient F_I provides a multilocus estimate of the ratios of differences of the probabilities of allelic identity by state for random genes sampled from two individuals. Departure from HW genotypic distributions was significant across sampled individuals at each site. The difference between values of F_I and $F_{(1)}$, which helps assess the relative contributions of mating among relatives (biparental inbreeding) and selfing to overall inbreeding levels (Vekemans and Hardy, 2004), varied from 0.00 (GRE) indicating potential mating among relatives, to 0.343 (BLU). These values are consistent with the expected range for a mixed mating woody species (Vekemans and Hardy, 2004). Values for the *Sp* statistic measuring the strength of spatial genetic structure signal ranged from 0.002 at sites BLU and BIG, for which the patterns of SGS were not significantly different from a random distribution of genotypes, and was similarly low (0.006) at site KB. Highest *Sp* (0.038) occurred at site GRE and is comparable with values for other tree species (Hardy et al., 2006). Inspection of individual pairwise assignments revealed that the signal for SGS at site GRE included a large number of genets at highly contagious spatial proximities, effectively within clumped stands of surveyed ramets.

Population genetic structure relative to sampling localities

Hierarchical Bayesian approaches based on the genotype data of 232 *M. leucadendra* individuals, used to characterise the scales of population genetic structure among the four study regions, revealed two genetic clusters among all samples. In all cases, the standard deviations of posterior $L(K)$ estimates generated from 20 STRUCTURE runs were very small (less than 0.3% of mean values) and the optimal solution for K=2 genetic clusters strongly differentiated the headwater KB from the three mainstream sites. A subsequent round of clustering analysis did not reveal further population substructure independent of spatial autocorrelation within either of the two identified groups. Moreover, the extent of pairwise genetic relatedness between individuals across all four sampling sites was not explained by geographic distance (Mantel tests; data not shown).

Fluvial signature: flood stream power distribution

Stream power distributions for the 1991 flood event revealed that local-scale catchment geophysical characteristics defined the effective force experienced during events of this amplitude (Figure 4.7a). Overall, the flow event was characterised by a very rapid rate of change in discharge and short duration (days). Discharge and stream power at BLU,

however, were far greater than at the headwater KB, as well as than at other tributary and downstream catchments (peak discharge 464.86 m^3s^{-1}, 8644.08 m^3s^{-1}; stream power 89.87 Nms^{-1}, 403.13 Nms^{-1} at KB and BLU respectively; Figure 4.7a). The tails of the flood distribution were also widest at site BLU and varied among catchments (Figure 4.7a). Together, these characteristics show that flood profiles vary widely between reaches within the study river system.

Fluvial signature: flood event distribution

For extreme event analysis, maximum likelihood estimates for optimal thresholds of discharge were 100 (67 exceedances in the data set) and 1000 (87 exceedances) for catchments KB and BLU respectively. Posterior distributions for the location, scale and shape parameters were based on μ=183.42, σ=123.64, ξ=0.1403 (-lnL=411.98) and μ=1733.39, σ=873.19, ξ=0.3068 (-lnL=679.42) for KB and BLU respectively. For both data sets, time series parameter plots and Gelman diagnostics indicated chain convergence was high (multivariate PSRF≈1.00; point estimate and 97.5% quantiles for μ, σ and ξ all ≈1.00).

Return level plots revealed considerable differences between catchments in the magnitude of flood discharge over return periods 1 to >1000 years (Figure 4.7b). The posterior values for 1-in-10 and 1-in-100 year return levels were *c*. 4500 m^3s^{-1} and 6800 m^3s^{-1} at catchment KB (Figure 4.7b, dashed line), compared to *c*. 9500 m^3s^{-1} and 12 000 m^3s^{-1} at catchment BLU (Figure 4.7b, solid line). For the KB catchment analysis, the upper bound of the credible envelope was less than 10 000 m^3s^{-1} up to the 200 year return period, whereas at BLU values both far exceeded this bound and were more variable (Figure 4.7). Further explorations of the BLU catchment data using both maximum likelihood and Bayesian models indicated large quantiles for return periods exceeding 50 years. This deviation from model fit might at least partly be explained by the high stochasticity between successive flood events that contributes to low flood predictability in the study system (Alexander et al., 1999a), and these trends were concordant with differences in the scale and distribution of peak values in the actual data (*n*=33 years).

Discussion

Headwater and mainstream locations in the Upper Burdekin river catchment differ by an order of magnitude in disturbance, as measured by extreme event analysis modelled over 33 years of daily flow data. The extent of flood variability detected between stream types and over the hydrological record is consistent with the conclusions drawn by previous comparisons of flow disequilibria in river systems when compared at a global scale. This reinforces the concept that flow variability in large dry tropics systems in the southern hemisphere is extreme (Puckridge et al., 1998; Alexander et al., 1999a). The genotypic signatures in *M. leucadendra* populations differed between locations in association with the order-of-magnitude differences in disturbance intensity and

variability. At the headwater catchment location (KB) the proportion of unique genotypes detected by spatial genetic analysis was high (all 90 sampled multilocus genotypes were unique) whereas in the mainstream locations clonal structure was much more prevalent (30% of sampled genotypes). This mainstream signature was consistent across three sampling sites each separated by more than 40 km, implying robust data signal. These findings support the hypothesis that vegetation responses to fluvial disturbance can influence differences in stem growth patterns and genetic structure in plant populations.

Plant spatial ecology: stem aggregation and the spatial range of clonal genotypes

Resprouting in flood-driven environments promotes genet survival. The capacity to resprout produces multiple, genetically identical above-ground stems, but stand stability may also increase local recruitment opportunities (Fielding et al., 1997, Karrenberg et al., 2002). Both of these processes should contribute to population genetic signatures in plant species that exist in river systems.

Clonal growth corresponded to a strong signal of clustered stem structure. In all cases the replicate genotypes coincided with geographically clustered groves of stems and spatial autocorrelation clonal sub-ranges of 4 to 15 metres, suggesting that clonal growth contributes its effects at spatially localised scales. This finding agrees with theoretical expectations that physiological aggregation is the prime mechanism by which clonal growth confers survival advantages on woody plants in the face of unpredictable disturbance events (Peterson and Jones, 1997).

I consider that my evidence suggests a link between disturbance, plant response and population genetic processes. At the headwater low-disturbance-intensity location (KB) all multilocus genotypes that I sampled were unique. However, in mainstream high-disturbance-intensity locations clonal structure was much more prevalent (30% of sampled genotypes) and consistent across all three mainstream sampling sites. This suggests that the positive relationship between disturbance intensity and resprouting (ramet production) can be expressed in a negative association between disturbance intensity and genetic diversity within populations. My findings therefore support the hypothesis that vegetative responses to disturbance can generate differences in genetic structure based on physical conditions experienced (Barsoum 2002).

While my analyses suggest that resprouting in the face of high disturbance probabilities has strong influence on local genetic structure, its effects appear to operate only across short distances. The complementary analyses at ramet and genet scales suggest at least one other process may be influential in determining the spatial genetic distribution of *M. leucadendra*. Analysis of pairwise genetic relatedness between all individuals between 20 m and 500 m revealed that the influence of distance on genetic relatedness was generally very weak, and accords with high genotypic diversity at all sampled catchments. Thus, processes other than the dominance of clonal genotypes arising as a

product of resprouting contribute to the signals of genetic variability at these distances. Moreover, mean genet size and the centroid distances between neighbouring genets showed high overlap, implying spatial aggregation independent of genetic identity. Thus, vegetative and sexual regeneration strategies could be complementary and both contribute to the establishment of clumps in *M. leucadendra*, which themselves could provide structural stability and increased establishment success.

Scales of interaction between flood disturbance and spatial genetic signatures

Resprouting in flood-driven environments promotes individual genet survival. Therefore it is reasonable to expect that the capacity to resprout confers specific advantages for species survival and niche dominance via enhanced disturbance tolerance and/or the transport and establishment of clonal propagules (Fielding et al., 1997; Karrenberg et al., 2002). These processes could be expected to generate population genetic signatures in river systems. Probabilistic assignment of individuals to population genetic clusters strongly grouped together the three sampled mainstream locations. Thus, there is no evidence to suggest that individuals at these locations represent members of isolated gene pools. This implies a high level of genetic admixture at broad spatial scales, here measured up to 150 km. This finding, however, does not imply that vegetative stem growth and dispersal via geomorphic disturbance as a mechanism that explains the broader scale of population structure in *Melaleuca leucadendra*. This is because clonal genotypes in *M. leucadendra* were detected only within 20 metre-long groves of trees within sampling locations, and did not generate a clustered genotype structure. This contrasts to the major role that sprouting and dispersive clonal growth mechanisms play in generating population genetic structure and grove distribution in better-studied riparian communities, such as in the section *Tacamahaca* 'balsam poplars' along rivers in western North America (Gom and Rood, 1999a; Rood et al., 2003). For example, Rood et al. (2003) showed that branch propagation and downstream dispersal of these vegetative fragments provide vigorous clonal saplings in *Populus balsamifera* and *P. balsamifera* subsp. *trichocarpa*. In the current study system, the clustered growth form and high genotypic diversity among mature groves implies the role of resprouting in generating population structure is strongly localised in time and space in riverine *M. leucadendra*.

Spatially aggregated clonal genotypes suggest that resprouting is a major driver of spatial biology in *M. leucadendra* at the established plant stage. I propose that the capacity to resprout is a candidate trait contributing to individual plant survival in river environments. Investigation of the diversity and distribution of clones at multiple headwater streams is evidently required to determine the generality of the patterns detected in this analysis. The analysis of stream power, which increases as a river increases in size, was used to identify the magnitude and scale of variability of flood events within the Upper Burdekin river system. This analysis indicated that the headwater creek (KB) had lower power, apparently associated with a lower proportion

of clonality. This result is somewhat unexpected and contrasts to that for cottonwoods, in which species in headwater streams (the *Tacamahaca* 'poplars') display a higher degree of clonal reproduction and are apparently adapted to high shear stress conditions, while species in downstream reaches (the *Aigeiros* 'cottonwoods'), characterised by finer sediments and lower stream velocities, display a higher proportion of seedling reproduction (Kranjcec et al., 1998). However, quite unlike northern temperate zones (Pabst and Spies, 2001), large dry tropics systems display unpredictable changes in habitat structure including in flood energy gradient, stream velocity and stream capacity relative to channel size and slope (Alexander et al., 1999b). This environmental unpredictability adds complexity to theories of niche construction not previously explored in woody vegetation. Whereas the distributions of cottonwood and herbaceous riparian species along environmental gradients can be associated with among-species differences in tolerance to stream stage and water table variability (Kranjcec et al., 1998; Silvertown et al., 1999), the distribution of the species *Melaleuca leucadendra* can be associated with within-species tolerance to hydrological variability (e.g. Fielding and Alexander, 1996). Selection for tolerance of multiple agents of environmental stress, for which resprouting reflects one important solution (Chong et al., 2007), could represent a major driver of biological threshold values and survivorship in *Melaleuca leucadendra* within the Myrtaceae-dominated Australian riparian vegetation community.

In this study, the scales of interaction between spatial and genetic signatures in the keystone riparian taxon, *Melaleuca leucadendra*, were evaluated in relation to flood disturbance. An events-based conceptual approach was valuable to critically evaluate genetic structure as evidence for the balance between vegetative and sexual regeneration strategies. My findings support hypotheses of disturbance-based selection for particular ecological traits, specifically resprouting, and that this process may influence spatial genetic structure. Differences in spatial genetic structure within *M. leucadendra* populations are related to differences in the magnitude and variability of disturbance events between stream types; this implies that disturbance variability could determine the relative advantages of vegetative and sexual regeneration for survivorship in the highly unpredictable riparian environment (Fielding and Alexander, 2001).

Vegetative and sexual regeneration strategies in *M. leucadendra* may be complementary, and both contribute to determining local population genetic structure of adult stands. One interpretation is that individuals arising from predominately sexual establishment events produce multiple resprout stems in response to disturbance. Resprouting, in turn, increases the probability of surviving successive disturbance events (Fielding and Alexander, 2001) and the probability of contributing to seed output in periods between disturbances, producing a positive feedback mechanism that links population genetic processes to environmental stresses via plant responses. This is concordant with the contention that *M. leucadendra* is a phenotypic 'Jack-of-all-trades' (Muth and Pigliucci, 2007), showing the ability to maintain fitness across a broad range of environmental

conditions and providing the mechanism by which the species becomes mono-dominant in high-discharge areas (e.g. Fielding and Alexander, 2001).

My results imply that vegetative and sexual reproductive mechanisms may both play important roles in the overall life history of *M. leucadendra*. The effects of these mechanisms have distinct spatio-temporal signatures. Resprouting as a clonal growth mechanism influences genetic structure principally through stem aggregation and genet persistence. High genotypic richness, independent of levels of clonality, implies that genetic variation is maintained by gene flow processes such as seed dispersal rather than the ecological interactions (growth, competition, reproduction) among neighbouring clonal genotypes. These findings support the theories that disturbance is an physical phenomenon that (i) moderates the effects of resprouting at the macroevolutionary scale (Bond and Midgley, 2003) and (ii) contributes to long-distance seed dispersal in open landscapes, represented as fat-tailed seed dispersal kernels (Nathan et al, 2008). Resprouting reflects a generalised biological solution allowing persistence and colonisation across a broad range of environmental perturbations which may explain why resprouting appears to be evolutionarily labile and not directly correlated to phylogenetic patterns of speciation or relatedness among congeners (Bond and Midgley, 2003, Vesk, 2006).

My findings support hypotheses of disturbance-based selection for particular ecological traits, specifically resprouting, and that this process may influence spatial genetic structure in plant populations. Of course, the effects of disturbance could be expected to differ depending on the scale of observation. First, spatially aggregated clonal genotypes suggest that resprouting is a major driver of spatial biology in *M. leucadendra* at the established plant stage. Second, differences in spatial genetic structure in *M. leucadendra* are related to differences in the magnitude and variability of disturbance events between stream types; this implies that disturbance variability within the river system could determine the relative advantages of vegetative and sexual regeneration for survivorship, and this balance is likely to change continually in the highly unpredictable riparian environment.

Studies such as this will improve our understanding of the limitations of mechanistic approaches and theoretical models used independently to assess plant trait evolution where environmental variability could constrain species success. Investigation of more locations that feature different hydrological disturbance regimes, including multiple headwater and mainstream sites both within and between river systems, is now needed to determine the strength of the relationship between disturbance and growth strategy detected in this study. *M. leucadendra* dominates flood-driven river systems in dry tropics northern Australia and displays clumped vegetative growth as well as high genetic diversity. The capacity to respond to environmental conditions via both vegetative and sexual regeneration strategies may explain niche specialisation and numerical dominance of riverine species in locations of extreme disturbance.

Tables and figures

Table 4.1. Allele size range, number of alleles per locus and expected heterozygosity for eight microsatellite loci used. Refer to Rossetto et. al (1999a, 2000) for locus sequences.

Locus name	Allele characteristics		
	Size range	No. alleles	H_E
scu 052	304–356	27	0.89
scu 084	168–210	33	0.93
scu 081	85–145	25	0.93
scu 097	108–164	21	0.91
scu 098	158–162	4	0.13
scu 053	205–253	8	0.70
scu 039	109–170	37	0.93
scu 014	96–136	21	0.89

Table 4.2. Genotypic diversity and geographic distance among *M. leucadendra* ramets sampled at three mainstream catchments (GRE, BLU, BIG) and one headwater catchment (KB). (Number of genetic individuals, G, derived from pairwise sibling match probability tests to evaluate Nc, the number of detected identical genotypes that represent replicates of the same genet sampled at distinct spatial locations, i.e. 'clones'. *** $p<0.001$ for each Psib = sibling match probability at $\alpha = 0.01$).

Site	Number of			Genotypic richness		Geographic distance between samples	
	stands	ramets N	genets $G=N-N_c$	proportion unique genotypes $N_g = G/N$	Simpson's diversity index D	ramets (m)	genets (m)
GRE	9	58	43***	0.74	0.988	0.81–16.81	0.22–200.16
BLU	10	53	33***	0.62	0.978	0.45–15.48	0.728–246.68
BIG	6	31	24***	0.77	0.981	0.51–10.18	0.762–588.41
KB	7	90	90***	1.00			0.100–545.07

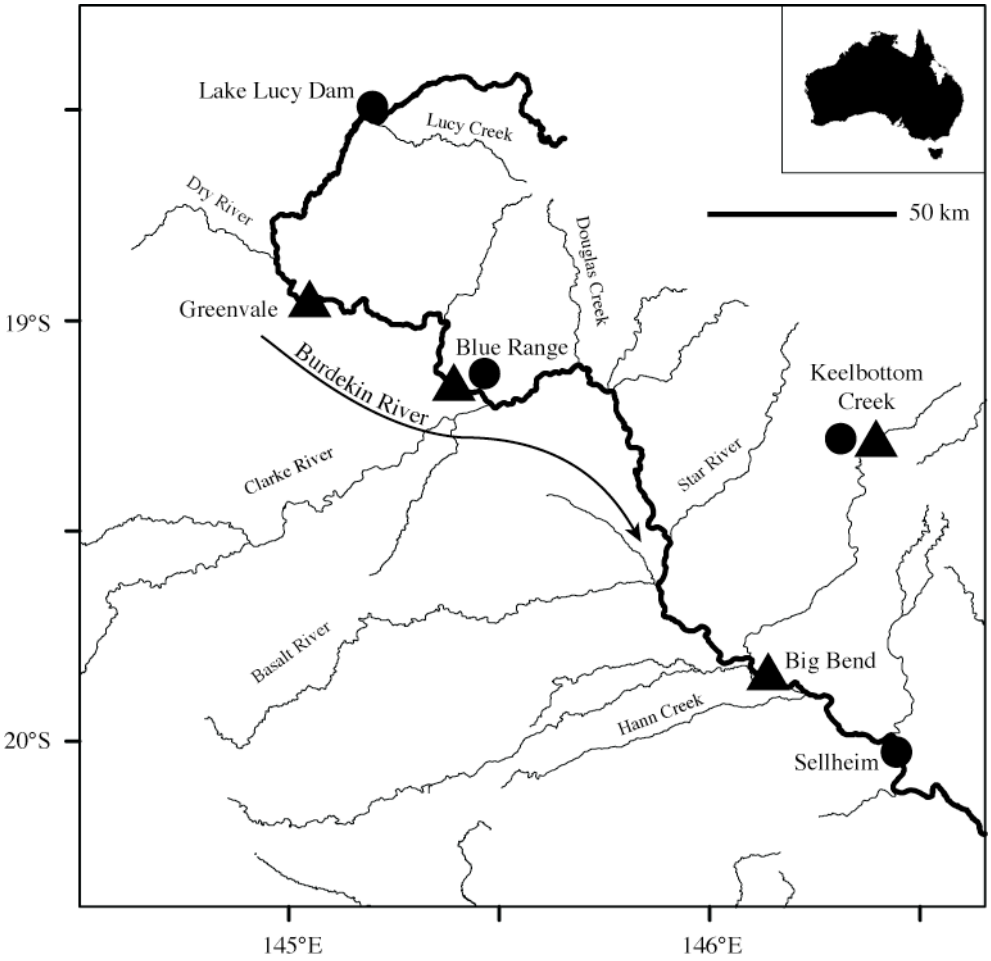


Figure 4.1. Study region in the Upper Burdekin River catchment, north-east Queensland, Australia. Sampling locations (triangles): Greenvale (GRE), Blue Range (BLU) and Big Bend (BIG) were mainstream sites; Upper Keelbottom Creek (KB) was a headwater site. Closest available gauging stations (circles), used for flood event analyses, are co-located within 1.1 km and 0.2 km of sampling sites at Blue Range and Keelbottom Creek respectively, 54.0 km upstream from Greenvale at Lake Lucy Dam, representing another headwater catchment, and 45.9 km downstream from Big Bend at Sellheim.

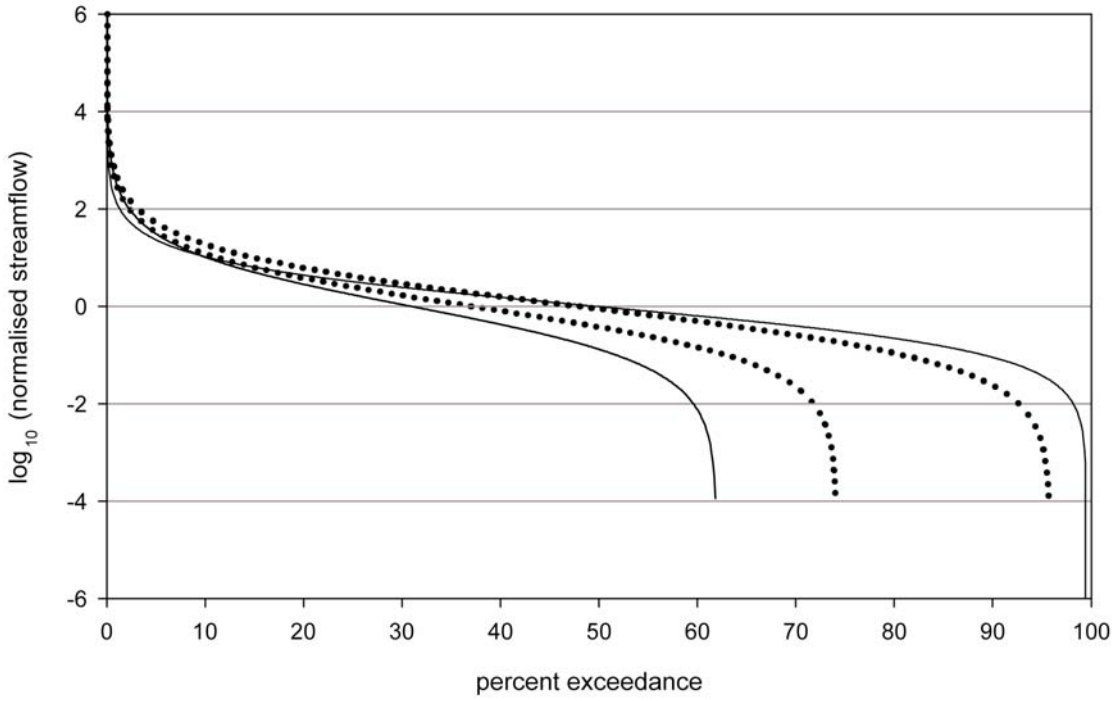


Figure 4.2. Predicted flood duration curve for Upper Burdekin River catchments 120107 BLU (upper solid line); 120002 SELL (upper dotted line); 120121 LUC (lower dotted line); 120102 KB (lower solid line). Plots represent log normalised streamflow (cumecs) $y = ln((a/x) - 1)/b$ where a = percent exceedance at cease to flow; b = constant controlling the slope of the FDC. Function values are from Post (2004).

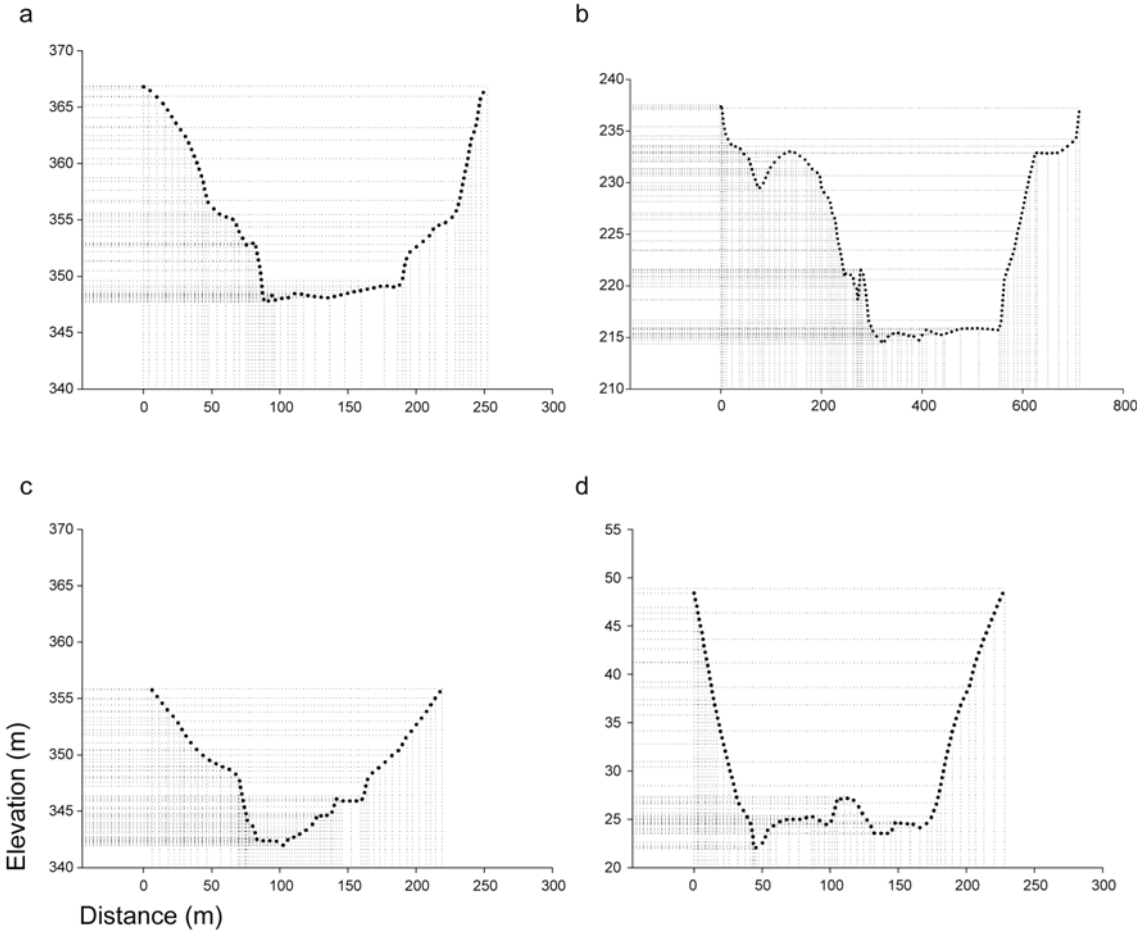


Figure 4.3. Gauging station site cross-sections for Upper Burdekin River catchments (a) BLU; (b) SELL; (c) KB; and (d) LUC used to calculate stream power distributions in this study. Data were obtained from the Department of Natural Resources & Management, Queensland, Australia.

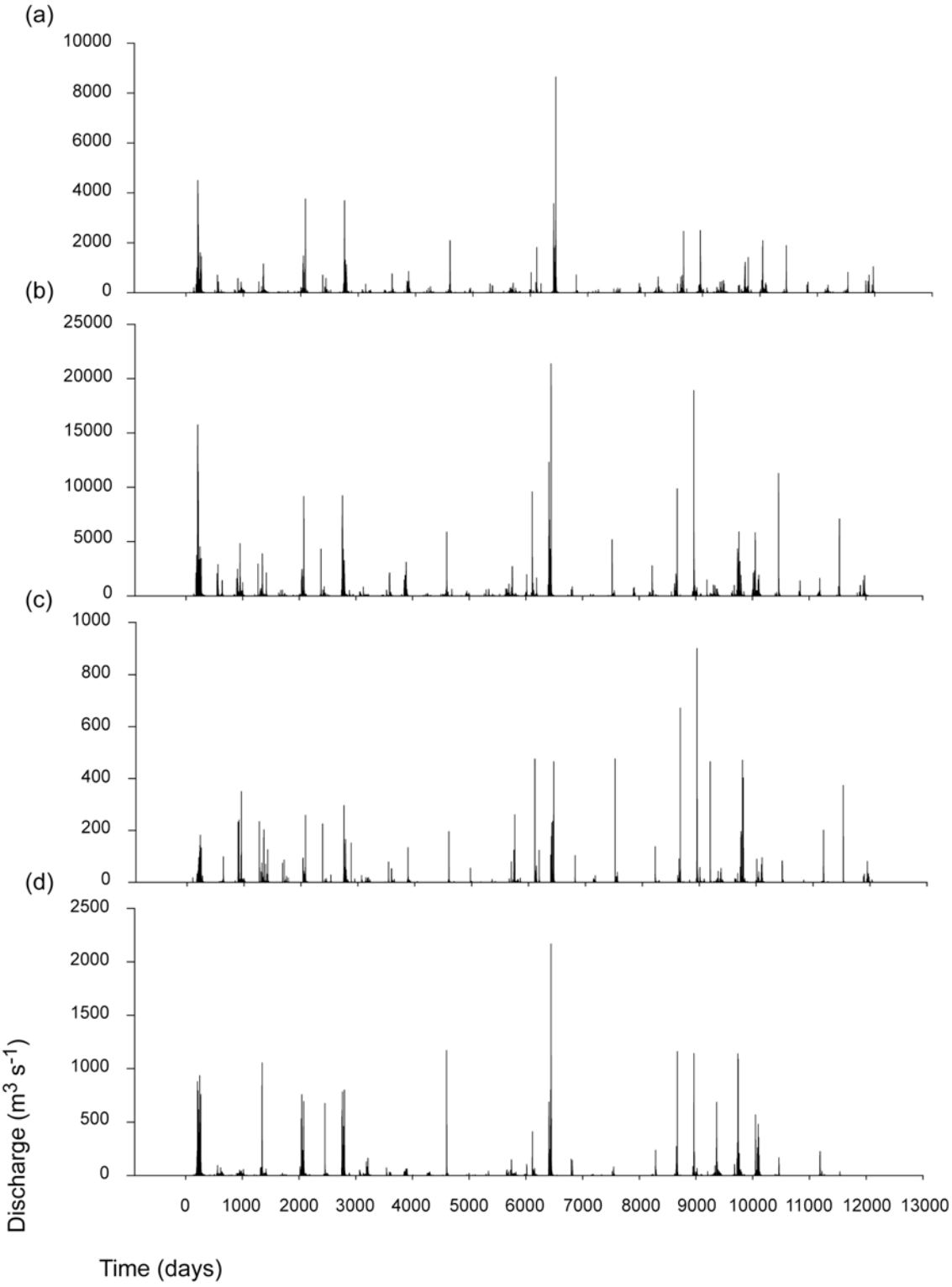
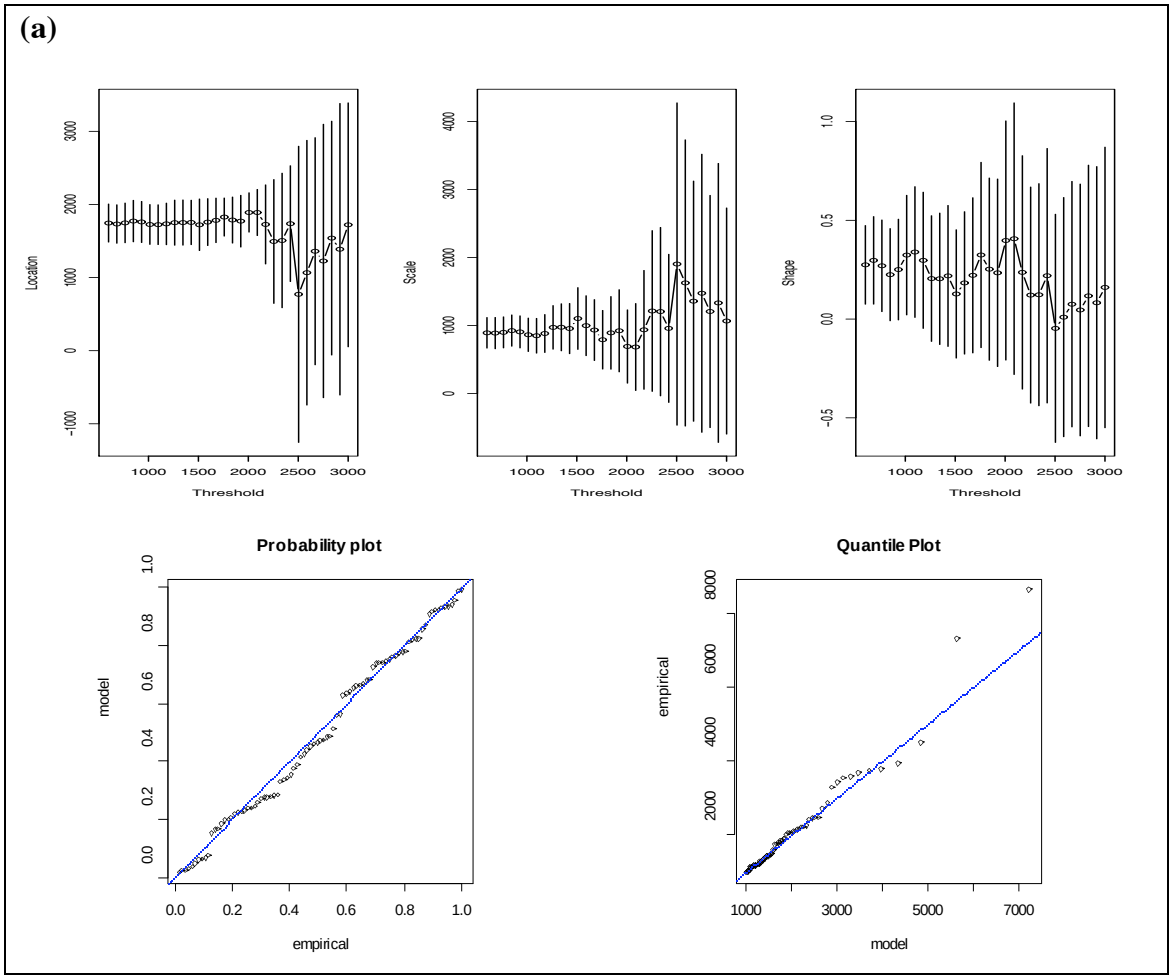


Figure 4.4. Hydrographs generated from 33 contiguous years daily discharge data (m^3s^{-1}) (1973–2006) for Upper Burdekin River catchments (a) BLU; (b) SELL; (c) KB; and (d) LUC

(a)


Location
Threshold
Scale
Threshold
Shape
Threshold
Probability plot
model
empirical
Quantile Plot
empirical
model

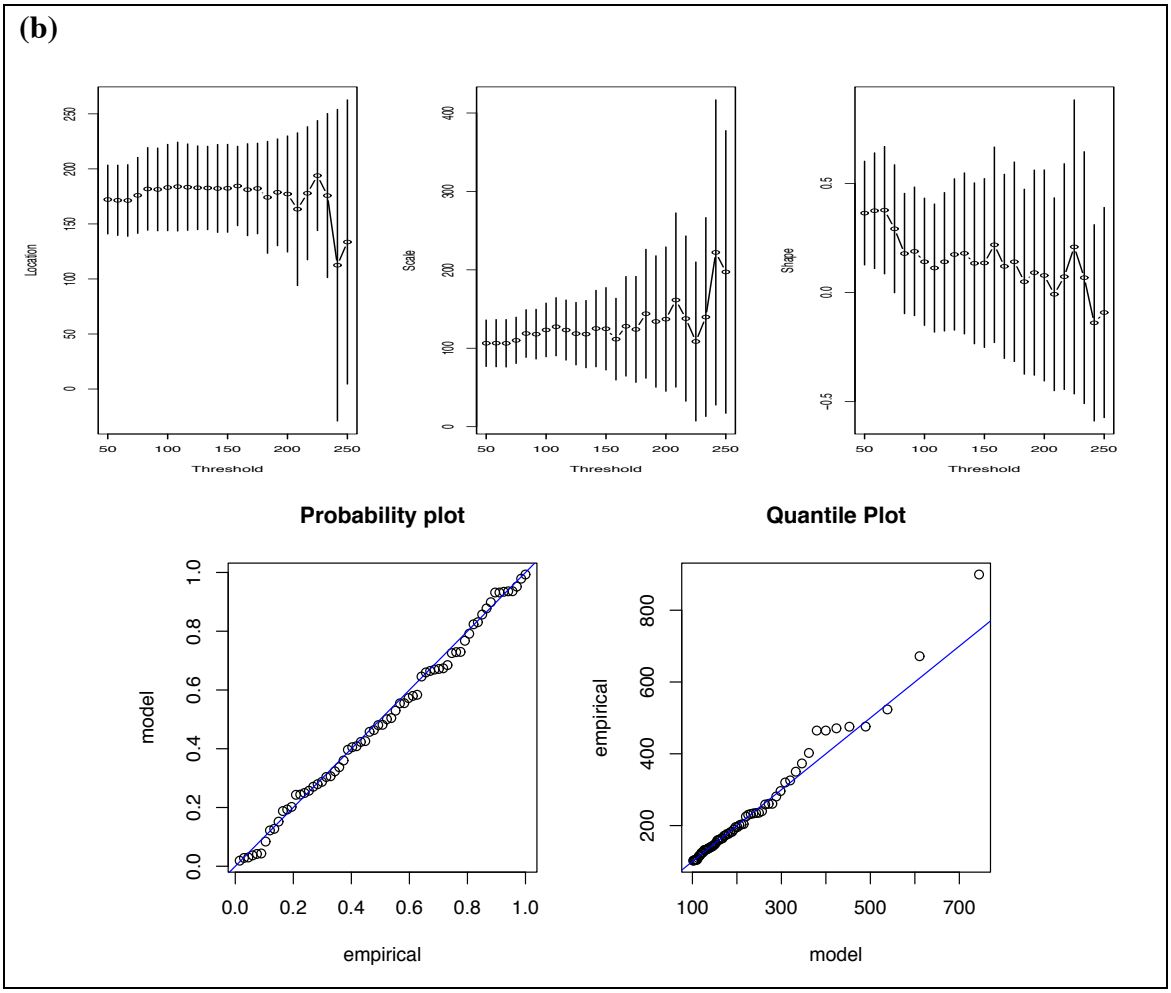


Figure 4.5. Threshold analysis and diagnostic plots for data fit to point process models as estimated using maximum likelihood approaches implemented in the extRemes v1.55 R package (Gilleland et al., 2004). These models were used to parameterise subsequent Bayesian point process analyses applied in this study. Plots shown here represent analyses based on 33 continguous years daily discharge data (m^3s^{-1}) (1973–2006) for Upper Burdekin River catchments **(a)** KB and **(b)** BLU. Optimal discharge thresholds derived were 100 (67 exceedances in the data set) and 1000 (87 exceedances) for catchments KB and BLU respectively. Posterior distributions for the location, scale and shape parameters used in the subsequent point process analyses were based on μ=183.42, σ=123.64, ξ=0.1403 (-lnL=411.98) and μ=1733.39, σ=873.19, ξ=0.3068 (-lnL=679.42) for KB and BLU respectively

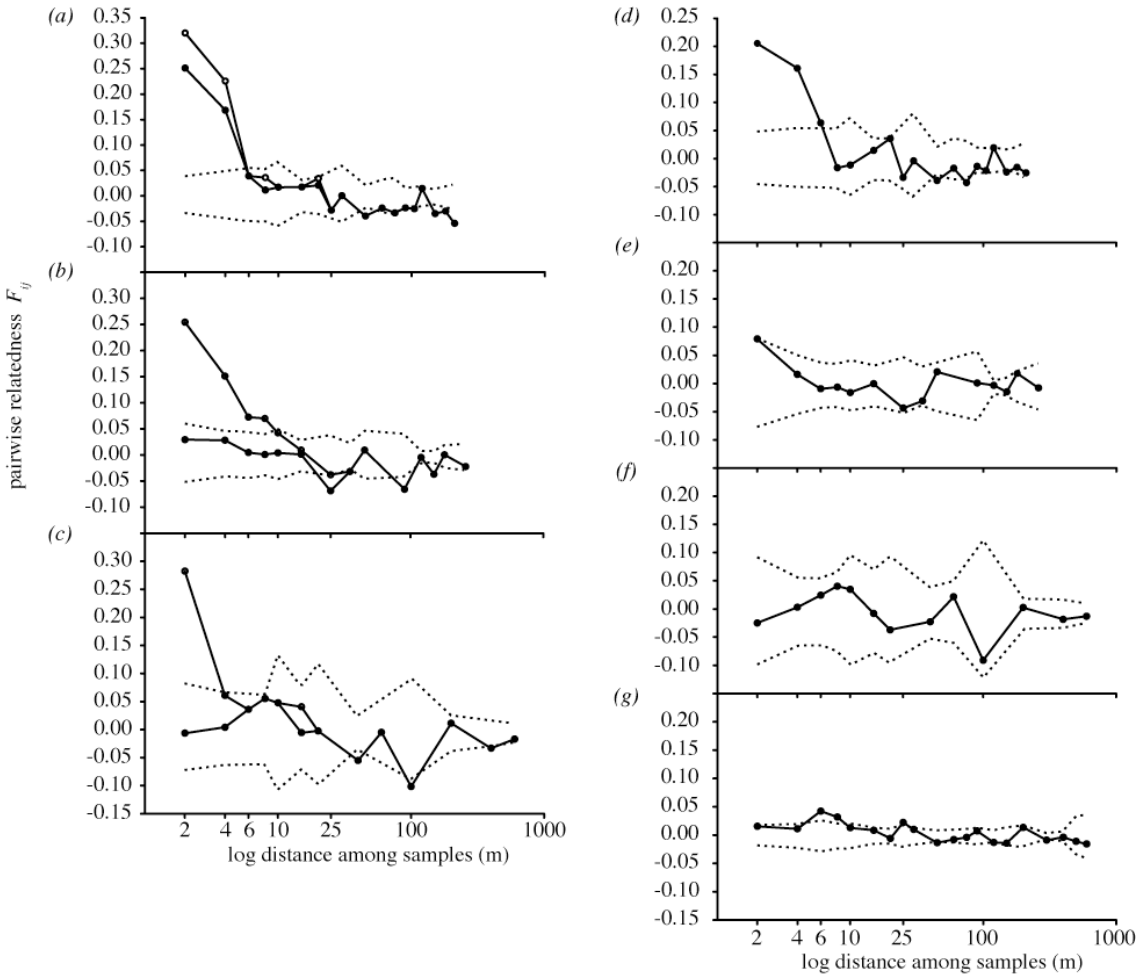


Figure 4.6. Spatial autocorrelation analysis of kinship coefficients for *Melaleuca leucadendra* clonal and genotypic structure at three mainstream catchments: *(a)* GRE; *(b)* BLU; *(c)* BIG. For each site, analyses for both ramet-level (open circles) and among-genet (closed circles) data are presented. Solid lines represent the mean kinship coefficient per distance class [F_{ij}] and dashed lines the limits of the jack-knife 95% confidence interval of no association based on 10 000 random permutations of all individuals among all geographic locations. The spatial distance where the ramet-level and among-genet correlograms merge corresponds to a probability of clonal identity <0.05 and estimates the radius of the clonal sub-range. Genet-level analysis correlograms showing mean kinship coefficients (circles) between individual *Melaleuca leucadendra* genets as a function of spatial distance at mainstream catchments *(d)* GRE; *(e)* BLU; *(f)* BIG; and headwater catchment *(g)* KB. Dotted lines delimit the 95% confidence envelope, based on 10 000 random permutations of all individuals among all locations, of the null hypothesis of random distribution of genotypes in space.

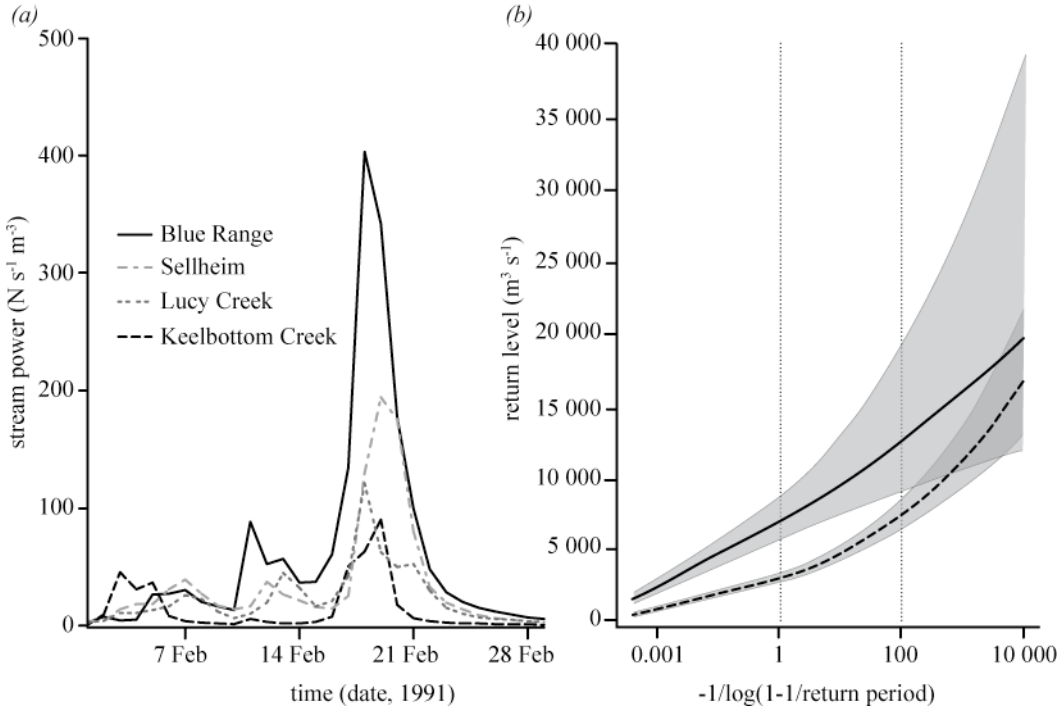


Figure 4.7. (a) Stream power distribution based on daily discharge data during the 1991 flood event at four gauging stations in the Upper Burdekin River catchment. (b) Return level plots of posterior distributions for flood discharge (m^3s^{-1}) and return periods 1 to 10 000 years based on point process Bayesian extreme event analysis of 33 years daily data (mid-1973 to 2006) at Upper Burdekin River; mainstream catchment, solid line = Bluewater; headwater catchment, dashed line = Keelbottom Creek. Plots represent medians (solid lines) and intervals (dashed lines) containing 90% of the prior/posterior probability.

Chapter 5—Discontinuities and directionality in population genetic connectivity at the landscape scale in *Melaleuca leucadendra* (L.) L.

Introduction

In environments associated with large rivers, fluvial processes act as primary ecosystem drivers by structuring habitat connectivity and change (Puckridge et al., 1998; Tabacchi et al., 1998; Bendix and Hupp, 2000). Disturbance and dispersal have important effects on changes to the spatial structure and regional dynamics of plant populations in river environments. Metapopulation models attempt to investigate dynamic demographic processes and their interactions between multiple locations (Wiens, 1997). The riverine vegetation studied in this thesis shows that multi-scale interactions between population persistence, spatial genetic structuring and life-history strategy occur (chapters 2 and 3) and that all three parameters are connected via the influence of flow variability (Chapter 4). Thus, *M. leucadendra* within the Burdekin River is an ideal study system in which to test predictions of metapopulation structure and the spatial scales of genetic connectivity.

Classical metapopulation concepts applied to river systems predict that propagule movement by water (hydrochory) results in unidirectional gene movement from upper to lower drainage areas and/or in the direction of prevailing stream flow (e.g. Merritt and Wohl, 2002). Empirical studies, however, typically suggest unclear signals of genetic structure among plant populations in river systems, indicating that multiple dispersal processes could explain regional patterns of genetic structure. For example, biotic dispersal agents such as birds and bats can override the simple unidirectional gene movement assumption by dispersing pollen and seed, and generating multiple clusters of bi-directional gene flow within a river system (Nilsson et al., 1991; Kubitzki and Ziburski, 1994; Vardon et al., 2001). This makes detecting the degree to which population genetic structure is influenced by propagule dispersal events and individual plant survival difficult. Furthermore, stochasticity in flooding regime within river systems can also introduce a high degree of unpredictability in propagule dispersal patterns and distances.

Theoretical paradigms of stream flow behaviour have been developed principally from research in small or perennial streams in northern hemisphere temperate latitudes (Johansson et al., 1996; Danvind and Nilsson, 1997; Honnay et al., 2001; Campbell et al., 2002). These models assume dynamic equilibrium between the incoming flow and the transport capacity of the river channel. Thus, disturbance events that cause shifts in channel structure and connectivity are predicted to occur over large time periods relative to the lifetime of plant populations. As a result, vegetation demography and structure have been modelled and interpreted with stream flow being considered a

constant parameter (Hanski, 1999), with patterns of reproductive phenology and population extinction and regeneration considered to reflect mean hydrographic trends (Mahoney and Rood, 1998; Pannell and Charlesworth, 1999; Tero et al., 2003). In contrast, large semi-arid river systems feature stochastic changes in connectivity due to frequent, yet highly unpredictable disturbance events. Despite this disturbance-driven environment, dominant plant species display a persistence distinct from counterparts in northern hemisphere systems (Fielding et al., 1997; Fielding and Alexander, 2001). For example, in northern Australian systems, large, long-lived plant species of the family Myrtaceae occur, including *M. leucadendra*. The life history and ecological success of these species do not fit models of succession and vegetation structure shifts that are predicted under environmental disturbance events (Chapter 2).

Geomorphically effective flood events could produce complex temporal shifts in genetic and spatial structure and connectivity. This is because these events influence individual genet survival and also re-structure stream configuration, thus altering pathways for gene flow. In this thesis, I have already demonstrated an association between catchment-scale hydrological regime and local spatial genetic structure as evidence for the importance of the clonal growth strategy of individual plants under selective disturbance regimes (Chapter 4). These findings imply that flow-driven disturbance and dispersal processes in river systems could play a formative role in shaping demographic structure and detectable patterns of spatial genetic relatedness in riverine *Melaleuca leucadendra*. Successive disturbance events continuously shift the probability distributions associated with survival and mortality associated with individual locations within the riverine environment. This process may feed back with traits such as clonal growth, as evidenced by differences in spatial genotypic structure and growth survival strategies detected at the among-population level in *M. leucadendra* (Chapter 4). Thus stream flow may act both directly and indirectly to influence population processes and demographic structure.

Stochastic floods generate unpredictable shifts in habitat structure and connectivity. This phenomenon is very different from the typical northern temperate model. Therefore, there is little reason to expect that genetic signatures reflect static states or persistent linear trends that are predicted under models of directional gene flow. For example, continuous feedback between fluvial processes and survival and dispersal probabilities suggests that populations in events-driven river systems are unlikely to operate under Hardy-Weinberg equilibrium, the assumption underlying conventional deterministic population dynamics models and coalescent approaches used to infer long-term gene flow (Manel et al., 2003). Thus, this approach may be inappropriate for *M. leucadendra* in particular, and all high-energy riverine taxa in general. In this context, non-equilibrium methods (BAYESASS v 1.3; Wilson and Rannala, 2003) were used to estimate rates of recent immigration between sampling locations and between genetic populations as inferred from individual assignment methods (Pritchard et al.,

2000). Faubet *et al*. (2007) present rigorous model testing procedures to evaluate BAYESASS model performance, but applications to real data sets are currently limited.

In this study, Bayesian model-based methods, which do not assume equilibrium, were used to infer the spatial scales of cryptic population genetic structuring in *Melaleuca leucadendra* in the Burdekin River system. The extent and directionality of contemporary gene flow was then used to evaluate genetic and demographic connectivity in relation to the fluvial regime. The aims of this study were to: (i) infer the spatial signal of genetic population structuring based on individual allelic (rather than spatial) identity, (ii) assess the relationship between hydrological and genetic connectivity using estimates of contemporary gene flow and migration, and (iii) infer the landscape-scale processes shaping genetic structure and differentiation in *Melaleuca leucadendra*.

Materials and Methods

Study area and sample sites

The study was conducted in the Upper Burdekin River, where seven sites were sampled (Figure 5.1). Catchment size varied three-fold among sampling locations (*c*. 200 km^2 to greater than 10000 km^2). The seven sampling localities were classified (and hereafter referred to) into 'headwater' and 'mainstream' stream types based on a combined function of differences in hydrological stream order, catchment size and flood discharge energy (Chapter 4). Two sites (LUC and KB) were classified as headwater, and five sites (GRE, LD, BLU, CLA, and BIG) were classified as mainstream. Headwater sampling sites represent the tributary streams Lucy Creek and Keelbottom Creek. Mainstream sites represent the major tributary Clarke River (CLA) and four main channel reaches on the Upper Burdekin River (Figure 5.1).

Samples for genetic analyses were collected from mature individuals of *M. leucadendra* from all sites in the dry season (June to December 2004). Previous study showed that the spatial extent of genotypic structuring due to clonal growth is typically restricted to 4–17 m in this system (Chapter 4). To minimise the chance of sampling replicate genotypes (clonal ramets), material used for genetic analyses was selected from previously identified genotypic individuals 10–500 m apart from both channel banks. Distances between sites ranged from 13 km to 170 km (Appendix 5A).

Genetic analysis

Total genomic DNA was extracted using the QIAGEN DNeasy Plant Mini Kit™ (QIAGEN, Valencia, CA), including the optional centrifugation step to remove excess precipitates. Prior to PCR amplification, secondary contaminants were reduced via a silica-plate cleanup protocol (Elphinstone et al., 2003) and the integrity of extracted DNA for each sample was assessed visually via agarose gel electrophoresis and

quantified by spectrophotometer estimates using a NanoDrop® ND-1000 (NanoDrop Technologies, Wilmington, DE). Candidate loci from *M. alternifolia* previously demonstrated to have cross-species amplification capability (Rossetto et al., 1999b; Rossetto et al., 2000) were optimised for 15 candidate loci using *M. leucadendra*. A subset of 8 loci was selected to screen across all samples. Loci were amplified using QIAGEN and Bioline DNA polymerase reagents with 5'-fluorescent tagged primers on a MJ Research DNA Engine Tetrad 2 Thermocycler (Bio-Rad Laboratories, Hercules, CA). DNA amplification of each locus followed a protocol where an initial 10 cycles of amplification included reduction of annealing temperature by 1°C per cycle for 10–15 cycles from 60°C and then followed by a further 20 cycles at the lowest temperature. Amplification products were analysed by fluorescent-dye detection on a MegaBACE 1000 (GE Healthcare) at the James Cook University Genetic Analysis Facility, Townsville, Australia and individual genotypes were scored using Genetic Profiler v. 2.2 (GE Healthcare).

Data analyses

Genotypic linkage equilibrium

Genotypic disequilibrium tests for each pair of loci in each sample were performed using GENEPOP 3.4 (Raymond and Roussett, 1995). I applied the *q* value approach to the false discovery rate method for each test using bootstrap methods to estimate the tuning parameter π (QVALUE v.1.1, Storey and Tibshirani, 2003; Storey et al., 2004) in order to examine deviations from linkage equilibrium between loci. The robust method (Storey, 2002) was then applied to account for small *P*-values and directly estimate pFDR. This approach has been advocated to control the proportion of statistically significant results that are type 1 errors, compared to more conventional approaches (e.g. Bonferroni methods) that aim to limit the chance of making even a single type 1 error irrespective of the cost to power in terms of type 2 errors (Verhoeven et al., 2005; Vähä et al., 2007).

Inference of spatial genetic relationships among demes

In the study system, clonal ramet growth in *Melaleuca leucadendra* structures the spatial distribution of genotypes at localised scales < 20 m (Chapter 4). Quantifying the spatial signature of population genetic structuring in the river system has not previously been addressed. Multiple complementary approaches were applied to evaluate genetic variability and differentiation in the study system at hierarchical spatial scales. First, I used three statistics to quantify genetic variability: gene diversity (H_E), allelic richness ($A_{R(X)}$) and private allelic richness ($pA_{R(X)}$), using rarefaction procedures implemented in HP-RARE 1.0 (Kalinowski, 2005). Hierarchical *F* statistics using Yang's (1998) algorithm (HIERFSTAT v0.04-4; Goudet, 2005) were used to estimate the relative genetic variation among sampling populations at three levels: (population, stream type, stream location). The likelihood-ratio *G*-statistic implemented in HIERFSTAT was used

to compute the statistical significance of each level of population differentiation via randomisation tests (n = 10000 permutations). The G-statistic approach permutes individuals among population groups within each level of interest, and thus accounts for the amount of variation at each level of population structure independent of the effects of lower levels (Goudet, 2005). All R computations (QVALUE, HIERFSTAT) were performed in R v 2.5.0 (R Development Core Team, 2007).

Genetic co-ancestry between pairs of individuals relative to a standardised sampling scale (210 m) was estimated using the kinship coefficient described in Loiselle et al. (1995) and implemented in SPAGEDI 1.2 (Hardy and Vekemans, 1999; Hardy and Vekemans, 2002; Vekemans and Hardy, 2004). Reference gene frequencies used pooled data (all sites). Average relatedness coefficients were estimated for F_1 = 0-2 m and the successive distance categories: 2–4, 4–6, 6–8, 8–10, 10–15, 15–30, 30–45, 45–60, 60–75, 75–100, and then in successive intervals to the maximal distance recorded at each sampling site. To visualise spatial genetic structure (SGS), average F_{ij} values were plotted against the logarithm of distance and regressed on $ln(d_{ij})$ to obtain the regression slope b (Hardy et al., 2006). To test for SGS under the null hypothesis that F_{ij} and d_{ij} were uncorrelated, the spatial positions of the individuals were permuted 10,000 times and confidence intervals obtained from jack-knifing over loci (Vekemans and Hardy, 2004; Hardy et al., 2006). SGS intensity was quantified by $Sp = -b/(F_1 - 1)$, where F_1 represents the average kinship coefficient between adjacent, neighbouring individuals (Fenster et al., 2003; Vekemans and Hardy, 2004) and using b calculated over comparable distance ranges for each site.

Isolation by distance between sampling localities was tested using a model of continuous population structure and restricted dispersal (Hardy and Vekemans, 1999). The average relationship coefficient $Rho = 2F_{ST}/1+F_{IT}$ (Ronfort et al., 1998) was estimated using pairwise permutation procedures implemented in SPAGEDI 1.2 (Hardy and Vekemans, 1999; Hardy and Vekemans, 2002; Vekemans and Hardy, 2004). Average relationship coefficients were estimated for d = 7 distance classes distributed across the total sample range (Hardy and Vekemans, 2002) and using pooled reference gene frequencies from all five mainstream sample localities. The spatial positions of the individuals and population locations were permuted 10000 times and confidence intervals obtained from jack-knifing over loci (Vekemans and Hardy, 2004; Hardy et al., 2006). Mantel tests (20000 permutations) were then used to examine the relationship between geographical distance and the genetic relationship between pairs of individuals in different sample localities as defined by $Rho/1-Rho$, using the program IBDWS version 3.14 (Jensen et al., 2005). The strength of IBD signal was quantified using the RMA regression slope b calculated over the total distance range, relative to the 95% confidence envelope (20,000 bootstraps) and implemented in IBDWS v. 3.14 (Jensen et al., 2005). I tested for a potential difference in dispersal signature as a function of stream type by analysing patterns of isolation-by-distance IBD using (i) the full data set comprising two headwater and five mainstream sample localities; and (ii)

data from mainstream localities only. A partial Mantel test was then performed to assess whether genetic divergence differed among mainstream and headwater population samples. The partial Mantel statistic r_M estimates the correlation between genetic similarity (matrix of pairwise relationship between individuals, *Rho*) and landscape configuration (binary matrix with stream type coded as 1 for headwaters; all others 0) while controlling for the effect of the geographic distance.

Inference of population genetic structure and migration

Bayesian-model-based clustering methods (STRUCTURE v.2.2, Pritchard et al., 2000) were used to assign individuals probabilistically to populations differentiated by allelic frequencies, independent of prior information on spatial identity or assumed Hardy-Weinberg equilibrium. For all analyses, individuals designated to unknown cluster origin were assigned to the admixture model assuming non-correlated allelic frequencies (Pritchard et al., 2000). For each model, to estimate 'true' genetic cluster number K, I set $K = 1$ to twice the number of sampling populations, and conducted 20 independent runs for each K-value to evaluate model performance. Initial runs comprised a burn-in of 6×10^5 followed by 1.2×10^6 iterations. Convergence and mixing behaviour at successive values of K were evaluated by inspecting time-series plots of the individual parameters across multiple runs. Optimal K was evaluated by examining the probability of individual assignments based on credible intervals across 20 runs for each K value, and calculating the second order rate of change of the likelihood function with respect to K (Evanno et al., 2005).

An hierarchical analysis was conducted to infer individual assignment within each proposed cluster until no further subdivisions were evident. Initial analysis was performed on the full data set comprising $n = 306$ individuals from seven sampling populations, without prior information on spatial origin. Subsequent hierarchical runs at two levels were performed using a burn-in of 6×10^4 followed by 1.2×10^5 iterations. I applied a third, asymmetric model to examine the effect of prior information (sampling population location) on model performance, because previous analyses indicated that spatial genotypic structure at headwater and mainstream locations was distinct (see Introduction). In this analysis, I identified genet origin for all $n = 132$ individuals sampled from two headwater locations (i.e. PopInfo option in STRUCTURE).

Bayesian non-equilibrium methods (BAYESASS v 1.3; Wilson and Rannala, 2003) were used to estimate the rates and directionality of recent immigration among sample localities and genetic clusters in our study system. The inference method implemented in BAYESASS estimates posterior probability distributions and credible intervals for immigration levels m (migration rate), indicating the amount of genetic variation present in the data relative to model simulations (width of credible intervals) (Wilson and Rannala, 2003). The inference model assumes linkage equilibrium within populations, but allows for deviations from Hardy-Weinberg equilibrium (Wilson and Rannala, 2003; Faubet et al., 2007). Migration rates among populations can be

asymmetric, but are assumed to be constant over short time scales (i.e. past two generations). Importantly, the inference model constrains the total proportion of migrant individuals into a population per generation to the interval [0, 1/3]. Here, I use the posterior mean population immigration rate as estimator to infer gene flow patterns and to determine estimates of non-migrant proportions among the genetic clusters inferred using individual assignment methods (STRUCTURE).

For each model detailed below, I conducted ten independent MCMC runs initiated at different random seeds (burn-in 2.9 x 10^6 followed by 6 x 10^6 iterations, sampling every 2000^{th} generation). To evaluate convergence between runs I calculated the Bayesian deviance for migration D_{assign} across runs (Faubet et al., 2007) and obtained the 95% credible intervals for each element of the migration matrix and calculated its width. I also compared the accuracy and relative bias of migration rate estimates across the replicate runs based on the relative mean square error, using the posterior means of the posterior distribution of migration rates (Faubet et al., 2007). Initial analyses indicated posterior distributions generated using rate priors 0.15, 0.3 were highly congruent (unpublished data). Only results for models using default priors (0.15) are presented as these settings correspond to consistent acceptance values between 40% and 60%.

Evidence for directional migration among all seven sampling populations was evaluated. As sampling size can affect model behaviour (Wilson and Rannala 2003) I compared the performance of two models: (i) using data from all individuals and (ii) using 23 randomly selected genotypes per sampling population. The magnitude of migration signal among genetic clusters previously inferred from STRUCTURE analyses (above) was assessed by implementing hierarchical models in BAYESASS. In this approach, all individuals were re-assigned to populations corresponding to the genetic clustering solution $K = 2$ within (i) mainstream and (ii) headwater locations. For the mainstream and headwater models analysed in BAYESASS, individuals were designated membership to population 1 or 2 corresponding to unequivocal STRUCTURE cluster assignments at $K = 2$ (discrete 90% credible envelopes across 20 runs). Remaining individuals were equivocal to cluster designation and were designated membership to a separate group, population 3.

Results

For each pair of the eight loci screened, the number of significant genotypic disequilibrium tests over all samples was higher than expected by chance (22 out of 117 at $P < 0.05$). Estimates of the tuning parameter π (Storey et al. 2004) indicated the overall proportion of true null hypotheses was high ($\pi_0 = 0.855$). Using a false detection rate level of 0.05, 13 locus pairs (11.1%) showed deviance from genotypic equilibrium ($P < 0.01$). One locus pair comparison was obtained in three out of seven sampling populations, one other in two populations. The robust method (Storey 2002) was then applied to account for small P-values and directly estimate pFDR. Under this model, π_0

was 0.835 and no locus pair comparisons were significant in multiple sampling populations. Therefore, I considered markers represent physically unlinked and informative polymorphic microsatellite loci used in subsequent analyses.

At the population level, average expected heterozygosity was 0.69 (SD ± 0.03), and average allelic richness was 8.43 (SD ± 1.09) when standardised to a sample size of 40 genotypic individuals (Table 5.1). At the stream type level, average allelic richness was 11.75 (SD ± 2.41) standardised to two populations per stream type. Genetic diversity indices of the two headwater populations ($H_E = 0.727$; $A_{R(40)} = 13.263$) were considerably higher than the mainstream populations ($H_E = 0.679$; $A_{R(40)} = 10.241$). Additionally, the distribution of private alleles was much higher in the headwater populations (30 out of 42 private alleles found in these two populations) (Table 5.1). The sum of private allelic richness over 7 loci in mainstream populations varied from 5.81 in GRE to 9.10 in BIG, compared to 13.01 and 15.32 in the headwater populations LUC and KB, with the average private allelic richness over all populations being 9.65 ± 3.35. Global likelihood-ratio *G*-statistic tests indicate there is both a strong effect of population within streamtype ($P = 0.0001$) and a modest effect of streamtype ($P = 0.0481$) on population genetic structuring. Population differentiation estimates based on inferred genetic clusters compared to *a priori* sampling locations were similar, but less strong (effect of genetic population within streamtype $P = 0.001$; effect of streamtype $P = 0.06$) (Table 5.2). Overall variance components (Yang 1998) were estimated at two levels: sampling population ("pop") and streamtype ("streamtyp", separating samples between headwater and mainstream populations). Hierarchical *F*-statistics type-coefficients revealed that differentiation among individuals contributed most to overall genetic variance ($F_{ind/total} = 0.402$, $F_{pop/total} = 0.131$, $F_{streamtyp/total} = 0.106$), as well as to variance at the sampling population and streamtype levels ($F_{ind/pop} = 0.312$, $F_{ind/streamtyp} = 0.331$) (Table 5.2). Consistent with these results, there was no evidence for a strong isolation by distance signal in *Melaleuca leucadendra* from the Burdekin system. The correlation between genetic similarity as measured by *Rho*/1–*Rho* and geographic distance was weak (Mantel tests: $P = 0.92$, $n = 306$; $P = 0.90$, $n = 174$ for full and mainstream models respectively). The strength of signal was very low and the 95% confidence interval envelope generated from permutation procedures encompassed zero, indicating an equivocal relationship (RMA $slope_{full}$: $b = 1.89 \times 10^{-6}$; bootstrap 95% CI: $(-2.189 \times 10^{-6}, 2.378 \times 10^{-6})$) (RMA $slope_{mainstream}$: $b = 5.03 \times 10^{-7}$; bootstrap 95% CI: $(-9.19 \times 10^{-7}, 9.02 \times 10^{-7})$). This implies that the degree of pairwise genetic relationship between individuals among sampling localities was not dependent on geographical separation. By contrast, genetic similarity/distance was tightly correlated with stream type (partial Mantel permutation test, $r_M = 0.955$; $P = 0.0033$), which suggests the extent of genetic differentiation in *M. leucadendra* among headwaters differs substantially from that among mainstream localities.

In all models, data structure inferred from the distribution of ln *P*(X K) estimates from multiple STRUCTURE runs and clustering solutions based on the modal *K* estimator

(Evanno et al., 2005) were congruent. In all cases, the standard deviations of $L(K)$ estimates generated from 20 runs were very small (less than 0.3% of mean values), suggesting a strong structuring signal. Analysis on the seven sample populations indicated an optimal clustering solution of $K = 2$, corresponding closely to differentiation between individuals from the two headwater locations and all others from five mainstream locations (figures 5.1 and 5.2a). Independent analyses on the headwater and mainstream sample populations again separated individuals into two clusters ($K = 2$) within both stream types. In the headwater model, individual membership among the two discrete genetic clusters (discrete 90% credible interval envelopes) was highly congruent with sample localities. The pattern of individual membership under the $K = 2$ model identified two discrete clusters each comprising greater than 95% of individuals from a single sample locality, whereas cluster 3 comprised individuals from both sample localities (Figure 5.2b). The mainstream model identified one cluster comprising a high proportion of individuals from the two most upstream localities (LD and GRE) whereas the remaining two clusters included individuals from all five sample localities. The proportion of equivocal membership assignments among mainstream samples was high (cluster 3) (Figure 5.2b). Subsequent STRUCTURE analyses on partitioned data did not reveal further clustering signal within mainstream and headwater groups. An independent, asymmetric STRUCTURE model implemented on the entire data set, incorporating prior population information for individuals from the two headwater locations, provided additional strong support for a clustering solution of $K = 2$ genetic clusters (data not shown), consistent with the initial naïve model. For each clustering level of analysis, the two *ad hoc* decision criteria for estimating the true number of genetic clusters in STRUCTURE analyses, *ln P*(X/K) and delta *K,* generally provided a single congruent solution suggesting strong data signal. Moreover, the estimates of population structure based on re-sampling analyses (23 randomly selected individuals per sampling population) provided structuring solutions consistent with the full data model indicating robust data signal, because this approach minimised bias of contagious genotypic association due to spatial proximity of sampled individual relative to others. These results together provide strong evidence that mainstream and headwater localities within the study river system reflect discrete genetic population signatures.

Among the five mainstream sample locations, estimates of posterior mean immigration rate m_{ql} varied across the allowed interval for migrant proportions [0, 0.33] consistent with adequate chain mixing behaviour. The inferred immigration rates between all population combinations correspond to narrow 95% CI widths (all < 0.115) compared to the simulation model that accepts all proposed changes in the Markov chain (migration rate 95% CI [1.15×10^{-7}, 0.144]; non-migration rate 95%CI [0.675, 0.992]) (Figure 5.2a,b). This signal was consistent across ten independent MCMC runs in the initial analysis incorporating data from all sampled individuals and in subsequent models comprising 23 randomly selected individuals per sampling locality. These

results indicate that the multilocus data set contributes significant information to infer migration rate and associated model parameters (Faubet et al., 2007).

For each model implemented, I evaluated model fit by comparing the deviance of the probability of individual assignment based on mean migration rate, D_{assign} (Faubet et al., 2007) and overall posterior log likelihood scores across ten independent MCMC runs. Inferences on immigration rates using the posterior mean estimates and 95% CI widths were congruent across runs. In the full model comprising all seven sample populations, the maximum deviance between runs corresponded to 36 log likelihood units and reflects sampling from a bimodal posterior probability distribution. In the streamtype models comprising independent analyses of headwater and mainstream sample populations, the maximum deviance corresponded to 24 log-likelihood units (mainstream model) and 2 log-likelihood units (headwater model). The root-mean-square error and relative bias of the mean had similar low values and remained in the same order of magnitude across runs (Faubet et al., 2007). Here I report conservative model parameter estimates, generated from the 'best' run with lowest deviance and best overall log-likelihood score, and analysis of 23 randomly selected individuals per sample locality/ genetic cluster.

Variable rates of genetic exchange were detected among mainstream samples (Figure 5.2a). Locations GRE, CLA and BIG showed non-migrant proportions close to the lower bound of the prior distribution for *m* (0.66) (Figure 5.2a). This indicates that external genotypes contribute disproportionately high signal to the allelic signatures of individuals sampled from these three sites. Posterior migrant rate estimates identified that locations BLU and LD represent potential sources of immigrant genotypes for those detected at locations GRE, CLA and BIG. Both CLA and BIG showed migrant contributions from BLU ($m = 0.26, 0.28$), and GRE from LD ($m = 0.28$) (Figure 5.2a). Thus in all cases, inferred gene movement patterns among sample localities were unidirectional source migrant genotypes and appear to be contributed from BLU and LD only. Evidence for migrant contributions from GRE, CLA and BIG to the other sampled localities was minimal (emigration rates for GRE, CLA, BIG all $m < 0.007$; CI widths < 0.06; non-migrant proportions at LD and BLU both > 0.98) (Figure 5.2a).

No evidence for strong genetic connectivity between the two headwater localities was detected, nor between the headwater sites and any mainstream site (Figure 5.2a,b). Immigration between the headwater and mainstream clusters was negligible (all headwater-mainstream population comparisons $m_{QL} < 0.008$; CI widths < 0.03) (Figure 5.2a). The probability of migrant exchange between headwaters was low (from KB into LUC $m_{ql} = 0.025$, 95% CI width 0.081; from LUC into KB $m_{ql} = 0.003$, 95% CI width 0.023, Figure 5.2a,b). Correspondingly, both headwater localities showed high mean non-migrant proportions > 0.93, but variance estimates for LUC were substantially greater than for KB (95% CI widths for non-migrant proportions 0.113, 0.051 respectively).

Analyses of separate models applied to mainstream and headwater locations and comprising reassignment of all individuals to populations based on STRUCTURE allelic clustering solutions ($K = 2$) resolved two discrete allelic populations within each stream type that showed low levels of migrant exchange, in addition to a third allelic population representing common genotypes and higher migration probabilities (Figure 5.2b). In the headwater model, non-migrant allelic proportions were very high ($m > 0.96$), corresponding to low probability of migrant exchange between the two geographically discrete sampling locations KB and LUC ($m < 0.001$; Figure 5.2b). The 'mixed membership' cluster 3 showed lower non-migrant proportions ($m = 0.86$; 95% CI width 0.173) although the signal for migrant origin (from cluster 1) was relatively low ($m = 0.11$; 95% CI width 0.154, Figure 5.2b). Similarly, the mainstream model resolved two discrete genetic clusters corresponding to high non-migrant proportions ($m > 0.97$; 95% CI < 0.08) and low emigration rates, whereas the 'mixed membership' cluster 3 showed lower non-migrant proportions and larger estimate variance ($m = 0.81$; 95% CI width = 0.24; Figure 5.2b).

Discussion

Genetic diversity in *Melaleuca leucadendra* sampled in the Burdekin River catchment did not conform to isolation by distance or strictly linear trends in river drainage pattern at the spatial scale assessed here (13 km to 170 km between sampled locations). There was no evidence of population genetic structure among individuals from mainstream regions. In contrast, a large number of private alleles occurred among individuals sampled from headwater regions. These findings suggest that multiple distinct patterns of genetic exchange have occurred within the river system. These patterns may have arisen because of temporal differences in genetic exchange due to variation in hydrological connectivity. For example, the pool of common genotypes that are widely distributed may reflect the outcome of historical periods of channel connectivity promoting genetic interchange. Alternately, where disjunct genotype pools occur, a reduction of landscape connectivity and fewer opportunities for long-distance dispersal may exist.

Differences in allelic structure and genetic connectivity between mainstream and headwater locations correspond broadly to current hydrological signatures in the river. Genetic clustering solutions inferred from individual assignment analysis suggest that admixture and high genotypic exchange operates across mainstream regions which are separated by more than 100 kilometres. Thus, the modern river landscapes feature high levels of connectivity and gene dispersal. However, inferred recent migration rates revealed that gene flow differed among sample localities, suggesting differential movement among local gene pools. For example, among the three mainstream locations (GRE, CLA and BIG) the combination of high migrant proportions and low emigration rates suggests that these sampling locations are repositories ("sinks") of broadscale gene flow contributed to, at least in part, by gene pools included in this study (LD and BLU).

The hierarchical analysis of allelic immigration rates within catchment types revealed that genotypic association (allelic clustering signal) was strongest among the three most upstream locations. Moreover, inferred gene movements were unidirectional and in the direction of more downstream locations, implying that altitudinal gradient in the modern channel landscape could partly explain directional gene dispersal patterns in the river. These results are consistent with theoretical expectations for 'classical' metapopulation dynamics and long-distance hydrochory (Tero et al., 2003). However, two genetic populations with low emigration rates were strongly resolved within each stream type, consistent with expectations that the inferred genetic clusters reflect independent allelic dynamics. This result implies that periods of historical disjunction in the river landscape caused loss of genetic connectivity between demes. However, hierarchical STRUCTURE analyses also revealed that within each stream type there existed a third group comprising admixed individuals, as assessed conservatively against the 90% credible interval envelope for posterior assignments to each cluster. The presence of cross-assigned individuals reflects the level of resolution at which genetic clusters are identified. Therefore, I investigated the strength of population genetic structuring signal accounting explicitly for all cross-assigned individuals within each stream type by estimating the posterior mean immigrant proportions in all three genetic clusters corresponding to the STRUCTURE solution K=2, using BAYESASS models. These analyses revealed a high proportion of cross-assigned genotypes representing the third cluster in both the headwater and mainstream regions. In each case, the cross-assigned allelic group showed greatest migrant proportions and estimate variance, suggesting that this allelic group corresponds to common and evolutionarily persistent genotypes within each stream type that are distributed across large scales. The occurrence of a high proportion of cross-assigned genotypes indicates that genetic connectivity is maintained but not saturated throughout each stream type. Thus, these results imply that the combined effects of ongoing gene flow and selective processes act to maintain a proportion of shared ancestral genotypes that persist in the study system as part of species evolutionary signature, that in turn is continuously re-shaped by temporal changes in genetic connectivity as evidenced at the population level.

At least two solutions could contribute to maintained high genetic diversity and occurrence of common genotypes at the regional scale not related to modern channel configuration, which varies continuously as a function of stochastic climate and flow dynamics (Alexander et al., 1999b). First, high fecundity throughout the lifetime (i.e. millions of seeds per reproductive event) coupled with opportunistic life histories could help maintain high genetic diversity. Second, stream flow acts as a physical dispersal vector not dictated by modern landscape configuration or position in altitudinal gradient. Flood events are a principal mechanism predicted to drive large stochastic deviations from mean spatial dispersal trends, increasing the probability of effective long-distance dispersal events at landscape scales (100's of kilometres) (Nathan, 2006).

These patterns of genetic exchange among populations are temporally as well as spatially dynamic, most likely reflecting fluxes in gene pool isolation and connectivity. Comparable evidence for complex genetic distributions in riverine plants associated with non-equilibrium hydrological conditions and non-hierarchical gene flow, rather than population size or spatial distribution, have been detected in the Australian endemic stream lily *Helmholtzia glaberrima* (Philydraceae). Using AFLP markers and demographic mapping, Prentis and Mather (2007, 2008) demonstrated that strong non-equilibrium conditions associated with persistent founder effects, rather than existing landscape features such as hydrographic networks, have likely generated persistent patterns of population genetic diversity and differentiation in *H. glaberrima*. Genetic differentiation between *H. glaberrima* populations as identified by micro-drainage indicated that opportunities for seed dispersal were constrained (Prentis and Mather, 2007), and that sampled populations may represent the offspring from only a limited number of colonist plants (Prentis and Mather, 2008). In a similar framework in the Burdekin River system, stream flow and channel structure are maintained in a non-equilibric state due to minimal channel 'recovery' between successive floods (Alexander et al., 1999), and thus follow different temporal trajectories of change. Therefore, shifts in habitat and genetic connectivity occur through time, changing the probabilities of among-population genetic exchange. High flow variability, including episodic floods, could thereby impose stochasticity in population-level SGS signal and represent one key mechanism explaining the detected unordered spatial distribution of genotypes at local scales (Chapter 4). Moreover, opportunities for populations to accumulate and maintain discrete genotypic signatures might be expected to principally reflect the distribution of fluvial disturbances. Differences in fluvial regime between stream types could help explain why individuals sampled from two headwater locations, featuring lower disturbance energy profiles, resolved two independent allelic populations whereas individuals from five mainstream locations showed high allelic overlap. For example, whereas substantial genetic differentiation (as assessed by RAPD markers) and floral trait differentiation characterised subpopulations of the short-lived Egyptian perennial *Alkanna orientalis* (Boraginaceae) sampled in different wadis of the Sinai desert, evidence was strong for extensive gene flow between two wadi subpopulations and the interconnecting plain (Wolff et al., 1997). Seed transport via flash floods could plausibly explain maintained gene flow between subpopulations of this riparian species, and provide a mechanism to override pollinator selection pressure and constrain persistent genetic differentiation for floral traits (Wolff et al., 1997). The findings of the present study on *Melaleuca leucadendra* thus complement documented evidence in other hydrological environments for the strong role of non-equilibrium conditions in shaping population genetic distributions in riparian species.

The present study has revealed dynamic patterns of genetic connectivity within the river system. Modern channel configuration has potentially contributed to hydrological connectivity over distances greater than 100 km, resulting in periods of connectivity

among spatially distant gene pools and thus estimates of large effective population sizes in *M. leucadendra*. The degree of connectivity, as well as opportunities for dispersal and establishment that produce spatial genetic structure, could be expected to follow continuously changing trajectories as a function of fluvial variability. Therefore temporal shifts in landscape structure that alter the potential for genetic connectivity may contribute to population-level allelic identity as well as diversity. For riverine systems in particular, energy distributions composed of multiple hydrological, hydraulic and geomorphic processes determine landscape shifts and survival and dispersal probabilities at the scales at which these landscape processes operate, in this study reflected by sampling locations.

Tables and figures

Table 5.1. Genetic variability indicies average gene diversity (H_E), average allelic richness ($A_{R(X)}$) and average and total private allelic richness ($pA_{R(X)}$) estimated at among-population and between-stream type levels, using rarefaction procedures implemented in HP-RARE 1.0 (Kalinowski, 2005). Average allelic richness was standardised to a sample size of $X = 40$ genotypic individuals per population and $X = 2$ populations per stream type.

Population type	Genetic variability index			
	$H_{E\,av}$	$A_{R\,av}$	$pA_{R\,av}$	$pA_{R\,total}$
All populations	0.69	8.43	9.65	42
Headwater	0.73	13.26	14.17	30
Mainstream	0.68	10.24	7.46	12

Table 5.2. Genetic variance estimates among populations assessed at two levels (population, stream type), using hierarchical *F* statistics andYang's (1998) algorithm (HIERFSTAT v0.04-4; Goudet, 2005), and based on sampled and inferred genetic populations, using the global likelihood-ratio *G*-statistic (randomisation tests: n = 10 000 permutations).

Population type	Genetic variance						
	$G_{pop[stream\ type]}$	$G_{stream\ type}$	$F_{ind/total}$	$F_{pop/total}$	$F_{stream\ type/total}$	$F_{ind/pop}$	$F_{ind/stream\ type}$
Sampled	$P = 0.0001$	$P = 0.0481$	0.402	0.131	0.106	0.312	0.331
Inferred	$P = 0.001$	$P = 0.060$					

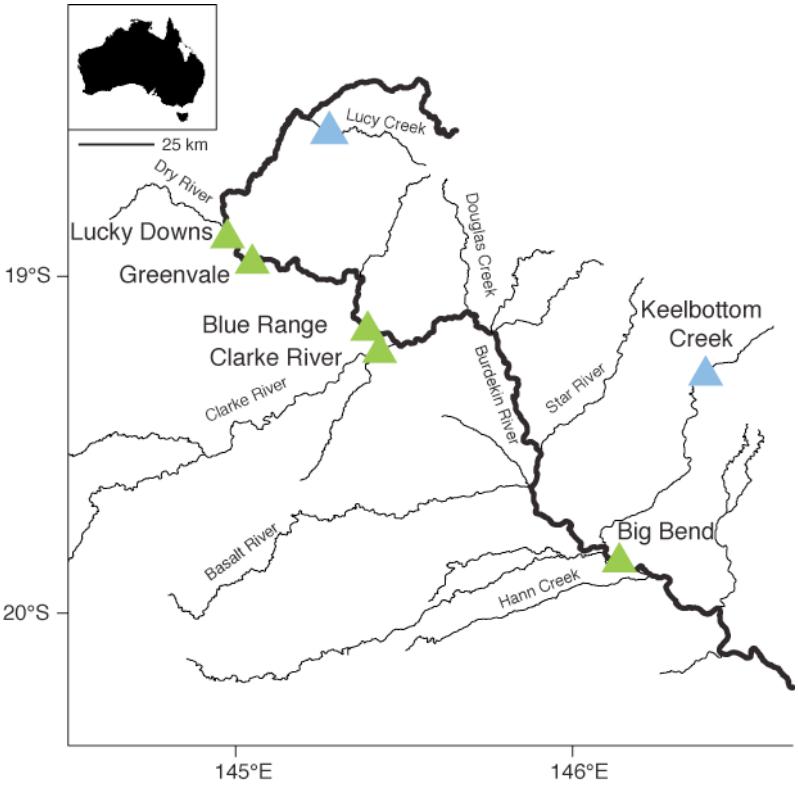


Figure 5.1

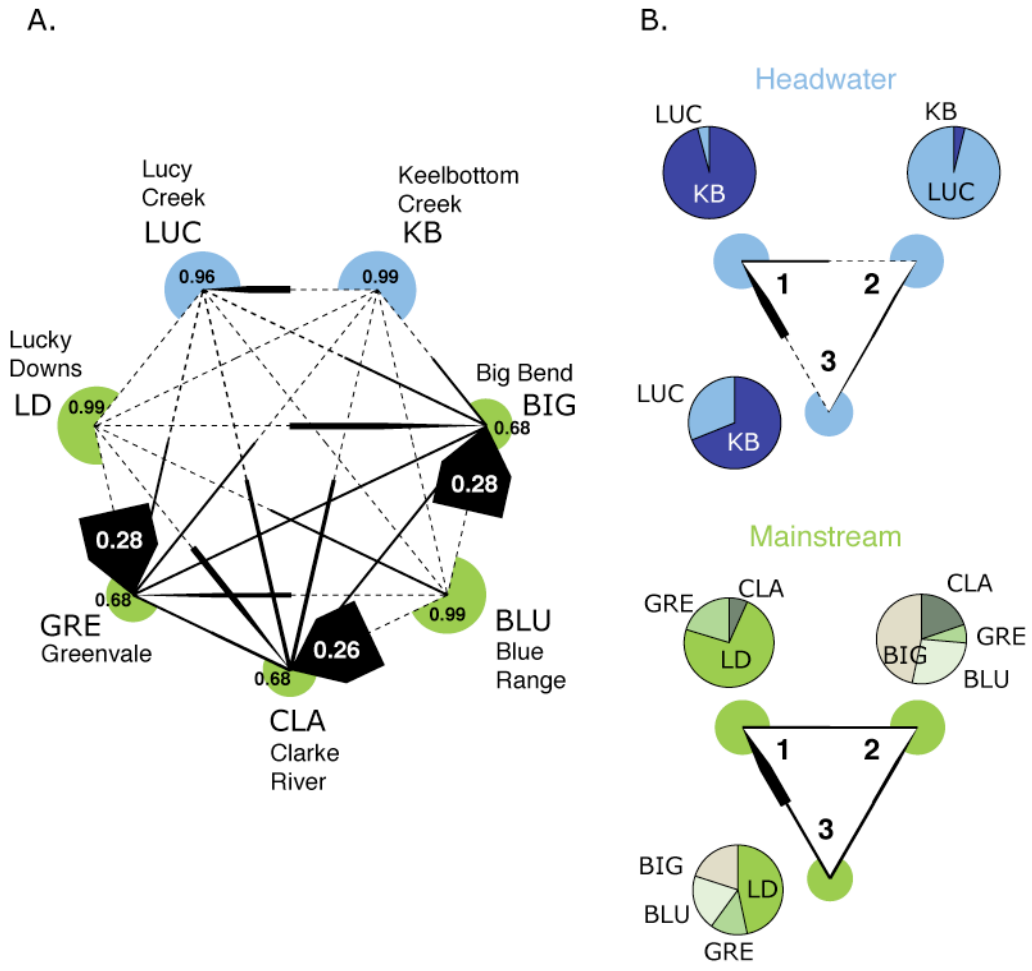


Figure 5.2

Figure 5.1. Location of seven sampled populations of *Melaleuca leucadendra* in the Upper Burdekin River catchment, north-east Queensland, Australia, comprising two headwaters (Lucy Creek (LUC) and Keelbottom Creek (KB) and five mainstream locations (Lucky Downs (LD), Greenvale (GRE), Blue Range (BLU), Clarke River (CLA), and Big Bend (BIG)).

Figure 5.2. Geographic distribution and genetic connectivity of *Melaleuca leucadendra* inferred from model-based population clustering methods and non-equilibrium estimates of gene flow. All values represent posterior model estimates obtained from one of ten independent runs showing lowest deviance (see text).

(A) Scales of genetic connectivity among the seven sampled populations. Circles at figure nodes and external values depict posterior mean estimates of population non-migrant proportions per generation; circle radius size is proportional to the order of magnitude of population non-migrant values. Lines depict posterior mean estimates of per-generation immigration rates between populations (migrant proportions) as inferred using BAYESASS models. Line thickness is proportional to order of magnitude differences in inferred immigration rates; dotted lines represent low signal for immigration rates ($m < 0.006$). Arrows show values for largest immigration rates; nodes at arrowheads show the direction (repository population) of inferred gene movement. Analyses were based on random sub-sampling of 23 genotypes per sampling population.

(B) Scales of genetic connectivity among the three allelic populations inferred from STRUCTURE clustering assignments at K=2, accounting for all cross-assignments as assessed against the 90% credible envelope of individual STRUCTURE assignments. Values represent proportional membership of individual genotypes from the seven sampled populations in each of the three allelic clusters. In both headwater and mainstream models, cluster 3 comprises all cross-assigned individual genotypes. Circle division represent proportional membership of individual genotypes from each of the seven sampling populations in each of the three allelic clusters, In the headwater model, allelic clusters 1 and 2 comprise a high proportion of individual genotypes from location KB and LUC respectively; all sampled genotypes (n=131) were included in this analysis. In the mainstream model, allelic cluster 1 (“upstream” cluster) comprises individual genotypes from the three most upstream sample locations only; allelic cluster 2 (“downstream” cluster) includes a high proportion of individual genotypes from the most downstream sample location. 15 randomly selected genotypes per sampling population (n=75) were used in the mainstream model analysis.

Chapter 6—Unclear species boundaries in the *Melaleuca leucadendra* group

Introduction

Species within the genus *Melaleuca* often display variability of diverse phenotypic traits. Conventional species-level diagnostic characters such as leaf and indumentum morphology, fruit and floral structures, and reproductive phenology are not consistent at intra-species and intra-population levels (Beardsell et al., 1993; Law et al., 2000). As a result, this genus is viewed as 'taxonomically difficult' (Bentham and Mueller, 1866; Blake, 1968; Barlow and Forrester, 1984; Byrnes, 1984; Rye and James, 1992; Beardsell et al., 1993; Orlovich et al., 1999).

Recent phylogenetic revision and novel tribal reclassification of the family Myrtaceae based on *matK* analyses of 68 genera suggest that homoplasy extends across key morphological attributes at the level of species including wood, fruit, and floral characters. This implies that morphological data alone are inadequate to resolve major clade relationships within the Myrtaceae (Wilson et al., 2001; Wilson et al., 2005; Biffin et al., 2007). In addition, key generic characters for *Melaleuca*, such as five basally-fused staminal groups, have been observed as evolutionarily labile features across closely related genera (e.g. Dawson, 1992). Life-history traits including growth form and regeneration strategy also vary at the congeneric level (Table 6.1), suggesting that robust circumscription of *Melaleuca* based on structural features is intractable. Multi-scale ecological and genetic relationships may influence ability to detect directional trends in evolutionary differentiation within and between currently recognised species and generic units (e.g. Craven and Lepschi, 1999).

The 'broad-leaved' *Melaleuca leucadendra* group comprises 16 recognised species (*sensu* Craven and Lepschi, 1999) and is ecologically dominant in dry tropics riparian systems across northern Australia. This presents a model system in which to evaluate the evolutionary and ecological drivers of phenotypic and genetic variation underlying cryptic species differentiation in *Melaleuca* and the family Myrtaceae. Novel species and populations associated with the *M. leucadendra* group have only recently been recognised (*M. ferruginea* and *M. triumphalis*; L. Craven, pers. comm., 2006) and species relationships within the genus and the *M. leucadendra* group remain unclear. Cook et al. (2008) resolved strong support for the *M. leucadendra* group as broadly monophyletic within the genus on the basis of chloroplast DNA (*ndhF*) data, in agreement with previous phylogenetic information obtained from the 18S-5.8S rDNA region (Brown et al., 2001). Data derived from the chloroplast and two nuclear DNA regions by Cook et al. (2008) provided no strong evidence for genetic isolation among *M. quinquenervia* and other morphologically defined taxa. Regional sharing of chloroplast haplotypes and reticulate patterns of evolution among the two nuclear

regions support the theory of recent or ongoing gene flow among members of the complex. Mechanisms constraining speciation rates are unclear, and this warrants investigation in the context of potential introgression events in relatively recent evolutionary history (c. 7 million years ago; Cook et al., 2008).

Research on the keystone riparian species *M. leucadendra* developed in this thesis suggests that fluvial processes, including episodic floods, impose strong selection for adaptive characters such as resprouting and clonal growth structure (chapters 2 to 4). Adaptive phenotypes appear to be shared across multiple lineages of taxa that occupy disturbance-driven environments, including the riparian Myrtaceae. Population-level studies using nuclear microsatellite markers revealed that *M. leucadendra* maintains high levels of genotypic variation and long-distance gene flow at the river system scale (chapters 4 and 5), despite stochastic environmental conditions and variable landscape scale connectivity. Thus, landscape fluvial processes are expected to influence the patterns of ecological and genetic differentiation in riparian taxa via evolutionary selection mechanisms such as the purportedly 'different ecologies' of Cook et al. (2008).

The challenge to resolve sub-tribal phylogenetic uncertainty in *Melaleuca* reflects the demand of evolutionary ecology research to critically evaluate evidence for species status in plants (Crandall et al., 2000; Templeton, 2001). Incorporating species phenotypic variation into phylogenetic sampling will allow direct tests of the taxonomic distribution of key adaptive characters and their underlying genetic variation (Crandall et al., 2000). This approach may help elucidate the genetic and environmental bases for functional trait variation in this ecologically important genus.

Species-level molecular phylogenetic analysis in plants is problematic due to the lack of high-resolution, yet evolutionarily conservative, loci such as the dloop in animals (Kress et al., 2005). The internal transcribed spacer region (ITS) of the rDNA in angiosperms has been broadly utilised for higher-resolution analyses of phylogenetic relationships in plants. This region still represents one of the most useful for assessing species-level genetic divergence in the nuclear genome (Kress et al., 2005). However, the mutational dynamics of ITS can be influenced by RNA secondary structure (e.g. Mayol and Rossello, 2001; Alvarez and Wendel, 2003). Therefore, assessing the structure and stability of the secondary structures of the RNA transcripts associated with ITS sequences is a useful primary strategy to evaluate evidence for divergent, intra-specific paralogues that could influence phylogenetic signal. In turn, utilising a combination of nuclear and chloroplast gene regions is recognised as an important technique to evaluate resolution and consistency in molecular phylogenetic analyses (Nylander et al., 2004; Brandley et al., 2005).

In this study, I infer the phylogenetic structure of the putatively ancestral ecotype *M. leucadendra*, which is dominant in flood-driven river channels. I utilise a nested sampling strategy across and within recognised morphotaxa comprising the 'broad-

leaved' *Melaleuca* species group, sometimes referred to as the *M. leucadendra* complex. This approach was used to incorporate the breadth of phenotypic variation into reconstruction of evolutionary genetic relationships in *M. leucadendra*. I utilise novel DNA sequences of three loci – one nuclear ribosomal (ITS) and two organellar (cpDNA; *trn*L-*trn*L-F and *rp*L16). Specifically, I (i) determine the relative utility of nuclear ITS, chloroplast *trnL* and *rp*L sequence regions to resolve closely related taxa of the *Melaleuca* genus, and infer a hypothetical phylogeny of the *M. leucadendra* species complex; (ii) investigate the influence of alternative model parameterisations, including ITS secondary structure information, on the ability to resolve topological relationships in the *Melaleuca* genus; and (iii) use the information on within-species ecological and genetic variation in M. *leucadendra* developed in this thesis to evaluate evidence for phylogenetic speciation.

Materials and methods

Taxon sampling

In total, 58 extant taxa within the Myrtaceae were sampled in this study. I used a nested sampling strategy to include (i) representatives of *Melaleuca leucadendra sensu lato* from multiple river reaches within the Burdekin River catchment as well as across its known distributional range (11 samples from Australia, Indonesia, and Papua New Guinea; Appendix 6a), (ii) all 16 nominal species (L. Craven, pers. comm. 2004) of the *M. leucadendra* group including 2-3 representatives of core species previously described as sympatric and/or potentially hybridising to *M. leucadendra* (i.e. *M. dealbata, M. quinquenervia, M. cajuputi, M. viridiflora, M. argentea*); and (iii) representatives of the genera *Callistemon* and *Calothamnus* that are considered related to *Melaleuca*, and which together comprise the sub-familial tribe Melaleuceae (Wilson et al., 2005). Outgroup taxa were selected on the basis of information from recent combined morphologic and molecular phylogenetic studies (Sytsma et al., 2004; Wilson et al., 2005) and to represent multiple Myrtoideae tribes: Kanieae (*Tristaniopsis*), Syzygieae (*Syzygium*), Myrteae (*Eugenia*), Eucalypteae (*Eucalyptus*), Leptospermioideae (*Asteromyrtus*), Lophostemoneae (*Lophostemon*), Xanthostemoneae (*Xanthostemon*) and Osbornieae (*Osbornia*). Results from previous analyses indicate that *Osbornia*, the monotypic Australasian mangrove shrub, is the closest sister to the Melaleuceae whereas members of the widespread genus *Eucalyptus* are more distant, although sympatric to riparian *Melaleuca* species (Craven and Lepschi, 1999; Brown et al., 2001; Sytsma et al., 2004; Wilson et al., 2005). Both *Osbornia* and *Eucalytpus* were included as outgroups in the final combined sequence alignment (52 taxa). Preliminary analyses using ITS secondary structure indicated that the sequences for the remaining genera were more divergent to Melaleucaceae species and were not used in analyses of the final combined data set of 52 taxa. In addition, no *M. sericea* sequence was obtained for ITS, so *M. sericea* was excluded from the final combined data set of 52 taxa. Only unique (non-identical) sequences were used in phylogenetic reconstruction.

Sample material was obtained either from field collected or young leaf material grown from seed (CSIRO Seed Centre, ACT, Australia) plus several herbarium samples (Lyn Craven, CSIRO, Canberra, Australia) were used for some outgroup taxa. Appendix 6a provides detailed voucher and taxon information.

DNA sequencing

Genomic DNA was extracted from silica-gel or herbarium-dried leaf material using the QIAGEN DNeasy Plant Mini Kit (QIAGEN, Hilden, Germany), including the optional centrifugation step for 5 min at maximum speed to optimise precipitate removal. Prior to DNA extraction, dried leaf tissue was ground using a Mini BeadBeater (BioSpec Products, Bartlesville, USA) until pulverised.

Novel sequences were derived for all 58 taxon samples used in this study. Three DNA regions from two genomes were amplified and sequenced per sample; the nuclear internal transcribed spacer including the 5.8S ribosomal gene, and two regions from the chloroplast genome (*trnL* intron and *trnL-F* intergenic spacer, hereafter *trnL*; *rpl*16 intron and flanking regions). For *rpl*16, amplification and sequencing primers used were *rpl*16 1661R and *rpl*16 71F (Jordan et al., 1996) for primary sequence alignment in addition to a new internal primer designed specifically for *Melaleuca* and utilised to obtain *rpL*16 sequences in one direction (*CCRP*). The primers used to amplify and sequence ITS were the universal primer ITS4 (White et al., 1990) in combination with ITS16 (Shepherd et al., 2004); for *trnL-F*, the universal primers 'c'–'f' were used (Taberlet et al., 1991). QIAGEN™ and Bioline™ brand reagents were used to conduct PCR in the following final concentrations: 1 unit *Taq* polymerase, 0.4 μM primer, 0.16 mM dNTPs, 0.5 mM (ITS, *rpl*16) or 1.0 mM (*trnL*) $MgCl_2$. Loci were amplified on a MJ Research DNA Engine Tetrad 2 Thermocycler (Bio-Rad Laboratories, Hercules, CA) and followed a standard protocol where 35 cycles of amplification included reduction of annealing temperature to 50°C from 96°C followed by final annealing at 72°C. The amplified PCR template was excised from agarose electrophoretic gels and purified using the MinElute PCR cleanup kit (QIAGEN). Purified PCR products were sequenced in both directions using an ABI 3700 DNA Sequencer (Macrogen Inc., Seoul, Korea). Raw electropherograms were processed using Sequencher 4.5 (Gene Codes Corp., 2005).

Data were derived wholly from direct sequencing of PCR products. To screen for potential intra-specific ITS paralogues, I closely inspected all ITS electropherograms for multiple peaks of equal strength. For the majority of ingroup (*Melaleuca*) taxa, I examined sequences derived from two or more samples from each individual species. Additionally, I constructed consensus secondary structure predictions for ITS1 and ITS2 (detailed below) to check for the presence of key conserved structural motifs (Mayol and Rossello, 2001) and screen for regions of slip-strand mispairing, which might indicate potential homoplasy between the aligned nucleotides of divergent outgroups (Biffin et al., 2007; Cook et al., 2008).

Sequence alignment

Consensus sequence alignments for each gene region required minimal manual editing of forward and reverse reads. In the ITS sequence alignment, I detected no evidence for incompatible site patterns across sequence positions. I conducted initial consensus analysis using ClustalX (Thompson et al., 1997) followed by manual inspection in BioEdit v5.0.6 (Hall, 1999; Hall, 2001). Appendix 6b lists locus sequence alignments used to conduct phylogenetic inference analyses.

ITS data—sequence alignment

To compose the final ITS alignment for phylogenetic analyses, I concatenated bases associated with the 18S, 5.8S and 26S rDNA conserved gene regions, retaining all bases conservatively associated with the variable internal spacer regions ITS1 and ITS2. To determine consensus gene and spacer regions applicable to my data set I screened multiple GenBank accessions for ITS sequences for taxa in four distinct Myrtaceae genera – *Melaleuca*, *Callistemon*, *Syzygium* and *Eucalyptus*. Specifically, I compared the delineation of 18S, 5.8S and 26S regions in each sequence with respect to the sequence nucleotide pattern, to infer the most conservative, biologically plausible nucleotide subsets to represent ITS1 and ITS2 in the current study.

Phylogenetic reconstruction

In all phylogenetic reconstructions, gaps in alignment were treated as missing data. Prior to combining data, I screened for incongruent phylogenetic signals among different gene regions by estimating individual gene region phylogenies using Bayesian Metropolis-Hastings Markov chain Monte-Carlo (MCMC) methods, checking for strongly supported, disparate bipartitions among gene regions (Castoe et al., 2005). Phylogenetic reconstructions using the combined dataset were subsequently inferred using both Bayesian MCMC and maximum parsimony (MP) methods.

Maximum Parsimony (MP) analyses were conducted using PAUP* v. 4.0b10 (Swofford, 2002). All characters were equally weighted in MP searches with heuristic search and inactive steepest descent options, 1000 random-taxon stepwise additions, tree bisection reconnection (TBR) branch-swapping and saving multiple parsimonious trees (MULTREES in effect). Support values for nodes in MP reconstructions were estimated using non-parametric bootstrapping, with 1000 heuristic searches and 100 random-taxon addition sequence replicates per bootstrap pseudo-replicate, and a strict 50% bootstrap consensus tree generated in PAUP*.

Model selection strategies

Accommodating uncertainty in model choice and parameter variability within combined datasets are known to be critical factors influencing the accuracy and evolutionary realism of phylogenetic inference (Huelsenbeck et al., 2004; Nylander et al., 2004; Alfaro and Huelsenbeck, 2006). I employed Bayesian and Akaike information criterion-

based approaches to evaluate model uncertainty and the effects of alternative model parameterisations on model posterior probabilities, inferred tree topologies and node support (Nylander, 2004a; Brandley et al., 2005; Castoe et al., 2005) in order to provide an informed phylogenetic hypothesis of the *Melaleuca leucadendra* group. Firstly, I identified the candidate suite of most appropriate four-state models of nucleotide evolution for MCMC analyses using Corrected Akaike Information Criterion (AIC_c) weights (95% credible set) as implemented in MrAIC v.1.4 (Nylander, 2004a). MrAIC invokes a profile of updating parsimony starting trees (estimated in PHYLIP) to optimise the maximum of the likelihood function across all searched evolutionary models, and therefore can provide a more heuristic search algorithm than implemented in ModelTest (Nylander, 2004a). Independent analyses using MrAIC were performed on the combined and all putative partitions of the dataset and used as decision criteria in the development of partitioned MCMC models based on combinations of gene regions: ITS1, ITS2, trnL, rpL (see below). Different model search algorithms are known to optimise different evolutionary models. Therefore, I also conducted model selection procedures using MrModelTest v.2.0 (Nylander, 2004b), and compared the 'best-fit' suites of models based on all available criteria; hLRT and estimated AIC_c (MrModelTest) and AIC_c (MrAIC).

Partitioning aims to divide data into biologically plausible sequence regions that have evolved under different evolutionary patterns, hence improving model accuracy and evolutionary realism (Nylander et al., 2004; Brandley et al., 2005). In addition to the AIC model selection procedures just described, I conducted Bayesian analyses on the ITS and combined data sets using alternative combinations of data partitions and character-substitution models, to evaluate the effects of partitioning scheme and model complexity on relative model performance including practical implications for topological inference. Datasets were partitioned on the *a priori* bases of gene identity (ITS1, ITS2, *trnL* and *rpL*16) and evolutionary constraints (i.e. ITS data set: ITS1, ITS2, stems and loops), summarised in Table 6.2 and Table 6.3 for the ITS and combined data sets respectively.

ITS data—secondary structure prediction

To examine the impact of ITS secondary structure information on phylogenetic interpretation in *Melaleuca*, I generated secondary structure predictions for taxa in my data set (after Biffin et al., 2007). In summary, the minimum-free-energy algorithm as implemented by Pfold (Knudsen and Hein, 2003; Mathews et al., 2004) was used to evaluate predicted secondary structures of the ITS1 and ITS2 RNA transcripts, using the software program RNAstructure v.4.3 (Mathews et al., 2004). RNA structures for ITS1 and ITS2 regions were subsequently visualised using the RnaViz v.2.0 package (De Rijk, 1997). I used the consensus secondary structure information to generate input for RNA-specific (stems and loops) models in PHASE analyses (see below).

ITS phylogeny—RNA models of sequence evolution

To estimate the posterior probability distribution of the *Melaleuca* ITS data set under alternative partitioning schemes, I used Bayesian MCMC analyses as implemented in the MCMCPhase module of the PHASE package (v.2.0b, 2005), utilising both four-state nucleotide and RNA-specific (stems and loops) substitution models not currently available in MrBayes. The RNA7C model considers nucleotide pairs as the elementary states and all changes to and from the mismatch state to be single substitutions. This model parameterisation was selected *a priori* on the bases of (i) maximum likelihood analyses supporting its appropriate fit for phylogenetic analyses of Myrtaceaeous lineages (Biffin et al., 2007); and (ii) preliminary analyses conducted in this study indicating that the majority rule consensus secondary structure predictions for Myrtaceae and those derived for *Melaleuca* taxa in my data set are congruent (E. Biffin pers. comm., 2006).

Default prior settings in PHASE were used – that is, equal topology priors, exponential branch length prior, Dirichlet prior for stationary state frequencies, and exponential prior for nucleotide substitution rate ratios. Six gamma rate categories and random starting trees were used. For models implementing fixed stationary state frequencies (SYMG), starting frequency values were set to equal (all 0.25) and not estimated during the analysis; all other model parameters were estimated during the analysis. For each model, I ran three independent runs of 6,000,000 generations each, sampling values every 100^{th} generation. To check for convergence and appropriate mixing, I compared generation plots for all substitution model parameters for each independent run. Final inferences were based on the combined samples from the conservative stationary phases of three independent runs (in total, $3x10^6$ samples; $1x10^6$ samples from each run).

The MrBayes "sumt" command was then used to generate a 50% majority rule consensus topology with posterior clade support values from these combined samples (after Telford et al., 2005). To evaluate alternative models via Bayes factor comparisons, marginal log-likelihood values (lnLs) were sampled from the posterior distribution of each run, retransformed into likelihoods, and the harmonic mean estimate of these likelihoods was calculated using Mathematica® v.5.2 (Wolfram Research Inc., 2005; after Brandley et al., 2005). In addition, I ran equivalent Bayesian analyses on the 4-state nucleotide models using default prior settings in MrBayes 3.1.2 to assess differences in tree topologies associated with potential differences in program algorithms. Bayes factor comparisons among PHASE models were conducted independently of comparisons among models generated from MrBayes analyses due to expected differences in program algorithms.

Bayesian MCMC phylogenetic inference on combined data

All MCMC phylogenetic analyses were conducted in MrBayes v.3.1.2 . Prior distributions for the model parameters specified for each selected model were applied

following Nylander *et al*. (2004), including using exponential priors on branch length and GTR substitution rate ratio parameters. I used one cold and three incrementally heated Metropolis-coupled chains, with heating parameter set to 0.2. For each final model, four independent runs initiated with random trees were run for a total of 3.0 x 10^7 generations, sampling trees every 100 generations. To determine the appropriate burn-in phase (i.e. the number of sampled generations before apparent stationarity), I assessed convergence and mixing behaviour across all substitution model parameters, for each independent run, for each model investigated, using Tracer v.3.1 (Rambout and Drummond, 2005) and output plots generated using the MrBayes sumt command. For the four independent runs, I examined generation density and distribution plots for all model parameters. To check for evidence of over-parameterisation and convergence of parameters after burn-in, I subsequently compared the mean and variance of model likelihoods, marginal posterior distributions and parameter generation plots for all runs. After confirming convergence, final inferences were based on the combined concatenated samples from the four independent runs. 50% majority rule consensus trees were computed to obtain posterior probabilities. Clades with >85% bootstrap support (MP analyses) and >0.95 posterior probability (Bayesian analyses) are considered well supported.

I employed Bayesian criteria for model selection among the mixed models. The utility of Bayesian approaches to comparing candidate models is increasingly being recognised in empirical studies (e.g. Irestedt et al., 2004). While Markov chain model jumping procedures are not currently available in software such as MrBayes, Bayes factors provide an advantageous means to assess alternative models because, unlike hierarchical likelihood-based tests, model marginal likelihoods derived from Bayesian MCMC analyses are not based on parameter point estimates. Model marginal likelihoods can reasonably be estimated from likelihood harmonic mean values, allowing direct and convenient utilisation of MCMC output (Nylander et al., 2004). A Bayes factor test for comparing models 1 and 2 examines the ratio of model posterior probabilities: that is, the odds that Model 1 (the marginal likelihood of the model, given the model parameters and the data) is preferred relative to Model 2. Therefore, the models being compared need not be 'nested' or indeed share the same parameters (Kass and Raftery, 1995; Irestedt et al., 2004). Bayes factors and relative Bayes factors were computed following Nylander et al. (2004) and Castoe et al. (2005). These calculations utilised the harmonic mean estimate of marginal likelihood values generated via MrBayes output (sumt command) to compare alternative models explored within PHASE (ITS data) and within MrBayes (combined data).

Results

Molecular variation and sequence distances

The combined concatenated sequence alignment (ITS1, ITS2, *trnL*, *rpL*16) comprised 2379 bp. In total, aligned data of 504 bp were obtained from the ITS regions, 723 bp from *trnL* and 1152 bp from *rpL*16. The proportion of parsimony-informative sites in the ITS region was 0.234 (118 sites), markedly higher than that detected in either of the chloroplast regions (0.047, 0.065 in *trnL* and *rpL*16 respectively) and the highly conserved 5.8S region (one indel only). Between ingroup taxa, pairwise sequence divergence ranged from 2.10% to 28.6% in ITS (*M. linariifolia* and *M. trichostachya*), 0.6% to 3.7% in *rpL*16, and 0.2% to 3.0% in *trnL* (Table 6.4). Individual gene trees reconstructed for *trnL* and *rpL*16 regions provided congruent, yet poorly resolved, phylogenetic estimates compared to ITS (Figure 6.1a–c). Therefore, I proceeded with data analyses on the ITS and combined-region data sets on the basis of no evident incongruent phylogenetic signal among gene regions.

ITS secondary structure analyses

The consensus, structurally partitioned ITS alignment comprised 145 paired stem nucleotides and 126 loop-bulge nucleotides in ITS1, and 109 paired stem and 124 loop-bulge nucleotides in ITS2. Conserved structural motifs detected in ITS1 and ITS2 secondary structure constructions were present across the analysed sequences including *M. leucadendra* and *Callistemon viminalis*, providing evidence that the sequence data represent functional copies of ITS across taxa (Figure 6.2a,b).

ITS structural partitioning

Model posterior likelihood was highest for the stems and loops model ($2\ln B_{10}$ 552.48; -lnL 2673.41) and lowest in the unpartitioned model (-lnL 2949.65; Table 6.2). However, the degree of taxic resolution was considerably greater in nucleotide models than the model allowing different rates in stems and loops, while major clades receiving high support (*Pp*>0.90) were consistently resolved regardless of model type. The majority consensus trees derived from alternative substitution models implemented in PHASE were highly congruent. For these tree sets, mean node support was very similar among the base unpartitioned model and structurally partitioned models (unpartitioned, ITS1 and ITS2, stems and loops models respectively; Figure 6.3a–c). On the basis of apparent congruence among ITS secondary structure models and topologies, and greater resolution in key tree structure under nucleotide models without increasing variability in node support, I used four-state nucleotide models as implemented in MrBayes for probabilistic analyses on the combined data set.

Maximum parsimony phylogenetic analysis

Heuristic MP analysis on the combined dataset resolved a congruent, but poorly resolved topology compared to Bayesian model approaches (detailed below; Figure 6.4). Total tree length recovered was 361. Index values of tree consistency, homoplasy and retention indicated that the MP model was moderately supported by the data (index values 0.507, 0.493, 0.738 respectively).

Bayesian nucleotide model selection and evaluation

The GTR model type was strongly supported as the best fit for both the combined and individual gene datasets under AIC_c, BIC and hLTR model selection criteria. Furthermore, each 99% confidence interval set contained a discrete and relatively small number of candidate models (one to three), indicating congruent model solutions (all GTRG-based models; Table 6.5).

On the basis of these results, and using AIC_c criteria, I selected the SYMG, GTR and GTRG models as the best fit candidate models for analysis of the individual datasets (ITS, *trnL* and *r*pL16 respectively) and the GTRG model for the combined dataset (Table 6.5). For the combined dataset, I employed these elementary models in a range of partitioning schemes based on gene identity to evaluate the effects of alternative model structure on posterior probabilities and topology (Table 6.6).

The estimated model likelihoods indicate a moderate increase in model fit from the base unpartitioned model to all others (increase of c. 80 log likelihood units; Table 6.6). Overall, the second most parameter-rich model (i.e. 4x spacer model with 29 free parameters, Table 6.6) was supported as the best-fit model on Bayes factor estimates. Notably, model fit was influenced by the identity of the substitution model applied to different data partitions, rather than model complexity alone. Thus, Bayes factor comparisons favoured models assigning SYMG, GTR and GTRG models respectively to the ITS, *trnL*, and *r*pL16 partitions over more parameter-rich models allocating a GTRG model to each data partition, although the gain in model fit (in terms of likelihood) was relatively small (differences between models less than ten log likelihood units). Relative Bayes factors support this trend and demonstrate decreasing relative gain as model complexity and number of parameters increases (Table 6.6), consistent with previous observations (Castoe et al., 2005). Within models, differences in harmonic mean estimates of marginal likelihood between independent MCMC runs was relatively low (3.2 to 14.1 units).

Examination of convergence and mixing across all model parameters in each candidate model indicated no evidence for parametric over-fitting. For instance, across all four independent MCMC runs of the best-fit 4x model, likelihood values and parameter estimates appeared to ascend rapidly to a stationary plateau and converged on very similar parameter and phylogenetic estimates. The posterior probability distributions of individual parameters showed discrete signatures throughout parameter space.

Effects of model parameterisation on Bayesian relative posterior probabilities, tree topologies and node support

Overall, posterior distributions of parameter estimates showed relatively low variance. Divergence across partitions was highest in the posterior distributions of substitution rate parameter estimates between the nuclear ITS and chloroplast regions. Comparison of parameter 95% credible intervals showed little overlap between *trnL* and/or *rpL*16 to ITS1 and ITS2 for the transversion ratios A-C, A-T and G-T in addition to A-T, in support of the spacer-based partitioning strategy used. Parameter estimates for ITS1 and ITS2 showed variance in the alpha shape of gamma distribution, but overall the degree of overlap was high (Table 6.7).

The majority-rule consensus trees obtained under the different combined-data models were highly congruent. Estimated mean tree lengths were short (0.36–0.54). Among the GTRG rate-variation models, topological uncertainty was positively associated with tree length uncertainty (Table 6.6). The normalised SD of tree length for the most complex model was 0.097, considerably higher than for the chosen (second-most complex) model (0.047). Identical consensus topologies were produced from the unpartitioned and the selected model. Posterior probability values for clades showed similar trends and mean node support was similar between models (0.93%; 0.92%). Among all models, differences in clade structure corresponded to changes at weakly supported nodes (*Pp* < 75%). On the basis of these trends I present results from analyses under the 4x model to infer phylogenetic relationships among the sampled taxa.

Bayesian MCMC phylogenetic inference under the best-fit combined-data model

The phylogenetic estimates for the 'broad-leaved' *Melaleuca leucadendra* group based on MCMC analyses indicate a paraphyletic grade at its base comprising representatives from the genera *Calothamnus*, *Callistemon* and *Melaleuca* (Figure 6.5). The *Melaleuca leucadendra* complex was resolved as a natural lineage within a paraphyletic gradation that includes representatives from currently distinct genera and distributional ranges (e.g. *Callistemon* and *Calothamnus*). These major clade relationships were consistent across individual and combined gene trees and across candidate evolutionary models.

Within this series *M. styphelioides*, *Calothamnus quadrifidus* and *M. cornucopiaeae*, and sampled taxa from the species complex *M. acacioides* were resolved as lineages basal to the *M. leucadendra* clade series (Clade A, *Pp* for lineages = 1.00, Figure 6.5). The species *M. acacioides* ssp. *acacioides* and *M. citrolens* were formerly included in a broad circumscription of *M. acacioides* F. Muell. and have overlapping distributional ranges in northern Australasia, but are distinct in ecology and phenology (*M. acacioides* ssp. *acacioides* coastal/mangrove, *M. citrolens* open forest; Barlow, 1986). The current phylogenetic results support delineation of these species as closely related taxa external to the *M. leucadendra* series (Figure 6.5). The New Caledonian endemic *M. pancheri*, previously classified in the genus *Callistemon* (see Craven and Dawson 1998), was

strongly associated with the *M. acacioides* species (*Pp* = 1.00) and the *M. leucadendra* series representing all shallower nodes (*Pp* = 0.72).

A key clade comprising the primarily southern-Australian *Callistemon* and *Melaleuca* lineages (Craven and Lepschi, 1999) resolved a distinct group at the base of the paraphyletic grade of the *M. leucadendra* series (Clade B, Figure 6.5). In contrast to the *M. leucadendra* species group, the species in Clade B are characterised by small pinnate leaf form and shrub/small tree growth habit , and vary in distributional range from restricted (south-east Australia, *M. deanei*) to widespread (eastern riparian systems, *M. trichostachya*) (Wrigley and Fagg, 1993; Craven and Barlow, 1997; Craven and Lepschi, 1999). Within this clade, *Callistemon pachyphyllus* and *C. viminalis* group as sister taxa to *M. deanei* (*Pp* = 0.99), although low variance in phylogenetic signal does not resolve polyphyletic relationships in this species group or interspecific associations with the sister lineage *M. styphelioides* (Figure 6.5).

The *Melaleuca leucadendra* group *sensu* Craven is paraphyletic. The *Melaleuca leucadendra* clade (Figure 6.5, shaded) groups together all sample taxa of the eastern species group *Melaleuca leucadendra s. l.* supported by high posterior probability and resolution of relationships at the species level. Within this clade, there was strong support for two major associations each containing multiple species samples (Figure 6.5). *M. triumphalis*, recently described by Craven (1998) from rock cliff habitat in the NT, northern Australia, is strongly associated with both eastern and western *M. argentea* samples together with *M. fluviatilis* (endemic to QLD), and *M. nervosa* (*Pp* = 0.94). The *M. argentea* taxa are weakly differentiated from each other (*Pp* = 0.79) but their relationship to *M. triumphalis* is unresolved, representing a polytomy between these three taxa (Figure 6.5).

The remaining taxa within the *Melaleuca leucadendra* group form a series of sub-clades based on species and/or geographic associations. The novel entity *M. ferruginea* (Craven) is strongly supported (*Pp* = 0.99) as a sister taxon to the core "Burdekin" *M. leucadendra* group, comprising four samples collected from geographically distinct river reaches within the Upper Burdekin catchment, north-east Queensland (*Pp* = 0.97). Clade A represents a strongly supported association (*Pp* = 0.95) among (1) the Burdekin-*ferruginea* group; (2) a monospecific *M. leucadendra* group comprising five samples from Indonesia, New Guinea and Australia (*Pp* = 0.96), (3) a group containing the more northerly distributed *M. quinquenervia* and *M. cajuputi* containing an Indonesian *M. viridiflora* and (4) *M. viridiflora* Queensland (Figure 6.4). One clade groups a single *M. leucadendra* sample, collected from a population previously identified as *M. argentea* (see Fielding and Alexander, 2001) together with three *M. dealbata* samples representing Australian and New Guinea collections (*Pp* = 0.97) and *M. lasiandra* (*Pp* = 0.93). These two groups resolve dichotomous relationships between taxa.

Relationships among the remaining terminal taxa vary in degree of support. A polytomy of three species (*M. quinquenervia*, *M. saligna*, *M. arcana*) represents the most poorly resolved section of the phylogenetic results. At the intraspecific level, support values for phylogenetic relationships were lowest in *M. cajuputi* ssp. *cajuputi* ($Pp < 0.60$). Samples representing three other non-endemic species *M. cajuputi* ssp. *platyphylla*,, *M. quinquenervia*, and *M. viridiflora* also occurred as paraphyletic taxa, but whether this results from misidentifications remains to be resolved.

Discussion

The suite of gene tree and evolutionary models assessed showed a gradation of phylogenetic signal, with highest resolution in the nuclear ITS. Evidence for ITS spacer motifs that are highly conserved across plants (ITS 1; Liu and Schardl, 1994) and eukaryotes (ITS 2; Schultz et al., 2005) were consistent across the sequences and genera used in this study, indicating that the ITS sequences generated in this study represent functional and informative data. Gene tree reconstructions incorporating all outgroup taxa indicated that the chloroplast loci *trnL* and *rpL*16 provide good phylogenetic signal at the generic to subgeneric level in the Myrtaceae. Among the taxa sampled in this study, *trnL* and *rpL*16 showed low phylogenetic signal among currently circumscribed intra-specific levels compared to nuclear ITS. Further studies utilising both nuclear and chloroplast markers and model evaluation within Bayesian frameworks will help identify the relative utility of candidate loci such as the *trnH-psbA* spacer region (Kress et al., 2005) and barcoding loci (Chase et al., 2007) to inform infra-species-level relationships in *Melaleuca*.

These data present another example that genera conventionally recognised as structurally distinct from *Melaleuca*, including *Callistemon* and *Calothamnus*, are well placed within a broader generic circumscription (Craven, 2006). In addition phylogenetic inferences based on the chloroplast gene trees and the combined-data topology were largely congruent. This indicates that differential sorting patterns among ancestral chloroplast haplotypes do not confound topological resolution and signals of introgression in the taxon *M. leucadendra* inferred from the nuclear ITS sequence data. Differences in topology and support corresponded consistently to clades with low support ($Pp<0.75$) regardless of analysis model used, whereas the signal for major clades showed consistent high support ($Pp>0.90$) across the different gene trees and combined data analyses. The RNA model accounting for base-pairing received the highest support for the ITS data based on posterior likelihood assessments, but the practical influence of model choice on inferred topologies was minimal among both the individual and combined-loci data sets. Congruent topological inferences were also resolved across extensive model analyses accounting for varied model parameterisations. Together, these findings suggest that the models analysed here provided congruent phylogenetic signal for well-supported branches delineating major clades. Analysis of secondary structure provided no evidence of pseudogenes in this

study or in (Cook et al., 2008). Potentially polymorphic DNA sequences may have been obtained for some samples of *M. arcana, M. nodosa, M. lanceolata*, *M. glomerata, M. sericea, M. fluviatilis* and *M. leucadendra*, *M. saligna* and *M. dealbata* as detected by Cook et al. (2008), but were eliminated from inclusion in the data set in this thesis. This warrants further investigation that recognises ITS polymorphisms to study the frequency and distribution of these potentialy polymorphic specimens. Further, more saturated sampling across phenotypes and within geographic regions will help determine the frequency and distribution of multiple divergent copies of nuclear genes. Alternatively, a population genetic approach to assessing introgression may be fruitful. Whichever approach, sampling and analytical design that could reflect potential introgression and incomplete homogenisation, or independent lineage sorting, will be of particular value.

I infer that the ITS and combined data sequence alignments contain robust support for major nodes independent of the evolutionary model used, but insufficient signal to resolve the shortest evolutionary branches that correspond to intra-species level relationships between *M. leucadendra* accessions. Therefore, my data reflect both the limits of marker resolution for intra-specific analyses and overall low sequence divergence values (<25%), corresponding to a high level of evolutionary relatedness within the suite of closely related taxa examined here. One potentially useful extension of the current analyses would be to employ reticulate and consensus split network methods (Huson and Bryant, 2006) on the wider sampling proposed to accommodate the multiple parallel edges (branches) associated with intra-species level relationships. This will facilitate deeper examination of evolutionary linkage and quantitative tests of hybridisation signals between and within taxa in the *M. leucadendra* lineage.

Cryptic phylogenetic signatures in the context of ecological differentiation among relatives were at least in part resolved for *Melaleuca leucadendra*. Interact between plant evolutionary and ecological processes shapes species-level patterns of phylogenetic relatedness. This interplay could be expected to be especially pronounced in groups such as *M. leucadendra* that inhabit disturbance-driven environments. For example, in river systems, the flow regime potentially influences the mechanisms of genetic variation and selection for ecologically adaptive heritable traits that dictate species-level evolutionary rates. Thus, in the current study, the detected high levels of genetic variation and exchangeability among taxa could explain the boundaries to phylogenetic resolution identified within the *M. leucadendra* species complex. Across analytical models, the nominal species, including the key taxa *M. leucadendra* and *M. dealbata*, were typically differentiated on very short branch lengths. The position of these taxa in the derived state in this analysis does not support the status of the *M. leucadendra* ecotype as ancestral for this species group. More likely taxa are those with affinities to *M. pancheri*, in this analysis at the base of the *M. leucadendra* group.

The *M. leucadendra* complex represents a congruent phylogenetic unit within which there are maintained opportunities for genetic exchange at the species level. This signal is consistent with its ecological circumscription as a specialised lineage occupying flood-prone riparian habitats (Barlow, 1988; Specht, 1990). Sampling multiple individuals at the river-system scale provided evidence for this reticulate signal in *M. leucadendra* resulting in indistinct phylogenetic boundaries among ecotypes, that could be expected to arise from genetic disjunction and disconnectivity at the landscape (river system) scale. The strong signal for introgression in *M. leucadendra* also supports the hypothesis of dynamic genetic connectivity at the population level, as assessed using nuclear polymorphic (microsatellite) markers (Chapter 5). Ongoing gene flow mediated by dispersal and disturbance is a mechanism that could constrain rates and directionality of speciation. Explicit tests of the relationships between clade structure and phenotypic and genotypic variation across the *M. leucadendra* complex will require extension of the multi-scale studies of genetic connectivity in the *M. leucadendra* ecotype demonstrated in this thesis. Sampling at the population level and lower, independent of current taxonomic circumscriptions, will potentially help interpret evolutionarily dynamic relationships within this large, biologically complex genus.

I propose that incorporating the breadth of phenotypic and ecological diversity that characterises the *Melaleuca* taxa in this study, and indeed across Myrtaceae lineages, is an important strategy to infer species-level function and evolutionary relatedness. I argue for a broadened phylogenetic concept for *Melaleuca* because the evolutionary interrelationships among sympatric taxa and potential for speciation reflect the combined influences of genetic and environmental processes. Based on my findings, one complementary research strategy could be to intensify hierarchical, population-level sampling and phylogenetic analysis within and across the putative species in the *M. leucadendra* complex, employing a suite of high-resolution markers to quantify the relationships between geographic and phenotypic identity. This approach would allow explicit testing of the null hypotheses of genetic and ecological exchangeability among currently differentiated species. Disturbance processes including the hydrological regime interact directly with population processes such as survivorship and gene flow, that in turn influence life-history evolution. Thus, assessing population-level genetic structure will allow new inferences on the mechanisms underlying species ecology related to detectable patterns of phylogenetic speciation. Future resolution of these trends will require sampling across current traditional taxonomic boundaries to resolve questions of genetic isolation and help identify the taxonomic boundaries—or continuum—of species.

Tables and figures

Table 6.1. Taxa putatively associated with the *Melaleuca leucadendra* species complex. Distribution codes are Papua New Guinea (PNG) and states and territories of Australia: Queensland (QLD); Western Australia (WA); Northern Territory (NT); New South Wales (NSW).

Species	Distribution	Habitat	Habit	References
M. arcana S.T.Blake	QLD (Cape York – Cooktown)	Moist, heathy hollows between coast and sand dunes	Tall shrub to small tree to 10 m.	1, 2, 3
M. argentea W.Fitzg.	WA, NT, QLD, PNG	Sand and gravel stream beds and banks; a "rheophyte"	Small to medium tree to 25 m	1, 2, 3
M. cajuputi Powell			Tree to 25 m; rarely a shrub to 1m	1, 2, 3, 4, 5
subsp. *cajuputi*	WA, NT, Indonesia	Peat swamp; sandy soil; coastal dunes		
subsp. *cumingiana* (Turcanzinow) Barlow	Burma, Thailand, Vietnam, Malaysia, Indonesia			
subsp. *platyphylla* Barlow	QLD (ne), Indonesia, PNG	Various. Lowland swamp forest; open forest on sandy soil; savanna swamp-monsoon forest ecotone; river banks adjacent to rainforest; swamp savanna on clay soil; grasslands; mangrove saline swamps and mud flats; clay pans		
M. clarksonii Barlow sp. nov.	QLD (Cape York)	Seasonally flooded regions; swamp and waterhole margins; woodland or open forest	Tree to 10 m; hard-barked	5, 1
M. dealbata S.T.Blake	WA, NT, QLD (Cape York – Bundaberg), PNG	Swamp; coastal	Medium-sized tree to 20 m	1, 2, 3
M. ferruginea Cowie sp. nov.	QLD	Floodplains	-	L. Craven

				pers. comm.
M. fluviatilis Barlow sp. nov.	QLD (Cape York–Rockhampton)	River beds; stream lines; light soils; a "rheophyte"	Shrub or tree to 30 m	1, 5
M. lasiandra F.Muell.	WA, NT, QLD	Red sands; swamps; stream lines	Shrub or tree to 5 m	1
M. leucadendra (L.) L.	WA, NT, QLD, Malesia	Watercourses; lagoons	Tree to 40 m	1, 2, 3
M. nervosa (Lindl.)Cheel				
forma *latifolia* Byrnes	WA, NT, QLD (nw)	Heavier soils	Tall shrub to 5 m or tree to 10 m	1, 2
forma *nervosa*	WA, NT, QLD (ne), PNG	Desert regions; stony or sandy ridges		
forma *pendulina* Byrnes	WA, NT, QLD	Levees		
M. quinquenervia (Cav.) S.T.Blake	QLD, NSW, New Caledonia, PNG	Coastal swamps; watercourses	Small to medium tree to 25 m	1, 2, 3
M. saligna Schauer	QLD (Torres Strait Is – Cooktown)	Watercourses; edge of swamps	Small tree to 10 m	1, 2, 3
M. sericea Byrnes	WA, NT	High water tables	Shrub or tree to 5 m	2
M. stenostachya S.T.Blake			Hard-barked shrub or small tree	
var. *stenostachya*	NT, QLD (n)	Dry soils; heavy or skeletal		1, 2, 3
var. *pendula* Byrnes	QLD (n)	Damp substrate		1, 2
M. triumphalis Craven	NT (Victoria River district)	Near perennial seepage; base of ephemeral waterfalls, top of scree slopes, crevices near cliff bases	Shrub to 2.5 m	1, 6
M. viridiflora Sol. ex Gaertn.			Small tree, often twisted habit, 10 m to occasionally 25 m	1, 2, 3
var. *viridiflora*	WA, NT, QLD, PNG	Swampy ground; high water tables		
var. *attenuata* Byrnes	QLD (n)	As for type		
var. *canescens* Byrnes	QLD (n)	Drier areas		
var. *glabra* (C.T.White) Byrnes	QLD (e), PNG	As for type		

1. Craven and Lepschi (1999); 2. Wrigley and Fagg (1993); 3. Blake (1968); 4. Miwa et al. (2001); 5. Craven and Barlow (1997); 6. Craven (1998); 7. Byrnes (1984).

Table 6.2. Summary of character substitution models and partitioning schemes under which the ITS data set (ntaxa = 52, nchar = 504) was analysed using PHASE 2.0 and MrBayes 3.1.2. All parameters excepting branch length and topology were allowed to be partition specific. Note calculations used to estimate ln*L* and Bayes factors generated from PHASE and MrBayes output differ between programs (e.g. see Brandley et al. 2005), and therefore values are directly comparable for model sets within (not between) software programs

Model	**No. of partitions**	**No. of free parameters**	**Model description**	**PHASE est. ln*L***	**2lnB_{10}, RBF**	**MrBayes est. *lnL***	**2lnB_{10}, RBF**
1x SYM+Γ	1	6	Single SYM+Γ model for the non-partitioned ITS data	-2949.65	Model 0	-2995.42	Model 0
2x SYM+Γ	2	12	One SYM+Γ model for each of ITS1, ITS2	-2944.55	10.2	-3031.73	-72.62, -12.10
1x GTR+I+ Γ	1	10	Single GTR+ I+ Γ model for the non-partitioned ITS data	-2952.24	-5.18	-2984.04	22.76, 5.69
2x GTR+I+ Γ	2	20	One GTR+ I+ Γ model for each of ITS1, ITS2	-2957.04	-14.78	-3029.66	-34.24, -2.45
stems(RNA7C+I+ Γ) +loops(GTR+I+ Γ)	4	17+ 20	For each of ITS1, ITS2: one GTR+ I+ Γ model for loops regions; one RNA7C+I+ Γ model for stems regions	-2673.41	552.48	-	-

Table 6.3. Summary of character substitution models and partitioning schemes under which the combined data set (ntaxa = 52, nchar = 2379) was analysed using MrBayes 3.1.2. For each model in each partition, all parameters excluding branch length and topology were allowed to be partition specific.

Model	No. of partitions	No. of free parameters	Model description
1x GTR+Γ	1	9	Single model for combined data: combined-data best-fit GTR+Γ
3x gene, GTR+Γ	3	27	Independent model for each of three gene regions ITS, trnL, rpL: combined-data best-fit GTR+Γ
3x gene, SYM+Γ (ITS) x GTR (trnL) x GTR+Γ (rpL)	3	23	Independent model for each of three gene regions ITS, trnL, rpL: SYM+Γ (ITS) xGTR (trnL) x GTR+Γ (rpL)
4x spacer, GTR+Γ	4	36	Independent model for each of three gene and spacer regions ITS1, ITS2, trnL, rpL: combined-data best-fit GTR+Γ
4x spacer, SYM+Γ (ITS1) x SYM+Γ (ITS2) x GTR (trnL) x GTR+Γ (rpL)	4	29	Independent model for each of three gene and spacer regions: SYM+Γ (ITS1) x SYM+Γ (ITS2) x GTR (trnL) x GTR+Γ (rpL)

Table 6.4. Summary sequence variation statistics for gene regions employed in this study: nuclear ITS, chloroplast *trnLF-C* and *rpL*16.

DNA region	Number of			Proportion of informative sites (total)
	Characters	variable sites	informative sites	
ITS1 + ITS2	504	224	118	0.234
ITS1	271	108	59	0.218
ITS2	233	116	59	0.253
trnL-F	723	65	34	0.047
rpl16	1152	124	75	0.065
ITS1 + ITS2 + *trnL-F* + *rpl*16	2379	413	227	0.095

Table 6.5. Summary of AIC_c values, AIC_c differences (Δ) and Akaike weights (w), showing all models contained in the 99% AIC confidence set, for the single-genome and combined data sets. Values were generated using MrAIC v.1.4 (Nylander 2004), which implements the 24 models of character substitution currently available in MrBayes v.3.1.2. l maximised log-likelihood; K estimable parameters including branch lengths

Model	l	K	AIC_c	ΔAIC_c	w	cum(w)
ITS: 504 characters						
SYM+Γ	-2851.6128	107	5975.5893	0.0000	0.4629	0.4629
GTR+ Γ	-2846.9390	110	5976.0155	0.4262	0.3740	0.8369
SYM+I+ Γ	-2851.6165	108	5978.8380	3.2487	0.0912	0.9281
GTR+ I+ Γ	-2846.9428	111	5979.3141	3.7248	0.0719	1.0000
trnL: 723 characters						
GTR	-1433.4826	109	3124.0842	0.0000	0.4485	0.4485
GTR+ Γ	-1432.3231	110	3124.5481	0.4639	0.3556	0.8042
GTR+I	-1433.5188	110	3126.9396	2.8554	0.1076	0.9117
GTR+ I+ Γ	-1432.3207	111	3127.3354	3.2512	0.0883	1.0000
rpL: 1152 characters						
GTR+ Γ	-2523.2147	110	5289.8876	0.0000	0.7743	0.7743
GTR+ I+ Γ	-2523.2225	111	5292.3527	2.4681	0.2257	1.0000
combined data: 2379 characters						
GTR+ Γ	-7402.2056	110	15035.1785	0.0000	0.7525	0.7525
GTR+ I+ Γ	-7402.2173	111	15037.4024	2.2239	0.2475	1.0000

Table 6.6. Posterior probability, Bayes factors and topology characteristics* of Bayesian analyses of the combined data set. RBF= relative Bayes factors; TL-tree length; NSD=normalised standard deviation of tree length.

Model	Partitions	Parameters	lnl	2lnB1,0	RBF	TL (mean)	TL (variance)	NSD
Nonpart	1	9	-7303.04	-	-	0.4306	0.000544	0.0542
lociGTRG	3	27	-7222.22	161.64	8.98	0.5380	0.002688	0.0964
Lociown	3	23	-7219.96	166.16	11.87	0.3603	0.000298	0.0479
ITS12GTRG	4	36	-7219.92	166.24	6.16	0.5344	0.002708	0.0974
ITS12own	4	29	-7216.10	173.88	8.69	0.3652	0.000293	0.0469

* Mean node support values representing arithmetic mean of the posterior clade probabilities on the 50% majority-rule consensus tree were comparable across models evaluated (nopart=0.93; 'best-fit' ITS12own=0.92).

Table 6.7. Mean and 95% credibility interval for each parameter sampled from the combined posterior distribution of four independent MCMC runs of the 4x-spacer, SYM+Γ model. Overall rate was set to average rate across locus partitions.

T	ITS1		ITS2		trnL		rpL	
r(A-C)	0.062	(0.0324–0.1011)	0.067	(0.0339–0.1091)	0.241	(0.1508–0.3456)	0.191	(0.1253–0.2720)
r(A-G)	0.204	(0.1486–0.2669)	0.194	(0.1376–0.2565)	0.208	(0.1192–0.3144)	0.169	(0.1055–0.2451)
r(A-T)	0.072	(0.0360–0.1177)	0.110	(0.0670–0.1620)	0.012	(0.0006–0.0356)	0.026	(0.0107–0.0467)
r(C-G)	0.047	(0.0218–0.0805)	0.036	(0.0134–0.0673)	0.139	(0.0561–0.2474)	0.110	(0.0497–0.1884)
r(C-T)	0.527	(0.4542–0.5990)	0.473	(0.4004–0.5467)	0.200	(0.1252–0.2886)	0.153	(0.1011–0.2151)
r(G-T)	0.087	(0.0493–0.1331)	0.121	(0.0765–0.1729)	0.202	(0.1224–0.2964)	0.352	(0.2632–0.4458)
alpha	0.322	(0.1836–0.5266)	0.140	(0.1014–0.2214)	-		0.162	(0.1092–0.2316)
pi(A)	0.250		0.250		0.276	(0.2458–0.3068)	0.266	(0.2424–0.2912)
pi(C)	0.250		0.250		0.201	(0.1747–0.2276)	0.166	(0.1465–0.1870)
pi(G)	0.250		0.250		0.177	(0.1518–0.2034)	0.160	(0.1405–0.1810)
pi(T)	0.250		0.250		0.346	(0.3144–0.3788)	0.407	(0.3801–0.4343)

a)

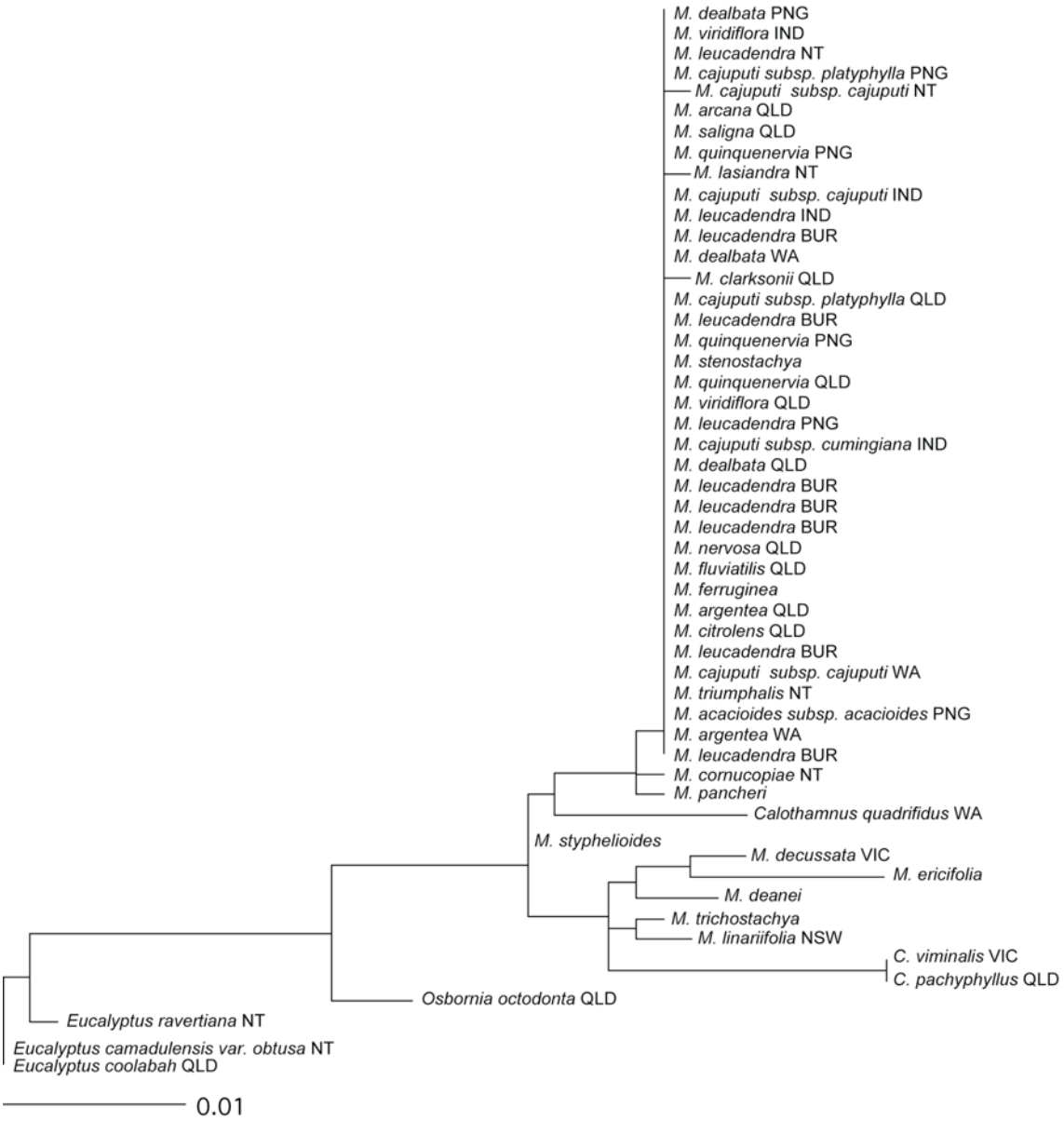


Figure 6.1a. 50% majority rule consensus trees inferred from Bayesian analysis of the individual gene region *trnL*, using the 'best-fit' model of character evolution GTR as assessed on AICc and Bayes factor model comparisons.

b)

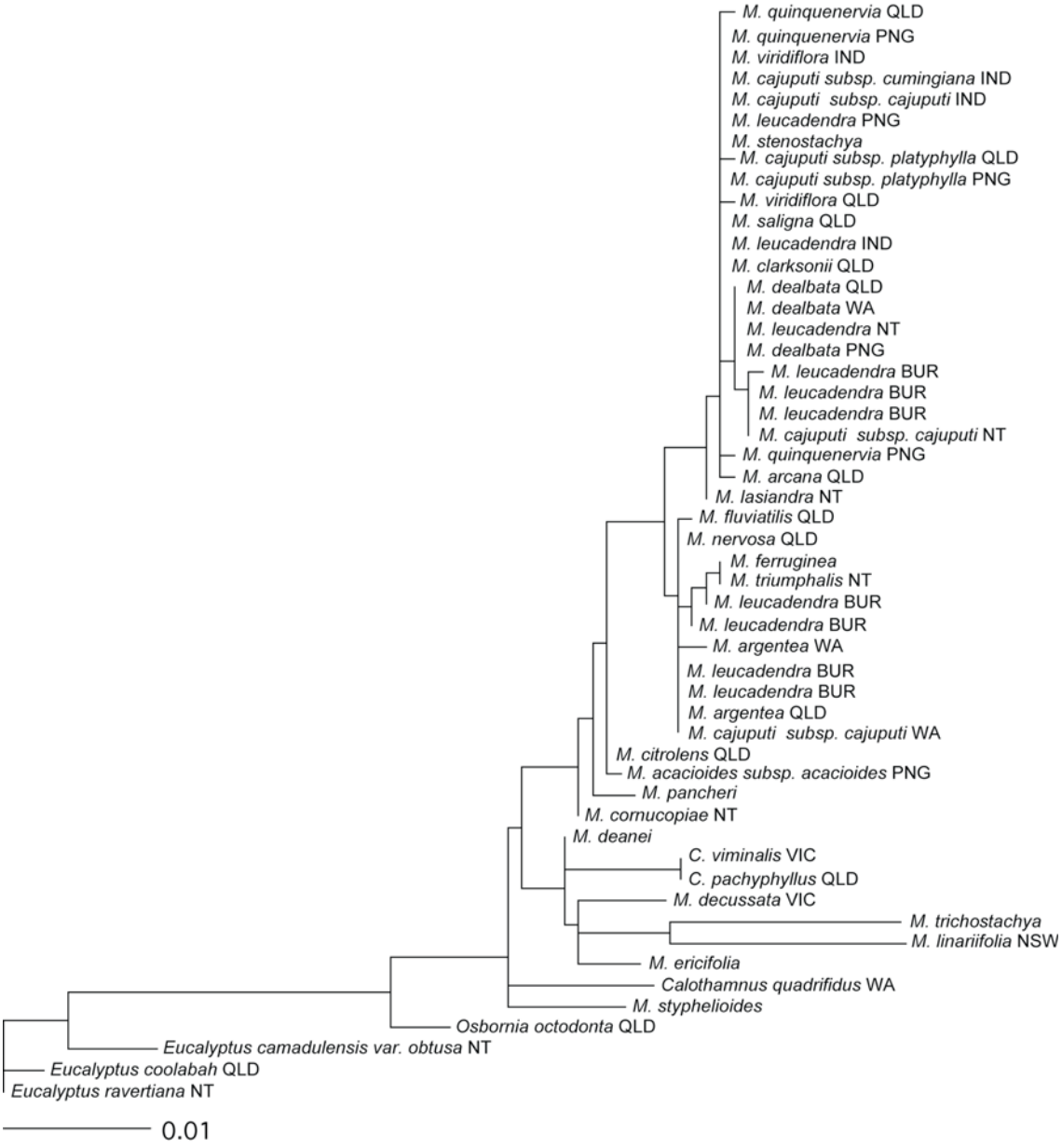


Figure 6.1b. 50% majority rule consensus trees inferred from Bayesian analysis of the individual gene region *rpl*16 using the 'best-fit' model of character evolution GTRG as assessed on AICc and Bayes factor model comparisons.

c)

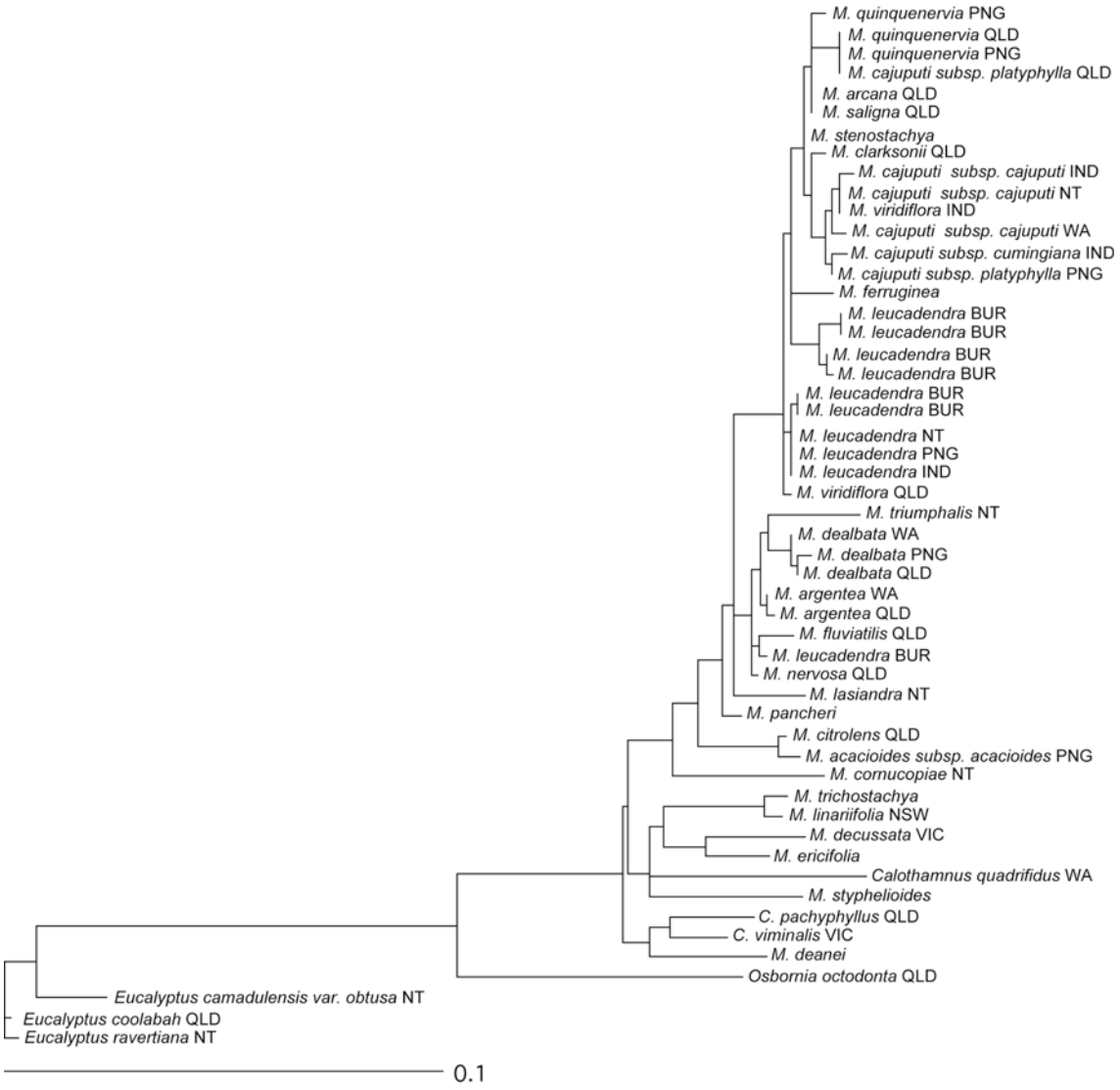


Figure 6.1c. 50% majority rule consensus trees inferred from Bayesian analysis of the individual gene region ITS using the 'best-fit' models of character evolution SYMG as assessed on AICc and Bayes factor model comparisons.

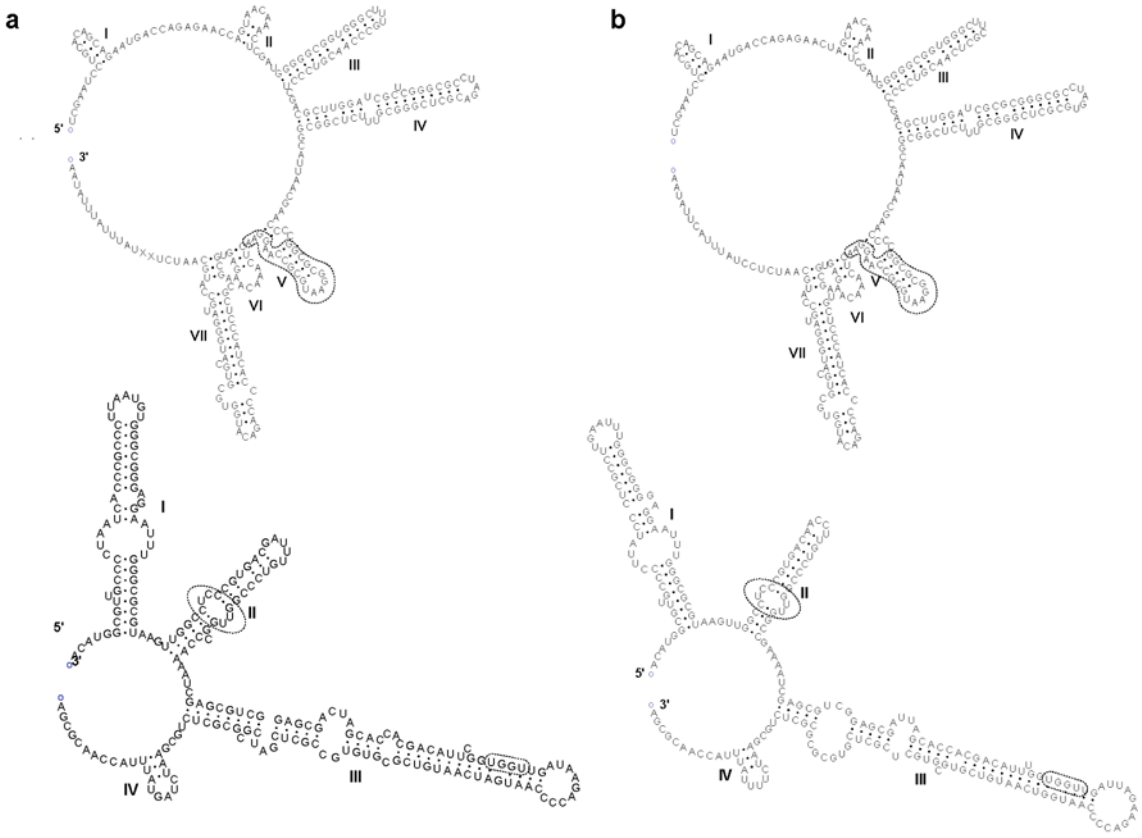


Figure 6.2. Secondary structure models for ITS1 and ITS2 spacer regions showing key structural motifs in (a) *Melaleuca leucadendra* (Big Bend, Upper Burdekin River, QLD); (b) *Callistemon viminalis* (VIC).

(a)

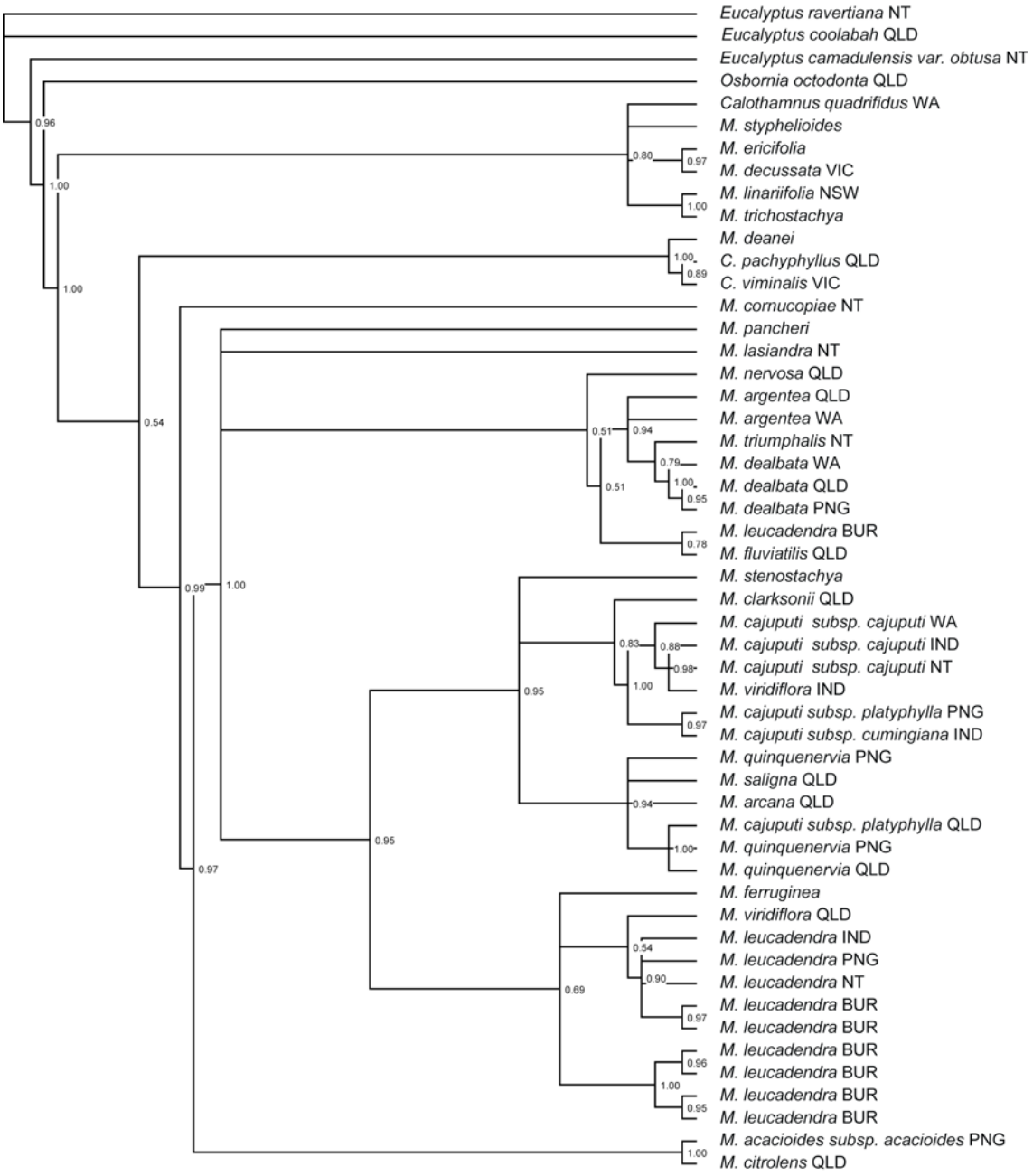


Figure 6.3a. The 50% majority rule consensus tree inferred from Bayesian analyses of the ITS data set using evolutionary models implemented in PHASE—partitioning strategy: unpartitioned model.

(b)

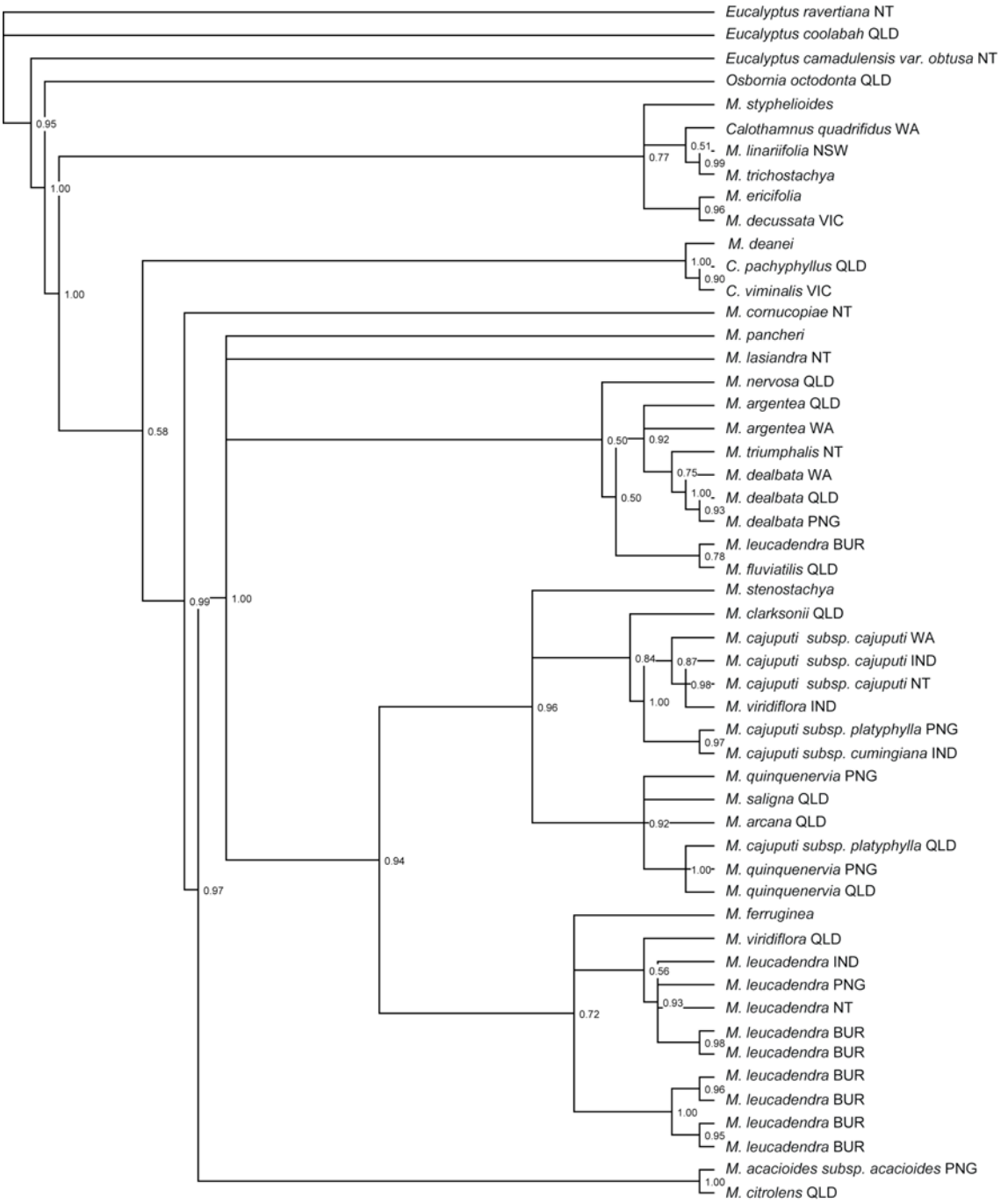


Figure 6.3b. The 50% majority rule consensus tree inferred from Bayesian analyses of the ITS data set using evolutionary models implemented in PHASE—data partitioned into ITS1 and ITS2 (SYMG).

(c)

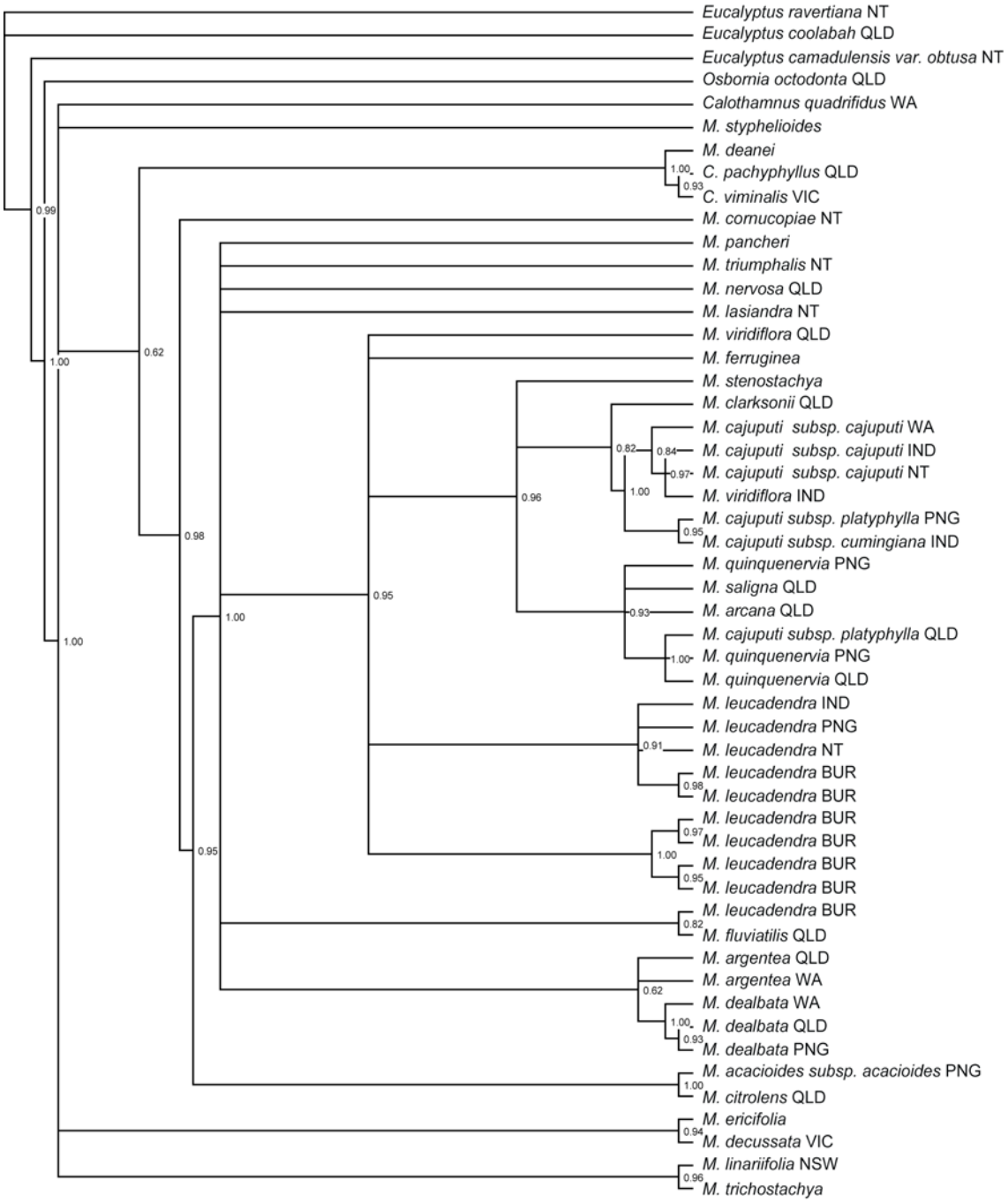


Figure 6.3. 50% majority rule consensus tree inferred from Bayesian analyses of the ITS data set using evolutionary models implemented in PHASE and alternative data partitioning strategies: (a) unpartitioned model; (b) data partitioned into ITS1 and ITS2 (SYMG); (c) RNA7C stems and loops model.

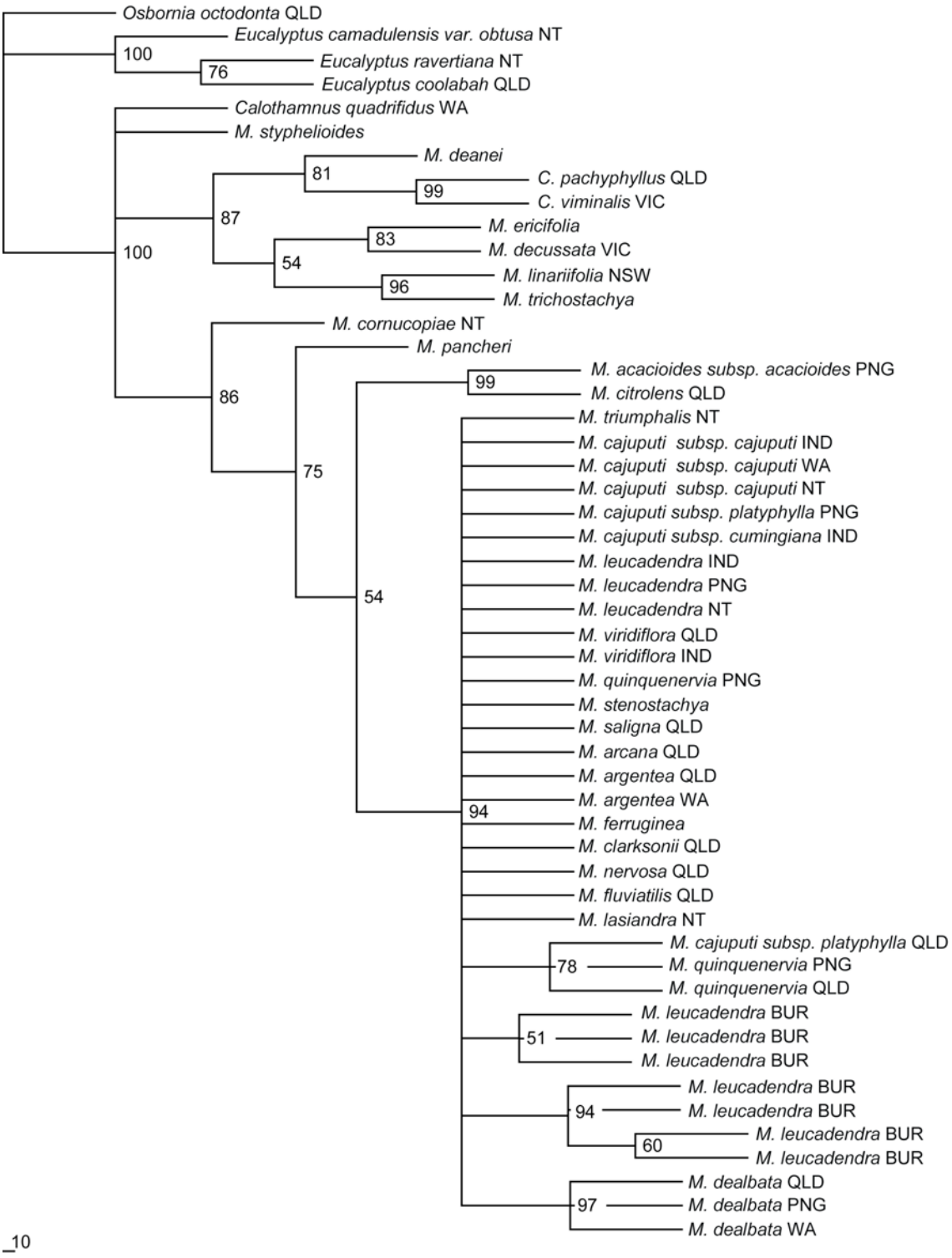


Figure 6.4. 50% majority rule consensus tree inferred from heuristic searches using MP methods in PAUP. Values refer to bootstrap support (100 random-taxon addition sequence replicates per bootstrap pseudo-replicate).

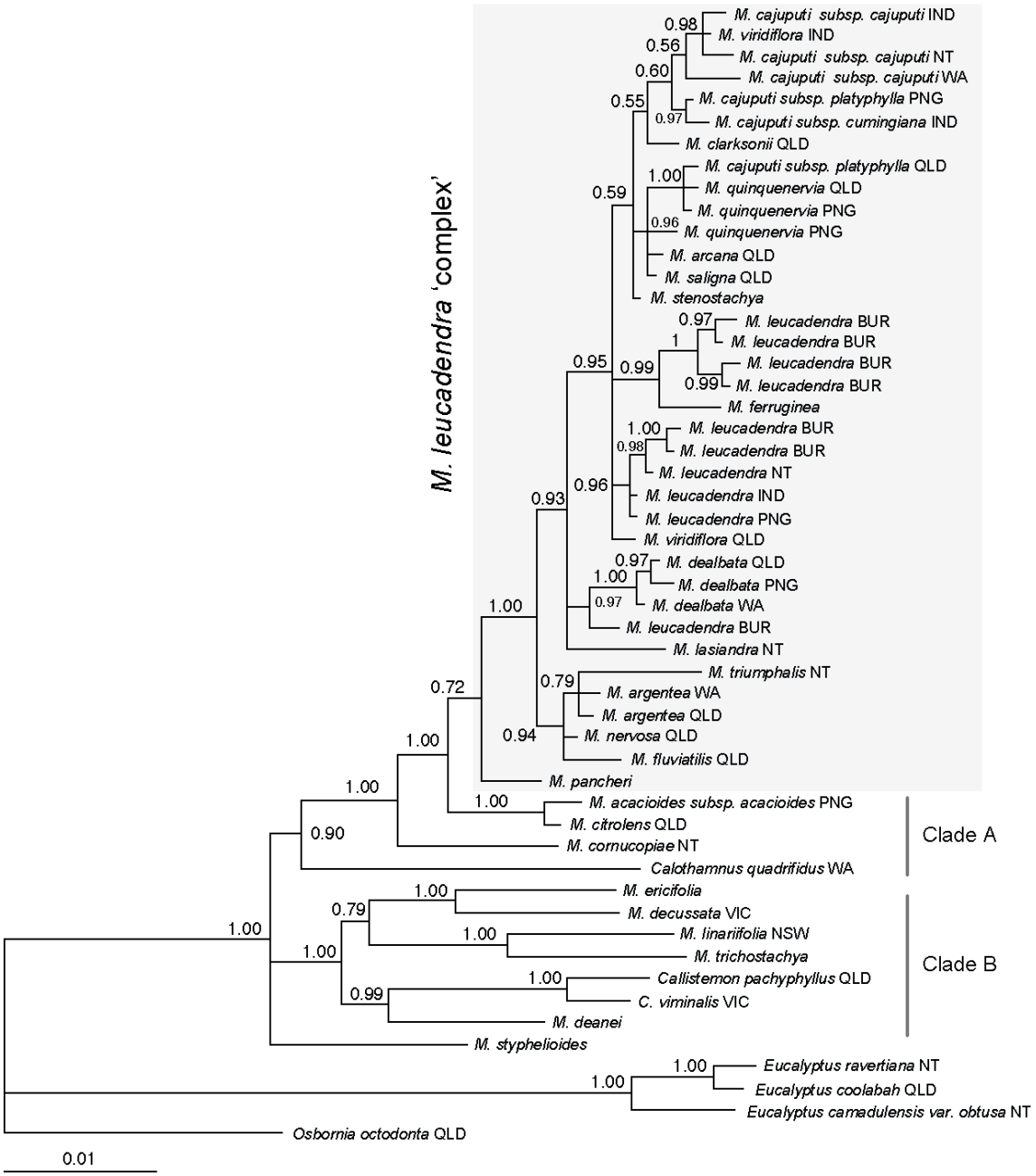


Figure 6.5. 50% majority rule consensus tree inferred from Bayesian analysis of the combined data set using the 'best-fit' partitioning strategy ITS1, ITS2 (SYMG), *trnL* (GTR), *rpL*16 (GTRG) as assessed on AIC_c and Bayes factor model comparisons.

Chapter 7—General discussion

Research synthesis

In this thesis I have explored the processes underlying plant persistence in a disturbance-driven lowland river system by investigating the ecology and genetic structure of a dominant riverine tree, *Melaleuca leucadendra,* at several scales. Using experimental and molecular approaches, I was able to make scale-explicit inferences regarding growth, survival and dispersal. I showed that clonal growth generated strong genotypic structure at a discrete spatial scale. This clonal growth mechanism is associated with dense aggregations of stems within groves of adult trees as well as high genotypic variation among individuals. An increased incidence of the clonal habit was observed in mainstream sites when compared to headwater sites, a finding consistent with these locations experiencing significantly greater hydrological disturbances (Chapter 4). Therefore, it is likely that disturbance promotes the clonal habit. Strong epicormic resprouting ability was also shown in *M. leucadendra* seedlings independent of seed genotype pool (Chapter 3). Resprouting ability was displayed in seedlings as young as five days after germination. Resprouting capacity in *M. leucadendra* was also disproportionate to plant size and growth rate from seed to seedling stages compared with co-occurring Myrtaceous riparian species, indicating that selection for resprouting is explained by factors other than resource foraging and utilisation, since resource distribution at scales relevant to seedlings is likely to be similar among species. Thus, reiterative stem growth plays a prominent role in the life history of *M. leucadendra* at both seedling and adult stages.

Selective forces that act on genetic diversity differ at individual and population levels. Clonal genotypes were detected at spatial scales less than 20 m and were correlated with high-energy riverine environments (Chapter 4), indicating a potentially strong link between environmental perturbation and individual growth strategy. Within sampling locations, there was no evidence for spatial genetic structuring at distances greater than 20 m. Genetic variation among sampling locations was also unrelated to geographical distance among stems or individuals within locations (chapters 4 and 5). This indicates a high level of genetic intermixing by processes distinct from those that structure growth form and determining individual genotypes. The influence of fluvial action on gene flow was observed between the largest spatial structuring scales measured in this study, that of headwater versus mainstream locations.

Resprouting in woody plants is one trait, probably among many, that constitutes a generalised solution for survival in variable-disturbance environments, in which disturbance may include fire, wind and floods. For riparian species, hydrological disturbances may impose an intense filtering process on phenotypic responses which, in turn, may determine the distribution of genotypes. Genetic differentiation at population

and species levels depends upon the persistence of discrete genotype pools, and the extent that either populations or species can be differentiated will depend on connectivity among them. Thus, consideration of the mechanisms that restrict or promote gene flow are also required to interpret the influences of different scales of connectivity and trait selection.

Spatial genetic analyses based on allelic population assignment provided insight into the extent of recent gene flow. Strong genetic differentiation was detected between the individuals sampled from mainstream and headwater locations, indicating that historical disjunction may limit genetic connectivity between these stream regions. However, admixture among mainstream populations was high even though they were located up to 160 km apart, demonstrating genetic and contemporary stream connectivity. In contrast, in samples from two headwater populations there were distinct allelic signatures with low probability estimates for genetic exchange between them. These patterns of genetic exchangeability were consistent with the absence of spatial genetic structure as assessed at a local scale (within 600 m), suggesting that processes maintain a disequilibrium genetic state and gene flow (Chapter 5).

For the *M. leucadendra* species group as a whole, it seems unlikely that individual species concepts will adequately explain relationships between currently circumscribed taxa. For example, I showed signals of reticulate branching patterns among congeners in the species group (Chapter 6). These findings support a lack of discrete genetic boundaries among taxa and imply recent or on-going gene flow and/or introgression.

Here I synthesise the information generated on the genotypic and phenotypic variation in *M. leucadendra* in the context of the hydrological regime. I use this synthesis to examine the processes that link survival, dispersal, and genetic structure in riverine woody species, and to develop and present ideas for new research pathways in riparian plant ecology.

Adaptive phenotypes in disturbance-driven river systems

Australian riverine environments are dominated by members of the genera *Melaleuca* and *Eucalyptus*. The prevalence of these genera in such disturbance-driven systems indicates a suite of phenotypic traits adapted to the prevailing environmental conditions which, in this study, is the flood-driven hydrological regime (i.e. Chapter 4). As resprouting has been observed as a generalist adaptive strategy among species occupying disturbance-prone niches, I tested the potential for different life stages to be adapted to a resprouting response. Using a cross-species experimental approach to compare differences in seedling resprouting capacity, I showed that resprouting is a prominent trait in *Melaleuca leucadendra* and *Eucalyptus camaldulensis* from the earliest post-cotyledon developmental stage (Chapter 3). In addition, resprouting appears uncoupled from resource allocation traits such as seed size and growth rate. This implies strong selection for the capacity to recover from physical damage at the

earliest life stages. This combination of traits is reflected by a broad spectrum of phenotypes that is a conspicuous feature of taxa in the Myrtaceae family. These Myrtaceous genera posses a combination of physiological and reproductive characteristics that support their ability to respond to stochastic and disturbance-prone environments (Chapter 2) and is indicative of bet hedging. In addition, typically predicted allometric relationships of seed size with adult phenotypes such as large size (habit) and longevity do not hold. Thus *Melaleuca leucadendra* may be seen as an outlier in functional trait space: the species occupies a particularly high-stress niche that lies well outside the predictable trait envelopes in proposed plant ecological strategy schemes (e.g. Westoby, 1998).

Connectivity and structure in river systems

Differences in the shape and predictability of stream flow distributions may generate differences in genetic structure and connectivity even at the within-river system scale. Large inter-annual and inter-season variation in flood patterns in the upper Burdekin catchment were detected in the 30-year data set analysed (Chapter 4), consistent with prior knowledge of Burdekin River discharges (Alexander et al., 1999b; Pringle, 2000). A feature of this variability is that floods are large and spatially heterogeneous, but unpredictable at the within-river scale, and cause continuous changes in channel geomorphology and habitat structure within the confines of the highly incised banks of the river (Alexander et al. 2000). Furthermore, parameters describing flood intensity (scale and location) and likelihood (shape) both differed between mainstream and headwater sites, revealing that flood predictability differs even at the within-sub-catchment scale.

The differences in flow regime assessed using flood-event modelling (Chapter 4) corresponded to an order-of-magnitude difference in flood energy between mainstream and headwater catchments. The probability of genetic connectivity among sampled locations, inferred using assignment methods and non-equilibrium models for genetic structure and gene flow (Chapter 5), was correlated with differences in flood energy among locations. Strong evidence for admixture was detected among mainstream locations whereas there was little evidence for genetic connectivity between mainstream and headwater locations—or between headwater locations. These different degrees of recurrent landscape-scale genetic exchange occur among locations that are fluvially connected, independent of geographic location. Together, these results imply that gene flow rather than persistent selection for genotypes governs gene pool dynamics at population scales and beyond.

Classical metapopulation theory predicts that dispersal and disturbance-driven population extinction can alter the genetic structure among populations and species (Husband and Barrett, 1996; Hanski, 2001; Tero et al., 2003). For example, in a riverine system, stream flow will result in a unidirectional gradient in genetic diversity along rivers. In turn, rare, catastrophic disturbance events are predicted to re-set the structure

and interactions of genotype pools. Consider that a conventional approach assumes that the form of the probability distribution being modelled for survival or dispersal in a dynamic population system results in a fit dominated by the majority of the observations. The lower and upper tails (or extremes) of the distribution need to be accommodated as they are likely to have a significant influence on population structure (Katz et al., 2005). However, our ability to quantify the tails of distributions are limited by our ability to build models that provide adequate prediction of abiotic events that have persistent effects on the physiological or developmental responses of the organism (or population). In effect, the tails of environmental driver distributions have a disproportionally large influence on overall survivorship and are the scales selection operates on. Thus, in ecological theory, events-based analyses would enable more accurate assessment of persistent organismal traits able to cope with the conditions in operation.

An events-based framework may be used to predict and compare the effects of climate-driven stream flow on plant survivorship within and between river systems. The distribution of flow events is erratic and generates three-dimensional effects on landscape connectivity. For example, in the Upper Burdekin River, disturbance generates non-reversible changes in channel structure with every successive flood, and these changes vary between river reaches (Alexander et al., 1999b). This pattern of continuous landscape shifts characterises large semi-arid and lowland systems in which the geomorphic linkages between river bed, banks, floodplain and tributary streams generate a mosaic of continuously changing environmental states. The linkage between the structure of the physical landscape and gene flow means that probabilities of individual plant survival and gene flow are unpredictable.

Species evolutionary interactions in river systems

My results imply that vegetative and sexual reproductive mechanisms both play important roles in the overall life history of *M. leucadendra*. The effects of these mechanisms have distinct spatio-temporal signatures. Resprouting as a clonal growth mechanism influences genetic structure principally through stem aggregation and genet persistence. High genotypic richness, independent of levels of clonality, implies that genetic variation is maintained by gene flow processes rather than the ecological interactions (growth, competition, reproduction) among neighbouring clonal genotypes. These findings support the theory that ecological factors such as disturbance moderate the effects of resprouting at the macroevolutionary scale (Bond and Midgley, 2003). This could explain why resprouting, although conferring fitness advantages, appears as an evolutionarily labile and widespread phenomenon that does not correlate directly to phylogenetic patterns of speciation or relatedness among congeners (Chapter 6). Resprouting reflects a generalised biological solution allowing persistence and colonisation across a broad range of environmental perturbations.

A corollary of this conclusion is that resprouting capacity probably reflects the physiological ability to tolerate high-stress conditions. Resprouting is indeed common, occurs in numerous plant growth forms, and across taxa that exist in diverse disturbance-driven systems (chapters 3 and 4). Therefore, the observable effects of disturbance could be expected to differ depending on the scale of observation. At the between-habitat level (beta trait variation), disturbance acts to group together taxa with similar physiological tolerance profiles, maintaining ecologically similar but phenotypically diverse species groups; at the within-habitat level (alpha trait variation), disturbance intensity may determine individual species occurrences corresponding to niche differentiation, and may even filter among the phenotype and genotype pools within a species, giving rise to population genetic structuring.

My results suggest that the filtering effects of disturbance act strongly at within-habitat scales, as reflected in niche specialisation in the study river system. Flow variability also acts as a dispersal vector, and therefore influences the likelihood of effective long distance dispersal (Nathan, 2006). Sampling in seven locations revealed two discrete allelic signatures that correlated to differences in catchment capacity rather than to the spatial distance between sampled individuals. These results suggest that gene flow is spatially extensive. The high overall level of allelic richness, independent of gene flow rates between populations, implies that stream flow processes influence the rates of genetic and ecological exchangeability.

Stochastic shifts in environmental states is a potential mechanism explaining the complex evolutionary trends detected in the *M. leucadendra* species group. The spatial genetic structure and labile biological characters of *M. leucadendra* imply that environmental variability, including natural disturbances, may act as a within-habitat filter of phenotypic selection. For example, differences in the expression of resprouting ability were detected at both genotypic (Chapter 4) and species levels (Chapter 3), suggesting that selective effects on population-level genotypic signatures have a persistent genetic basis, which could help explain within-habitat niche dominance in this taxon. The river flow regime could also shape contemporary gene flow processes (dispersal), contributing to complex phylogenetic signals. Within the study system, discrete allelic clusters were detected at the within-river system scale corresponding to differences among individuals from headwater and mainstream areas (chapters 4 and 5). These results imply that connectivity in this river system is spatio-temporally dynamic and has included periods of historical habitat discontinuity, leading to evolutionary differentiation as evidenced at the among-population scale (Chapter 5). In comparison, rates of potential gene flow and overall genotypic richness were high across *M. leucadendra* allelic populations (chapters 4 and 5), suggesting maintained evolutionary opportunities for genetic exchange. Thus, stochastic processes including the flow regime could generate cryptic population- and species-level genetic structure, as reflected in the heterogeneous phylogenetic clustering signal in the *M. leucadendra* species complex (Chapter 6).

These explanations are consistent with the apparently complex and poorly-resolved phylogenetic signals within and among Myrtaceous lineages and other southern hemisphere floras that inhabit dynamic physical landscapes (e.g. Sytsma et al., 2004). In these groups, selective demand for diverse life-history solutions for survival is reflected in high phenotypic variance within and among taxa in the same environment (variation at the within-habitat, or alpha level) (cf. Bond and Midgley, 2003; Pausas et al., 2004). These selective processes have a grouping effect when viewed at the habitat (i.e., beta) scale (sensu Silvertown et al., 2006; Ackerly and Cornwell, 2007), causing taxa to appear as phenotypically diverse, ecologically sympatric units in the riparian environment. Interplay between disturbance and plant vital processes can thereby result in stochastic shifts in population-level genetic structure and connectivity that could continuously re-shape species' evolutionary trajectories, as reflected in complex mosaic patterns of species phylogenetic relatedness.

Taken together, this evidence implies that environmental processes strongly shape functional ecology and evolution in the *M. leucadendra* species group, the members of which are sympatric in riparian habitats. Under this scenario, the rate of speciation under convergent selection for functional traits is expected to be strongly moderated by environmental forces (cf. Widmer 2002) whereas genetic variation at sub-species levels is promoted by mechanisms that generate dynamic gene flow processes. These processes could contribute to high phenotypic variance as expressed in *M. leucadendra*.

Proposal for specific research directions

Addressing population and species concepts

An important research objective arising from this thesis is the need to develop a strategy to quantify the interchangeability of plant species. Such an approach will require integration of information on genetic structure and changing environmental states. One primary step is to quantify differences in trait variation among co-occurring genotypes, phenotypes and taxa that are recognised as close relatives. Decomposing trait values into alpha and beta components is clearly needed, because this approach quantifies the deviance of a taxon's trait value relative to that of co-occurring taxa (Ackerly & Cornwell 2007), and provides a common environmental context applicable to comparisons between genotypes as well as between species. In the context of disturbance-driven riparian systems, this approach could help categorise the strength of traits, such as resprouting, as determinants of niche separation between genotypes or species, which may ultimately explain geographic distributions within this biogeographic zone.

This approach requires the responses of suites of potentially correlated plant traits to be mapped in association with prevailing environmental conditions. It may also be extended to predictions of future environmental (disturbance) scenarios. Given the results presented here, I propose that use of hydrological threshold values derived from

flood events analysis (Chapter 4; Coles and Tawn, 1996; Katz et al., 2002) is a likely important axis along which to parameterise the niche space of riparian species in trait decomposition analyses. Threshold values represent tolerances to environmental disturbance (Silvertown et al., 1999). The resolution of threshold models relative to biological response could then be reiteratively updated using information from empirical research. Such an approach has already been suggested for studying long-distance dispersal (e.g. Nathan, 2005).

In turn, trait data can be overlaid on a population-level phylogenetic network to test hypotheses of phenotypic variation and ecological overlap among taxa (Crandall et al., 2000). This analysis is relevant at genotypic as well as species levels because it is at intra-species scales that heritable trait evolution may contribute phenotypic effects and speciation (Chapter 6; Whitham et al., 2003). Finally, generating consensus split-networks models will help accommodate multiple parallel, but not necessarily bifurcating, phylogenetic relationships between closely related taxa (Templeton, 2001; Huson and Bryant, 2006). Combining information from population genetic and phylogenetic analyses, using individuals across the species complex, will help identify the distribution of ecologically adaptive characters in an evolutionary framework.

General conclusions

The results of this thesis suggest the existence of generalised solutions to survive environmental variability within the riparian habitat (chapters 3 and 4). This conclusion is reflected in the diverse phenotypes displayed among sympatric riparian species (e.g., Chapter 2). This notion suggests that in riverine environments, the filtering effects of fluvial disturbance promote sustained ecological adaptive capacity and species persistence. Fluvial action also promotes gene flow via seed dispersal, providing a mechanism that maintains diverse and large gene pools (Chapter 5). However, climate-driven fluvial processes are spatially and temporally unpredictable and may generate stochastic patterns in genetic connectivity between local populations across large spatial extents. Thus, the riverine habitat represents a complex but ideal system in which to examine questions of genetic and ecological exchangeability and investigate concepts of the structure of biological units.

The riparian system studied here provides an example of how extremely variable physical and biological phenomena interact. Species success is explained by vital plant processes (e.g., dispersal, survival, regeneration, and gene flow). Conventional approaches to measuring these processes include tracking the movement of dispersed seeds or predicting changes by modelling population demography. These approaches can capture only some of the variability associated with population dynamics because the typical observation period (years) is short relative to individual plant lifetimes and is unlikely to capture extreme, but infrequent disturbance events that impose the selective conditions that determine population and genetic structure. The distribution of

disturbances, including variability in both inter-peak intervals and peak events, affect both individual plant survivorship and long-distance dispersal, generating feedback between the environment, biological traits, and genetic relatedness. Process-based models that examine within-habitat differences in the shapes of biological tolerance and trait frequency distributions under environmental conditions, such as extreme-value analysis incorporating flood and long-distance dispersal events, offer the potential for new insights into the spatial and temporal scales over which these processes interact.

Research conclusions

In this thesis I have developed the argument that a multi-scale research framework is needed to interpret the phenotypic diversity (ecological response) and the genetic consequences of such variability (genotypic relatedness) in *M. leucadendra* in the context of the environment in which they exist.

Resprouting represents a growth mechanism that may directly influence genet survivorship under extreme disturbance. This research revealed that resprouting capacity is a fundamental species trait and is evident both at seedling and adult life stages. Resprouting in seedlings is common in many riparian species and I found evidence for expression of this trait in *M. leucadendra* and *E. camaldulensis* at seedling and mature life stages (chapters 3 and 4). I also found that adult trees of *M. leucadendra* in high disturbance areas showed greater incidence of resprouting than in lower disturbance areas. These findings suggest that the expression of the multi-stemmed habit is variable within *M. leucadendra*, but may contribute to survival during both recruitment and persistence phases. For example, in *M. leucadendra*, as well as in northern latitude riparian tree species such as *Populus tremuloides* and *P. tremula*, resprouting as a clonal growth mechanism may reflect an adaptation that promotes resource acquisition and growth during long intervals between hydrological disturbances, as well as survival of high-force disturbances. The capability to resprout may thus contribute to numerical dominance of *M. leucadendra* in mainstream sites in the Burdekin catchment that experience high-energy yet erratic disturbance. Analyses of demographic and morphological structure in *M. leucadendra* at multiple locations that differ in fluvial dynamics will complement the genotypic studies presented in this thesis, and will help determine the generality of the prospective association between increasing resprouting and fluvial disturbance.

My findings imply that differences in resprouting frequencies between locations are associated with differences in allelic signatures at the within-river scale, and both are related to disturbance signature (Chapter 4). Nevertheless, the stochastic and severe nature of ecological disturbance, experienced within the life-spans of individual trees, could help explain the level of connectivity between populations separated by large distances. In *M. leucadendra*, gene flow was evident between mainstream sites, which may sustain high genetic exchangeability among allelic populations. Studying spatial

genetic structure and contemporary gene flow beyond the ecological neighbourhood scale, here greater than 500 m (chapters 4 and 5), revealed that gene flow processes that underlie genetic variation do exist.

The pattern of stream flow in large semi-arid rivers is an exemplar of heavy-tailed phenomena that reflect hydrological and geomorphic variability within catchments, and at seasonal, annual and decadel timescales. I have shown that these effects potentially interact with demographic and genetic processes because they act as agents of extreme disturbance and dispersal. Disturbances are recurrent, impacting on genet survival and generating environmental disequilibrium. Moreover, the findings from this thesis suggest that spatial genotypic structure interacts with disturbance signature at the within-habitat scale. This implies that flow mechanisms could directly moderate the genetic architecture and maintenance of adaptive traits. These interactions could play key roles in explaining the spatial and temporal distributions of ecological specialisation and the potential for sympatric speciation (Widmer, 2002). Phylogenetic hypotheses generated in this thesis (Chapter 6) suggest that the species complex represents an evolutionarily and functionally congruent unit. Gene flow and hybridisation between taxa within the complex appears high, indicating that genotypic variability among interacting demes is common.

The research presented here utilised an events-based approach (extreme-value statistical theory) as a method to explore environmental variability. Many biological and environmental processes, such as dispersal and disturbance, reflect multi-modal distributions in which infrequent, but large-magnitude events exert disproportionate influence on survivorship, dispersal and genetic variation. In turn, phylogenetic models infer gene-level mechanisms and processes underlying evolutionary character change and genetic differentiation, and this strongly dictates our inferences on conceptual and operational biological units. These scale-dependent distributions are not adequately explained by existing spatial biology or genetic models alone. Applying information on ecological trait and spatial genetic variation, integrated with physical disturbance profiles, onto phylogenetic frameworks will allow deeper insights into the evolution of species' phenotypic and genotypic signatures.

The data I present here imply that high levels of genotypic and phenotypic variability in *Melaleuca leucadendra* are fundamental to the continued persistence of this species in this environment. *Melaleuca* persists in the riparian ecotone and as the dominant riverine taxon of the Australian dry tropics. Within the *M. leucadendra* complex, there seems to be little evidence for long-term isolation among member taxa. Varying environmental conditions likely influence patterns of genotypic shifts and gene flow, damping the probability of detecting evolutionary differentiation among species as circumscribed by phenotypic characters. Thus functional richness and reticulate phylogenetic associations in *Melaleuca leucadendra* result from dynamic ecological and genetic exchange in the riverine environment.

References

ABERNETHY, B. & RUTHERFURD, I. D. (2001) The distribution and strength of riparian tree roots in relation to riverbank reinforcement. *Hydrological Processes,* 15**,** 63-79.

ACKERLY, D. D. & CORNWELL, W. K. (2007) A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecology Letters,* 10**,** 135 - 145.

ALEXANDER, J., FIELDING, C. R. & JENKINS, G. (1999a) Plant-material deposition in the tropical Burdekin River, Australia: implications for ancient fluvial sediments. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 153**,** 105-125.

ALEXANDER, J., FIELDING, C. R. & POCOCK, G. D. (1999b) Flood behaviour of the Burdekin River, tropical north Queensland, Australia. IN MARRIOT, S. B. & ALEXANDER, J. (Eds.) *Floodplains: interdisciplinary approaches*. London, The Geological Society of London.

ALFARO, M. E. & HUELSENBECK, J. P. (2006) Comparative performance of Bayesian and AIC-based measures of phylogenetic model uncertainty. *Systematic Biology,* 55**,** 89-96.

ALVAREZ, I. & WENDEL, J. F. (2003) Ribosomal ITS sequences and plant phylogenetic inference. *Molecular Phylogenetics and Evolution,* 29**,** 417-434.

ARENS, P., COOPS, H., JANSEN, J. & VOSMAN, B. (1998) Molecular genetic analysis of black poplar (*Populus nigra* L.) along Dutch rivers. *Molecular Ecology,* 7**,** 11-18.

ARMSTRONG, D. P. & WESTOBY, M. (1993) Seedlings from large seeds tolerate defoliation better: a test using phylogenetically independent contrasts. *Ecology,* 74**,** 1092-1100.

ARNAUD-HAOND, S., ALBERTO, F., TEIXEIRA, S., PROCACCINI, G., SERRAO, E. A. & DUARTE, C. M. (2005) Assessing genetic diversity in clonal organisms: Low diversity or low resolution? Combining power and cost efficiency in selecting markers. *Journal of Heredity,* 96**,** 434-440.

ARONNE, G. & DE MICCO, V. (2004) Hypocotyl features of *Myrtus communis* (Myrtaceae): a many-sided strategy for possible enhancement of seedling establishment in the Mediterranean environment. *Botanical Journal of the Linnean Society,* 145**,** 195-202.

BACLES, C. F. E., LOWE, A. J. & ENNOS, R. A. (2006) Effective seed dispersal across a fragmented landscape. *Science,* 311**,** 628.

BARLOW, B. A. (1986) Contributions to a revision of *Melaleuca* (Myrtaceae): 1-3. *Brunonia,* 9**,** 163-177.

BARLOW, B. A. (1988) Patterns of differentiation in tropical species of *Melaleuca* L. (Myrtaceae). *Proceedings of the Ecological Society of Australia,* 15**,** 239-247.

BARLOW, B. A. & FORRESTER, J. (1984) Variation in indumentum morphology in the *Melaleuca leucadendra* complex (Myrtaceae). *Brunonia,* 7**,** 277-288.

BARSOUM, N. (2002) Relative contributions of sexual and asexual regeneration strategies in *Populus nigra* and *Salix alba* during the first years of establishment on a braided gravel bed river. *Evolutionary Ecology,* 15**,** 255-279.

BARSOUM, N., MULLER, E. & SKOT, L. (2004) Variations in levels of clonality among *Populus nigra* L. stands of different ages. *Evolutionary Ecology,* 18**,** 601-624.

BEARDSELL, D. V., O'BRIEN, S. P., WILLIAMS, E. G., KNOX, R. B. & CALDER, D. M. (1993) Reproductive biology of the Australian Myrtaceae. *Australian Journal of Botany,* 41**,** 511-526.

BEHRENS, C. N., LOPES, H. F. & GAMERMAN, D. (2004) Bayesian analysis of extreme events with threshold estimation. *Statistical Modelling,* 4**,** 227-244.

BELL, D. T. (1999) Australian trees for the rehabilitation of waterlogged and salinity-damaged landscapes. *Australian Journal of Botany,* 47**,** 697-716.

BELLINGHAM, P. J. & SPARROW, A. D. (2000) Resprouting as a life history strategy in woody plant communities. *Oikos,* 89**,** 409-416.

BENDIX, J. & HUPP, C. R. (2000) Hydrological and geomorphological impacts on riparian plant communities. *Hydrological Processes,* 14**,** 2977-2990.

BENTHAM, G. & MUELLER, F. (1866) Volume 3: Myrtaceae to Compositae. *Flora Australiensis: a description of the plants of the Australian Territory*. London, Lovell Reeve and Co.

BIFFIN, E., HARRINGTON, M. G., CRISP, M. D., CRAVEN, L. A. & GADEK, P. A. (2007) Structural partitioning, paired-sites models and evolution of the ITS transcript in *Syzygium* and Myrtaceae. *Molecular Phylogenetics and Evolution,* 43**,** 124-139.

BLAKE, S. T. (1968) A revision of *Melaleuca leucadendron* and its allies (Myrtaceae). *Contributions from the Queensland Herbarium,* 1**,** 1-114.

BOEGE, K. & MARQUIS, R. J. (2005) Facing herbivory as you grow up: the ontogeny of resistance in plants. *Trends in Ecology and Evolution,* 20**,** 441-448.

BOND, W. J. & MIDGLEY, J. J. (2001) Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology and Evolution,* 16**,** 45-51.

BOND, W. J. & MIDGLEY, J. J. (2003) The evolutionary ecology of sprouting in woody plants. *International Journal of Plant Sciences,* 164**,** S103-S114.

BORCARD, D., LEGENDRE, P. & DRAPEAU, P. (1992) Partialling out the spatial component of ecological variation. *Ecology,* 73**,** 1045-1055.

BRANDLEY, M. C., SCHMITZ, A. & REEDER, T. W. (2005) Partitioned Bayesian analyses, partition choice, and the phylogenetic relationships of scinid lizards. *Systematic Biology,* 54**,** 373-390.

BROWN, G. K., UDOVICIC, F. & LADIGES, P. Y. (2001) Molecular phylogeny and biogeography of *Melaleuca*, *Callistemon* and related genera (Myrtaceae). *Australian Systematic Botany,* 14**,** 565-585.

BYRNES, N. B. (1984) A revision of *Melaleuca* L. (Myrtaceae) in northern and eastern Australia, I. *Austrobaileya,* 1**,** 65-76.

CAIN, M. L., MILLIGAN, B. G. & STRAND, A. E. (2000) Long-distance seed dispersal in plant populations. *American Journal of Botany,* 87**,** 1217-1227.

CALDERÓN, I., ORTEGA, N., DURAN, S., BECERRO, M., PASCUAL, M. & TURON, X. (2007) Finding the relevant scale: clonality and genetic structure in a marine invertebrate (*Crambe crambe*, Porifera). *Molecular Ecology,* 16**,** 1799 - 1810.

CALLICOTT, J. B. (2002) Choosing appropriate temporal and spatial scales for ecological restoration. *Journal of Bioscience,* 27**,** 409-420.

CAMPBELL, G. S., BLACKWELL, P. G. & WOODWARD, F. I. (2002) Can landscape-scale characteristics be used to predict plant invasions along rivers? *Journal of Biogeography,* 29**,** 535-543.

CANADELL, J. & LOPEZ-SORIA, L. (1998) Lignotuber reserves support regrowth following clipping of two Mediterranean shrubs. *Functional Ecology,* 12**,** 31-38.

CASTOE, T. A., SASA, M. M. & PARKINSON, C. L. (2005) Modeling nucleotide evolution at the mesoscale: the phylogeny of the Neotropical pitvipers of the *Porthidium* group (Viperidae: Crotalinae). *Molecular Phylogenetics and Evolution,* 37**,** 881-898.

CELLOT, B., MOUILLOT, F. & HENRY, C. P. (1998) Flood drift and propagule bank of aquatic macrophytes in a riverine wetland. *Journal of Vegetation Science,* 9**,** 631-640.

CHARPENTIER, A. (2001) Consequences of clonal growth for plant mating. *Evolutionary Ecology,* 15**,** 521-530.

CHASE, M. W., COWAN, R. S., HOLLINGSWORTH, P. M., VAN DEN BERG, C., MADRINAN, S., PETERSEN, G., SEBERG, O., JORGSENSEN, T., CAMERON, K. M., CARINE, M., PEDERSEN, N., HEDDERSON, T. A. J., CONRAD, F., SALAZAR, G. A., RICHARDSON, J. E., HOLLINGSWORTH, M. L., BARRACLOUGH, T. G., KELLY, L. & WILKINSON, M. (2007) A proposal for a standardised protocol to barcode all land plants. *Taxon,* 56**,** 295-299.

CHAVES, M. M., MAROCO, J. P. & PEREIRA, J. S. (2003) Understanding plant responses to drought: from genes to the whole plant. *Functional Plant Biology,* 30**,** 239-264.

CHONG, C., EDWARDS, W. & WAYCOTT, M. (2007) Differences in resprouting ability are not related to seed size or seedling growth in four riparian woody species. *Journal of Ecology,* 95**,** 840-850.

COLES, S. G. & TAWN, J. A. (1996) A Bayesian analysis of extreme rainfall data. *Applied Statistics,* 45**,** 463 - 478.

CONDE, L. F., ROCKWOOD, D. L. & FISHER, R. F. (1981) Growth studies on *Melaleuca*. IN GEIGER, R. K. (Ed.) *Proceedings of Melaleuca Symposium*. Florida.

COOK, L. G., MORRIS, D. C., EDWARDS, R. D. & CRISP, M. D. (2008) Reticulate evolution in the natural range of the invasive wetland tree species *Melaleuca quinquenervia*. *Molecular Phylogenetics and Evolution,* 47**,** 506-522.

COOKE, B. D. (1987) The effects of rabbit grazing on regeneration of sheoaks, *Allocasuarina verticilliata* and saltwater ti-trees, *Melaleuca halmaturorum*, in the Coorong National Park, South Australia. *Australian Journal of Ecology,* 13**,** 11-20.

CORANDER, J., WALDMANN, P. & SILLANPAA, M. J. (2003) Bayesian analysis of genetic differentiation between populations. *Genetics,* 163**,** 367-374.

CORDES, L. D., HUGHES, F. M. R. & GETTY, M. (1997) Factors affecting the regeneration and distribution of riparian woodlands along a northern prairie river: the Red Deer River, Alberta, Canada. *Journal of Biogeography*, 24, 675-695.

CORNELISSEN, J. H. C., LAVOREL, S., GARNIER, E., DIAZ, S., BUCHMANN, N., GURVICH, D. E., REICH, P. B., TER STEEGE, H., MORGAN, H. D., VAN DER HEIJDEN, M. G. A., PAUSAS, J. G. & POORTER, H. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany,* 51**,** 335-380.

COSTA, J. E. & O'CONNOR, J. E. (1995) Geomorphically effective floods. IN COSTA, J. E., MILLER, A. J., POTTER, K. W. & WILCOCK, P. R. (Eds.) *Natural and anthropogenic influences in fluvial geomorphology: Geophysical Monograph 89*. Washington DC, American Geophysical Union.

CRANDALL, K. A., BININDA-EMONDS, O. R. P., MACE, G. M. & WAYNE, R. K. (2000) Considering evolutionary processes in conservation biology. *Trends in Ecology and Evolution,* 15**,** 290-295.

CRAVEN, L. (2006) New combinations in *Melaleuca* for Australian species of *Callistemon* (Myrtaceae). *Novon,* 16**,** 468-475.

CRAVEN, L. A. (1998) A result of the 1996 Mueller commemorative expedition to northwestern Australia: *Melaleuca triumphalis* sp. nov. (Myrtaceae). *Muelleria,* 11**,** 1-4.

CRAVEN, L. A. & BARLOW, B. A. (1997) New taxa and new combinations in *Melaleuca* (Myrtaceae). *Novon,* 7**,** 113-119.

CRAVEN, L. A. & LEPSCHI, B. J. (1999) Enumeration of the species and infraspecific taxa of *Melaleuca* (Myrtaceae) occurring in Australia and Tasmania. *Australian Systematic Botany,* 12**,** 819-927.

DALE, M. R. T. (1999) *Spatial pattern analysis in plant ecology,* Cambridge, Cambridge University Press.

DANVIND, M. & NILSSON, C. (1997) Seed floating ability and distribution of alpine plants along a northern Swedish river. *Journal of Vegetation Science,* 8**,** 271-276.

DAVIES, K. A. & GIBLIN-DAVIS, R. M. (2004) The biology and associations of *Fergusobia* (Nematoda) from the *Melaleuca leucadendra* complex in eastern Australia. *Invertebrate Systematics,* 18**,** 291-319.

DAWSON, J. W. (1992) *Flore de la Nouvelle-Calédonie et Dépendances.18: Myrtaceae - Leptospermoideae,* Paris, Muséum National d'Histoire Naturelle.

DE JONG, N. H. (2000) Woody plant restoration and natural regeneration in wet meadow at Coomonderry Swamp on the south coast of New South Wales. *Marine and Freshwater Research,* 51**,** 81-89.

DE RIJK, P. (1997) RnaViz. *.The University of Antwerp, Flanders, Belgium.*

DEILLER, A., WALTER, J. N. & TRÉMOLIÈRES, M. (2001) Effects of flood interruption on species richness, diversity and floristic composition of woody regeneration in the Upper Rhine alluvial hardwood forest. *Regulated Rivers: Research and Management,* 17**,** 393-405.

DEL TREDICI, P. (2001) Sprouting in temperate trees: a morphological and ecological review. *Botanical Review,* 67**,** 121-140.

DIAZ, S. & CABIDO, M. (2001) Vive la différénce: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution,* 15**,** 646-655.

DOUHOVNIKOFF, V., MCBRIDE, J. R. & DODD, R. S. (2005) *Salix exigua* clonal growth and population dynamics in relation to disturbance regime variation. *Ecology,* 86**,** 446-452.

DUNN, G. M., TAYLOR, D. W., NESTER, M. R. & BEETSON, T. B. (1994) Performance of twelve selected Australian tree species on a saline site in southeast Queensland. *Forest Ecology and Management,* 70**,** 255-264.

ECKERT, C. G., LUI, K., BRONSON, K., CORRADINI, P. & BRUNEAU, A. (2003) Population genetic consequences of extreme variation in sexual and clonal reproduction in an aquatic plant. *Molecular Ecology,* 12**,** 331-344.

EDWARDS, W. & GADEK, P. (2002) Multiple resprouting from diaspores and single cotyledons in the Australian tropical tree species *Idiospermum australiense*. *Journal of Tropical Ecology,* 18**,** 943-948.

ELPHINSTONE, M. S., HINTEN, G. N., ANDERSON, M. J. & HOCK, C. J. (2003) An inexpensive and high-throughput procedure to extract and purify total genomic DNA for use in population studies. *Molecular Ecology Notes,* 3**,** 317-320.

ENNOS, R. A. (2001) Inferences about spatial processes in plant populations from the analysis of molecular markers. IN SILVERTOWN, J. & ANTONOVICS, J. (Eds.) *Integrating Ecology and Evolution in a Spatial Context*. London, Blackwell Science Ltd.

EVANNO, G., REGNAUT, S. & GOUDET, J. (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular Ecology,* 14**,** 2611 - 2620.

EVERITT, B. L. (1968) Use of the cottonwood in an investigation of the recent history of a flood plain. *American Journal of Science*, 266, 417-439.

FALSTER, D. S., WARTON, D. I. & WRIGHT, I. J. (2003) (S)MATR: Standardised major axis tests and routines. Version 1.0. *http://www.bio.mq.edu.au/ecology/SMATR*.

FAUBET, P., WAPLES, R. S. & GAGGIOTTI, O. E. (2007) Evaluating the performance of a multilocus Bayesian method for the estimation of migration rates. *Molecular Ecology,* 16**,** 1149-1166.

FENSTER, C. B., VEKEMANS, X. & HARDY, O. J. (2003) Quantifying gene flow from spatial genetic structure data in a metapopulation of *Chamaecrista fasciculata* (Leguminosae). *Evolution,* 57**,** 995-1007.

FIELDING, C. R. & ALEXANDER, J. (1996) Sedimentology of the Upper Burdekin River of North Queensland, Australia - an example of a tropical, variable discharge river. *Terra Nova,* 8**,** 447-457.

FIELDING, C. R. & ALEXANDER, J. (2001) Fossil trees in ancient fluvial channel deposits: evidence of seasonal and longer-term climatic variability. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 170**,** 59-80.

FIELDING, C. R., ALEXANDER, J. & NEWMAN-SUTHERLAND, E. (1997) Preservation of *in situ*, arborescent vegetation and fluvial bar construction in the Burdekin River of North Queensland, Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 135**,** 123-144.

FISCHER, M. & VAN KLUENEN, M. (2002) On the evolution of clonal plant life histories. *Evolutionary Ecology,* 15**,** 565-582.

GAINES, S. D. & DENNY, M. W. (1993) The largest, smallest, highest, lowest, longest, and shortest: extremes in ecology. *Ecology,* 74**,** 1677-1692.

GARWOOD, N. C. (1996) Functional morphology of tropical tree seedlings. Chapter 3. IN SWAINE, M. D. (Ed.) *The ecology of tropical forest tree seedlings*. Paris, UNESCO.

GELMAN, A. & RUBIN, D. B. (1992) Inference from iterative simulation using multiple sequences. *Statistical Science,* 7**,** 457-511.

GILLELAND, E., KATZ, R. & YOUNG, G. (2004) extRemes: Extreme value toolkit. R package version 1.55. http://www.assessment.ucar.edu/toolkit/.

GOM, L. A. & ROOD, S. B. (1999a) Patterns of clonal occurrence in a mature cottonwood grove along the Oldman River, Alberta. *Canadian Journal of Botany,* 77**,** 1095-1105.

GOM, L. A. & ROOD, S. B. (1999b) The discrimination of cottonwood clones in a mature grove along the Oldman River in southern Alberta. *Canadian Journal of Botany,* 77**,** 1084-1094.

GOODSON, J. M., GURNELL, A. M., ANGOLD, P. G. & MORRISSEY, I. P. (2001) Riparian seed banks: structure, process and implications for riparian management. *Progress in Physical Geography,* 25**,** 301-325.

GOUDET, J. (2005) HIERFSTAT, a package for R to test and compute hierarchical *F*-statistics. *Molecular Ecology Notes,* 5**,** 184-186.

GREEN, P. T. & JUNIPER, P. A. (2004) Seed-seedling allometry in tropical rain forest trees: seed mass-related patterns of resource allocation and the 'reserve effect'. *Journal of Ecology,* 92**,** 397-408.

GUILLOT, G., ESTOUP, A., MORTIER, F. & COSSON, J. F. (2005) A spatial statistical model for landscape genetics. *Genetics,* 170**,** 1261-1280.

GURVICH, D. E., ENRICO, L. & CINGOLANI, A. M. (2005) Linking plant functional traits with post-fire sprouting vigour in woody species in central Argentina. *Austral Ecology,* 30**,** 789-796.

GUTSCHICK, V. P. & BASSIRIRAD, H. (2003) Extreme events as shaping physiology, ecology and evolution of plants: toward a unified definition and evaluation of their consequences. *New Phytologist,* 160**,** 21-42.

HALL, T. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series,* 41**,** 95-98.

HALL, T. (2001) BioEdit version 5.0.6., Department of Microbiology, North Carolina State University. Distributed by the author at http://www.mbio.ncsu.edu/BioEdit/bioedit.html.

HANSKI, I. (1999) Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. *Oikos,* 87**,** 209-219.

HANSKI, I. (2001) Spatially realistic models of metapopulation dynamics and their implications for ecological, genetic and evolutionary processes. IN SILVERTOWN, J. & ANTONOVICS, J. (Eds.) *Integrating ecology and evolution in a spatial context*. Oxford, Blackwell Science Ltd.

HANSSON, L., FAHRIG, L. & MERRIAM, G. (Eds.) (1995) *Mosaic landscapes and ecological processes,* Suffolk, Chapman & Hall.

HARDY, O. J., MAGGIA, L., BANDOU, E., BREYNE, P., CARON, H., CHEVALLIER, M. H., DOLIGEZ, A., DUTECH, C., KREMER, A., LATOUCHE-HALLE, C., TROISPOUX, V., VERON, V. & DEGEN, B. (2006) Fine-scale genetic structure and gene dispersal inferences in 10 Neotropical tree species. *Molecular Ecology,* 15**,** 559-571.

HARDY, O. J. & VEKEMANS, X. (1999) Isolation by distance in a continuous population: reconciliation between spatial autocorrelation analysis and population genetics models. *Heredity,* 83**,** 145-154.

HARDY, O. J. & VEKEMANS, X. (2002) SPAGeDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Molecular Ecology Notes,* 2**,** 618-620.

HARMS, K. E. & DALLING, J. W. (1997) Damage and herbivory tolerance through resprouting as an advantage of large seed size in tropical trees and lianas. *Journal of Tropical Ecology,* 13**,** 617-621.

HASTINGS, A., BYERS, J. E., CROOKS, J. A., CUDDINGTON, K., JONES, C. G., LAMBRINOS, J. G., TALLEY, T. S. & WILSON, W. G. (2007) Ecosystem engineering in space and time. *Ecology Letters,* 10**,** 153 - 164.

HILDREW, A. G. & TOWNSEND, C. R. (2007) Freshwater Biology - looking back, looking forward. *Freshwater Biology,* 52**,** 1863-1867.

HOFSTETTER, R. H. (1988) The current status of *Melaleuca quinquenervia* in Southern Florida. IN CENTER, T. D., DOREN, R. F. & HOFSTETTER, R. H. (Eds.) *Proceedings of the symposium on exotic pest plants*. University of Miami, Florida, United States Department of the Interior, National Park Service.

HONNAY, O., VERHAEGHE, W. & HERMY, M. (2001) Plant community assembly along dendritic networks of small forest streams. *Ecology,* 82**,** 1691-1702.

HOWE, H. F. & SMALLWOOD, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology & Systematics,* 13**,** 201-228.

HUELSENBECK, J. P., LARGET, B. & ALFARO, M. E. (2004) Bayesian phylogenetic model selection using reversible jump Markov Chain Monte Carlo. *Molecular Biology and Evolution,* 21**,** 1123-1133.

HUGHES, F. M. R. (1997) Floodplain biogeomorphology. *Progress in Physical Geography*, 21, 501-529.

HUGHES, F. M. R., ADAMS, W. M., MULLER, E., NILSSON, C., RICHARDS, K. S., BARSOUM, N., DECAMPS, H., FOUSSADIER, R., GIREL, J., GUILLOY, H., HAYES, A., JOHANSSON, M., LAMBS, L., PAUTOU, G., PEIRY, J.-L., PERROW, M., VAUTIER, F. & WINFIELD, M. (2001) The importance of different scale processes for the restoration of floodplain woodlands. *Regulated Rivers: Research and Management*, 17, 325-345.

HUSBAND, B. C. & BARRETT, S. C. H. (1996) A metapopulation perspective in plant population biology. *Journal of Ecology,* 84**,** 461-469.

HUSON, D. H. & BRYANT, D. (2006) Application of phylogenetic networks in evolutionary studies. *Molecular Biology and Evolution,* 23**,** 254-267.

HUTCHISON, D. W. & TEMPLETON, A. R. (1999) Correlation of pairwise genetic and geographic distance measures: inferring the relative influences of gene flow and drift on the distribution of genetic variability. *Evolution,* 53**,** 1898-1914.

IMBERT, E. & LEFÈVRE, F. (2003) Dispersal and gene flow of *Populus nigra* (Salicaceae) along a dynamic river system. *Journal of Ecology,* 91**,** 447-456.

IRESTEDT, M., FJELDSÅ, J., NYLANDER, J. A. A. & ERICSON, P. G. P. (2004) Phylogenetic relationships of typical antbirds (Thamnophilidae) and test of incongruence based on Bayes factors. *Evolutionary Biology,* 4**,** 23.

IWASA, Y. (2000) Dynamic optimization of plant growth. *Evolutionary Ecology Research,* 2**,** 437-455.

IYER, M., KOBE, R. K. & WALTERS, M. B. (2003) Carbon allocation in roots: To forage or for storage? *Ecological Society of America Annual Meeting Abstracts***,** 165.

JACKSON, R. B., POCKMAN, W. T. & HOFFMANN, W. A. (1999) Chapter 5. The structure and function of root systems. IN PUGNAIRE, F. I. & VALLADARES, F. (Eds.) *Handbook of functional plant ecology*. New York, Marcel Dekker Inc.

JAKALANIEMI, A., KAUPPI, A., PRAMILA, A. & VAHATAINI, K. (2004) Survival strategies of *Silene tatarica* (Caryophyllaceae) in riparian and ruderal habitats. *Canadian Journal of Botany,* 82**,** 491-502.

JENIK, J. (1994) Clonal growth in woody plants: a review. *Folia Geobotanica Phytotaxonimica,* 29**,** 291-306.

JENSEN, J. L., BOHONAK, A. J. & KELLEY, S. T. (2005) Isolation by distance, web service. *BMC Genetics,* 6:13.

JOHANSSON, M. E., NILSSON, C. & NILSSON, E. (1996) Do rivers function as corridors for plant dispersal? *Journal of Vegetation Science,* 7**,** 593-598.

JOHNSON, D. H. (1999) The insignificance of statistical significance testing. *Journal of Wildlife Management,* 63**,** 763-772.

JONES, C. G., LAWTON, J. H. & SHACHAK, M. (1994) Organisms as ecosystem engineers. *Oikos,* 69**,** 373 - 386.

JORDAN, W. C., COURTNEY, M. W. & NEIGEL, J. E. (1996) Low levels of intraspecific genetic variation at a rapidly evolving chloroplast DNA locus in North American duckweeds (Lemnaceae). *American Journal of Botany,* 83**,** 430-439.

JUNK, W. J., BAYLEY, P. B. & SPARKS, R. E. (1989) The flood pulse concept in river-floodplain systems. *Canadian Journal of Fisheries and Aquatic Sciences: Special Publications,* 106**,** 110-127.

KALINOWSKI, S. T. (2005) HP-RARE 1.0: a computer program for performing rarefaction on measures of allelic richness. *Molecular Ecology Notes,* 5**,** 187-189.

KARRENBERG, S., EDWARDS, P. J. & KOLLMANN, J. (2002) The life history of Salicaceae living in the active zone of floodplains. *Freshwater Biology,* 47**,** 733-748.

KASS, R. E. & RAFTERY, A. E. (1995) Bayes factors. *Journal of the American Statistical Association,* 90**,** 773-795.

KATZ, R. W., BRUSH, G. S. & PARLANGE, M. B. (2005) Statistics of extremes: modeling ecological disturbances. *Ecology,* 86**,** 1124 - 1134.

KATZ, R. W., PARLANGE, M. B. & NAVEAU, P. (2002) Statistics of extremes in hydrology. *Advances in Water Resources,* 25**,** 1287-1304.

KITAJIMA, K. (1996) Cotyledon functional morphology, patterns of seed reserve utilization and regeneration niches of tropical tree seedlings. Chapter 8. IN SWAINE, M. D. (Ed.) *The ecology of tropical forest tree seedlings*. Paris, UNESCO.

KITAJIMA, K. & FENNER, M. (2000) Ecology of seedling regeneration. IN FENNER, M. (Ed.) *Seeds: the ecology of regeneration in plant communities*. Oxon, CABI Publishing.

KNUDSEN, B. & HEIN, J. (2003) Pfold: RNA secondary structure prediction using stochastic context-free grammars. *Nucleic Acids Research* 31**,** 3423-3428.

KRANJCEC, J., J.M., M. & ROOD, S. B. (1998) The responses of three riparian cottonwood species to water table decline. *Forest Ecology and Management*, 110, 77-87.

KRESS, W. J., WURDACK, K. J., ZIMMER, E. A., WEIGT, L. A. & JANZEN, D. H. (2005) Use of DNA barcodes to identify flowering plants. *Proceedings of the National Academy of Sciences of the United States of America,* 102**,** 8369-8374.

KUBITZKI, K. & ZIBURSKI, A. (1994) Seed dispersal in flood plain forests of Amazonia. *Biotropica,* 26**,** 30-43.

KUDOH, H. & WHIGHAM, D. F. (2001) A genetic analysis of hydrologically dispersed seeds of *Hibiscus moscheutos* (Malvaceae). *American Journal of Botany,* 88**,** 588-593.

LACEY, C. J. & JOHNSTON, R. D. (1990) Woody clumps and clumpwoods. *Australian Journal of Botany,* 38**,** 299-334.

LADIGES, P. Y. & FOORD, P. C. (1981) Salinity and waterlogging tolerance of some populations of *Melaleuca ericifolia* Smith. *Australian Journal of Ecology,* 6**,** 203-215.

LAMB, E. G. & CAHILL, J. F. (2006) Consequences of differing competitive abilities between juvenile and adult plants. *Oikos,* 112**,** 502-512.

LANDHAUSSER, S. M. & LIEFFERS, V. J. (2002) Leaf area renewal, root retention and carbohydrate reserves in a clonal tree species following above-ground disturbance. *Journal of Ecology,* 90**,** 658-665.

LAVOREL, S. & GARNIER, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology,* 16**,** 545-556.

LAW, B., MACKOWSKI, C., SCHOER, L. & TWEEDIE, T. (2000) Flowering phenology of Myrtaceous trees and their relation to climatic, environmental and disturbance variables in northern New South Wales. *Austral Ecology,* 25**,** 160-178.

LEGENDRE, P. (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology,* 74**,** 1659-1673.

LEGENDRE, P., DALE, M. R. T., FORTIN, M.-J., GUREVITCH, J., HOHN, M. & MYERS, D. (2002) The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography,* 25**,** 601-615.

LEGENDRE, P. & FORTIN, M.-J. (1989) Spatial pattern and ecological analysis. *Vegetatio,* 80**,** 107-138.

LEHTILÄ, K. (1999) Chapter 10. Impact of herbivore tolerance and resistance on plant life histories. IN VUORISALO, T. O. & MUTIKAINEN, P. K. (Eds.) *Life history evolution in plants*. the Netherlands, Kluwer Academic Publishers.

LEISHMAN, M. R. & WESTOBY, M. (1994) The role of large seed size in shaded conditions: experimental evidence. *Functional Ecology,* 8**,** 205-214.

LEVIN, S. A. (1992) The problem of pattern and scale in ecology. *Ecology,* 73**,** 1943-1967.

LICHSTEIN, J. W., SIMONS, T. R., SHRINER, S. A. & FRANZREB, K. E. (2002) Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs,* 72**,** 445-463.

LIU, J. S. & SCHARDL, C. L. (1994) A conserved sequence in internal transcribed spacer 1 of plant nuclear rRNA genes. *Plant Molecular Biology,* 26**,** 775-778.

LLORET, F., ESTEVAN, H., VAYREDA, J. & TERRADAS, J. (2005) Fire regenerative syndromes of forest woody species across fire and climatic gradients. *Oecologia,* 146**,** 461-468.

LOCKHART, C. (1996) Aquatic heterophylly as a survival strategy in *Melaleuca quinquenervia* (Myrtaceae). *Canadian Journal of Botany,* 74**,** 243-246.

LOCKHART, C., AUSTIN, D. F. & AUMEN, N. G. (1999) Water level effects on growth of *Melaleuca* seedlings from Lake Okeechobee (Florida, USA) littoral zone. *Environmental Management,* 23**,** 507-518.

LOISELLE, B. A., SORK, V. L., NASON, J. & GRAHAM, C. (1995) Spatial genetic structure of a tropical understory shrub, *Psychotria officinalis* (Rubiaceae). *American Journal of Botany,* 82**,** 1420-1425.

LUNDQVIST, E. & ANDERSSON, E. (2001) Genetic diversity in populations of plants with different breeding and dispersal strategies in a free-flowing boreal river system. *Hereditas,* 135**,** 75-83.

MAHONEY, J. M. & ROOD, S. B. (1998) Streamflow requirements for cottonwood seedling recruitment: an integrative model. *Wetlands,* 8**,** 634-645.

MALANSON, G. P. (1993) *Riparian landscapes,* Cambridge, Cambridge University Press.

MANEL, S., SCHWARTZ, M. K., LUIKART, G. & TABERLET, P. (2003) Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology and Evolution,* 18**,** 189-197.

MATHEWS, D. H., DISNEY, M. D., CHILDS, J. L., SCHROEDER, S. J., ZUKER, M. & TURNER, D. H. (2004) Incorporating chemical modification constraints into a dynamic programming algorithm for prediction of RNA secondary structure. . *Proceedings of the National Academy of Sciences USA,* 101**,** 7287-7292.

MAYOL, M. & ROSSELLO, J. A. (2001) Why nuclear ribosomal DNA spacers (ITS) tell different stories in *Quercus*. *Molecular Phylogenetics and Evolution,* 19**,** 167-176.

MCLELLAN, A. J., PRATI, D., KALTZ, O. & SCHMID, B. (1997) Structure and analysis of phenotypic and genetic variation in clonal plants. IN DE KROON, H. & VAN GROENENDAEL, J. (Eds.) *The ecology and evolution of clonal plants*. Leiden, Springer-Verlag.

MELICK, D. R. (1990a) Flood resistance of *Tristaniopsis laurina* and *Acmena smithii* from riparian warm temperate rain-forest in Victoria. *Australian Journal of Botany,* 38**,** 371-381.

MELICK, D. R. (1990b) Regenerative succession of *Tristaniopsis laurina* and *Acmena smithii* in riparian warm temperate rain-forest in Victoria, in relation to light and nutrient regimes. *Australian Journal of Botany,* 38**,** 111-120.

MENSFORTH, L. J. & WALKER, G. R. (1996) Root dynamics of *Melaleuca halmaturorum* in response to fluctuating saline groundwater. *Plant and Soil,* 184**,** 75-84.

MERRITT, D. M. & WOHL, E. E. (2002) Processes governing hydrochory along rivers: hydraulics, hydrology, and dispersal phenology. *Ecological Applications,* 12**,** 1071-1087.

MISRA, R. K. & SANDS, R. (1992) A comparison of sap flux and water relations of leaves of various isolated trees with special reference to foundation movement in clay soil. *Plant and Soil,* 140**,** 269-278.

MISRA, R. K. & SANDS, R. (1993) Water extraction by isolated trees and its possible impact on building foundations on clay soils. *Australian Journal of Soil Research,* 31**,** 25-37.

MIWA, M., TANAKA, R., YAMANOSHITA, T., NORISADA, M., KOJIMA, K. & HOGETSU, T. (2001) Analysis of clonal structure of *Melaleuca cajuputi* (Myrtaceae) at a barren sandy site in Thailand using microsatellite polymorphism. *Trees,* 15**,** 242-248.

MOLES, A. T. & WESTOBY, M. (2006) Seed size and plant strategy across the whole life cycle. *Oikos,* 113**,** 91-105.

MORITZ, M. A. (1997) Analyzing extreme disturbance events: fire in the Los Padres National Forest. *Ecological Applications,* 7**,** 1252-1262.

MULLER, I., SCHMID, B. & WEINER, J. (2000) The effect of nutrient availability on biomass allocation patterns in 27 species of herbaceous plants. *Perspectives in Plant Ecology, Evolution and Systematics,* 3**,** 115-127.

MULLIGAN, D. R. & PATRICK, J. W. (1985) Carbon and phosphorus assimilation and deployment in *Eucalyptus pilularis* Smith seedlings with special reference to the role of cotyledons. *Australian Journal of Botany,* 33**,** 485-496.

MUTH, N. Z. & PIGLIUCCI, M. (2007) Implementation of a novel framework for assessing species plasticity in biological invasions: responses of *Centaurea* and *Crepis* to phosphorus and water availability. *Journal of Ecology*, 95, 1001-1013.

NATHAN, R. (2005) Long-distance dispersal research: building a network of yellow brick roads. *Diversity and Distributions,* 11**,** 125-130.

NATHAN, R. (2006) Long-distance dispersal of plants. *Science,* 313**,** 786-788.

NATHAN, R., SCHURR, F. M., SPEIGEL, O., STEINITZ, O., TRAKHTENBROT, A. & TSOAR, A. (2008) Mechanisms of long-distance seed dispersal. *Trends in Ecology and Evolution*, 23, 638-647.

NIKNAM, S. R. & MCCOMB, J. (2000) Salt tolerance screening of selected Australian woody species: a review. *Forest Ecology and Management,* 139**,** 1-19.

NILSSON, C., GARDFJELL, M. & GRELSSON, G. (1991) Importance of hydrochory in structuring plant communities along rivers. *Canadian Journal of Botany,* 69**,** 2631-2633.

NOLAND, T. L., MOHAMMED, G. H. & SCOTT, M. (1997) The independence of root growth potential on light level, photosynthetic rate, and root starch content in jack pine seedlings. *New Forests,* 13**,** 105-119.

NYLANDER, J. A. A. (2004a) MrAIC.pl. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.

NYLANDER, J. A. A. (2004b) MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.

NYLANDER, J. A. A., RONQUIST, F., HUELSENBECK, J. P. & NIEVES-ALDREY, J. L. (2004) Bayesian phylogenetic analysis of combined data. *Systematic Biology,* 53**,** 47-67.

ORLOVICH, D. A., DRINNAN, A. N. & LADIGES, P. Y. (1999) Floral development in *Melaleuca* and *Callistemon* (Myrtaceae). *Australian Systematic Botany,* 11**,** 689-710.

OUBORG, N. J., PIQUOT, Y. & VAN GROENENDAEL, J. (1999) Population genetics, molecular markers and the study of dispersal in plants. *Journal of Ecology,* 87**,** 551-568.

PABST, R. J. & SPIES, T. A. (2001) Ten years of vegetation succession on a debris-flow deposit in Oregon. *Journal of the American Water Resources Association,* 37**,** 1693-1708.

PACIOREK, C. J., CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. (2000) The demographics of resprouting in tree and shrub species of a moist tropical forest. *Journal of Ecology,* 88**,** 765-777.

PAN, J. J. & PRICE, J. S. (2002) Fitness and evolution in clonal plants: the impact of clonal growth. *Evolutionary Ecology,* 15**,** 583-600.

PANNELL, J. R. & CHARLESWORTH, B. (1999) Neutral genetic diversity in a metapopulation with recurrent local extinction and colonization. *Evolution,* 53**,** 664-676.

PARKS, J. C. & WERTH, C. R. (1993) A study of spatial features of clones in a population of bracken fern, *Pteridium aquilinum* (Dennstaedtiaceae). *American Journal of Botany,* 80**,** 537 - 544.

PARRIS, K. M. (2006) Urban amphibian assemblages as metacommunities. *Journal of Animal Ecology,* 75**,** 757-764.

PASCUAL, G., MOLINAS, M. & VERDAGUER, D. (2002) Comparative anatomical analysis of the cotyledonary region in three Mediterranean basin *Quercus* (Fagaceae). *American Journal of Botany,* 89**,** 383-392.

PATE, J. S., FROEND, R. H., BOWEN, B. J., HANSEN, A. & KUO, J. (1990) Seedling growth and storage characteristics of seeder and resprouter species of Mediterranean-type ecosystems of S.W. Australia. *Annals of Botany,* 65**,** 585-601.

PAUSAS, J. G., BRADSTOCK, R. A., KEITH, D. A., KEELEY, J. E. & GCTE (2004) Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology,* 85**,** 1085-1100.

PAZ, H. (2003) Root/shoot allocation and root architecture in seedlings: variation among forest sites, microhabitats, and ecological groups. *Biotropica,* 35**,** 318-332.

PEARSON, D. M. (2002) The application of local measures of spatial autocorrelation for describing pattern in north Australian landscapes. *Journal of Environmental Management,* 64**,** 85-95.

PETERSON, C. J. & JONES, R. H. (1997) Clonality in woody plants: a review and comparison with clonal herbs. IN DE KROON, H. & VAN GROENENDAEL, J. (Eds.) *The ecology and evolution of clonal plants*. Leiden, Backhuys Publishers.

PETTIT, N. E. & FROEND, R. H. (2001a) Availability of seed for recruitment of riparian vegetation: a comparison of a tropical and a temperate river ecosystem in Australia. *Australian Journal of Botany,* 49**,** 515-528.

PETTIT, N. E. & FROEND, R. H. (2001b) Variability in flood disturbance and the impact on riparian tree recruitment in two contrasting river systems. *Wetlands Ecology and Management,* 9**,** 13-25.

PETTIT, N. E., FROEND, R. H. & DAVIES, P. M. (2001) Identifying the natural flow regime and the relationship with riparian vegetation for two contrasting Western Australian rivers. *Regulated Rivers: Research and Management,* 17**,** 201-215.

PFENNINGER, M. (2002) Relationship between microspatial population genetic structure and habitat heterogeneity in *Pomatius elegans* (O.F. Müller 1774) (Caenogastropoda, Pomatiasidae). *Biological Journal of the Linnean Society,* 76**,** 565-575.

PICKETT, S. T. A. & OSTFELD, R. S. (1995) The shifting paradigm in ecology. IN KNIGHT, R. L. & BATES, S. F. (Eds.) *A new century for natural resources management*. Washington DC, Island Press.

PIERCE, S., LUZZARO, A., CACCIANIGA, M., CERIANI, R. M. & CERABOLINI, B. (2007) Disturbance is the principal α-scale filter determining niche differentiation, coexistence and biodiversity in an alpine community. *Journal of Ecology,* 95**,** 698-706.

POST, D. A. (Year) A new method for estimating flood duration curves: an application to the Burdekin River catchment, North Queensland, Australia. IEMS 2004: Proceedings of the International Environmental Modelling and Software Society. 14–17 June 2004. Osnabruck, Germany. City.

PRATT, P. D., RAYAMAJHI, M. B., VAN, T. K., CENTER, T. D. & TIPPING, P. W. (2005) Herbivory alters resource allocation and compensation in the invasive tree *Melaleuca quinquenervia*. *Ecological Entomology,* 30**,** 316-326.

PRENTIS, P. J. & MATHER, P. B. (2007) Micro-geographic landscape features demarcate seedling genetic structure in the stream lily, *Helmholtzia glaberrima*. *Aquatic Botany*, 87, 111-115.

PRENTIS, P. J. & MATHER, P. B. (2008) Fine-scale patterns of genetic variation indicate non-equilibrium gene frequency in the stream lily, *Helmholtzia glaberrima*. *Freshwater Biology*, 53, 973-980.

PRENTIS, P. J., VESEY, A., MEYERS, N. M. & MATHER, P. B. (2004) Genetic structuring of the stream lily *Helmholtzia glaberrima* (Philydraceae) within Toolona Creek, south-eastern Queensland. *Australian Journal of Botany*, 52, 201-207.

PRINGLE, A. W. (2000) Evolution of the east Burdekin Delta coast, Queensland, Australia 1980-1995. *Zeitschrift für Geomorphologie,* 44**,** 273-304.

PRITCHARD, J. K., STEPHENS, M. & DONNELLY, P. (2000) Inference of population structure using multilocus genotype data. *Genetics,* 155**,** 945-959.

PUCKRIDGE, J. T., SHELDON, F., WALKER, K. F. & BOULTON, A. J. (1998) Flow variability and the ecology of large rivers. *Marine and Freshwater Research,* 49**,** 55-72.

QUINN, G. & KEOUGH, M. (2004) *Experimental design and data analysis for biologists,* Cambridge, United Kingdom, Cambridge University Press.

R DEVELOPMENT CORE TEAM (2007) R: a language and environment for statistical computing. Vienna, R Foundation for Statistical Computing.

RAMBOUT, A. & DRUMMOND, A. J. (2005) Tracer v.1.3. Distributed by the authors at http://evolve.zoo.ox.ac.uk/beast/.

RAYMOND, M. & ROUSSETT, F. (1995) GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity,* 86**,** 248-249.

REEKIE, E. G. (1999) Chapter 5. Resource allocation, trade-offs, and reproductive effort in plants. IN VUORISALO, T. O. & MUTIKAINEN, P. K. (Eds.) *Life history evolution in plants*. the Netherlands, Kluwer Academic Publishers.

REES, M. & VENABLE, D. L. (2007) Why do big plants make big seeds? *Journal of Ecology,* 95**,** 926-936.

REMMERT, H. (Ed.) (1991) *The Mosaic-Cycle Concept of Ecosystems,* Berlin, Springer-Verlag.

REUSCH, T. B. H., STAM, W. T. & OLSEN, J. L. (2000) A microsatellite-based estimation of clonal diversity and population subdivision in Zostera marina, a marine flowering plant. *Molecular Ecology,* 9**,** 127-140.

RONFORT, J., JENCZEWSKI, J., BATAILLON, T. & ROUSSET, F. (1998) Analysis of population structure in autotetraploid species. *Genetics,* 150**,** 921-930.

ROOD, S. B., KALISCHUK, A. R. & MAHONEY, J. M. (1998) Initial cottonwood seedling recruitment following the flood of the century of the Oldman River, Alberta, Canada. *Wetlands,* 18**,** 557-570.

ROOD, S. B., KALISCHUK, A. R., POLZIN, M. L. & BRAATNE, J. H. (2003) Branch propagation, not cladoptosis, permits dispersive, clonal reproduction of riparian cottonwoods. *Forest Ecology and Management,* 186**,** 227-242.

ROSSETTO, M., HARRISS, F. C. L., MCLAUCHLAN, A., HENRY, R. J., BAVERSTOCK, P. R. & LEE, L. S. (2000) Interspecific amplification of tea tree (*Melaleuca alternifolia* - Myrtaceae) microsatellite loci - potential implications for conservation studies. *Australian Journal of Botany,* 48**,** 367-373.

ROSSETTO, M., MCLAUCHLAN, A., HARRISS, F. C. L., HENRY, R. J., BAVERSTOCK, P., LEE, L. S., MAGUIRE, T. L. & EDWARDS, K. J. (1999a) Abundance and polymorphism of microsatellite markers in the tea tree (*Melaleuca alternifolia*, Myrtaceae). *Theoretical & Applied Genetics,* 98**,** 1091-1098.

ROSSETTO, M., SLADE, R. W., BAVERSTOCK, P. R., HENRY, R. J. & LEE, L. S. (1999b) Microsatellite variation and assessment of genetic structure in tea tree (*Melaleuca alternifolia* - Myrtaceae). *Molecular Ecology,* 8**,** 633-643.

ROUSSET, F. (1997) Genetic differentiation and estimation of gene flow from *F*-statistics under isolation by distance. *Genetics,* 145**,** 1219-1228.

RYE, B. L. & JAMES, S. H. (1992) The relationship between dysploidy and reproductive capacity in Myrtaceae. *Australian Journal of Botany,* 40**,** 829-848.

SAINTILAN, N. & WILTON, K. (2001) Changes in the distribution of mangroves and saltmarshes in Jervis Bay, Australia. *Wetlands Ecology and Management,* 9**,** 409-420.

SAKAI, A. & SAKAI, S. (1998) A test for the resource remobilization hypothesis: tree sprouting using carbohydrates from above-ground parts. *Annals of Botany,* 82**,** 213-216.

SASAKI, A. & ELLNER, S. (1995) The evolutionarily stable phenotype distribution in a random environment. *Evolution,* 49**,** 337-350.

SAVERIMUTTU, T. & WESTOBY, M. (1996) Seed longevity under deep shade in relation to seed size. *Journal of Ecology,* 84**,** 681-689.

SCHULTZ, J., MAISEL, S., GERLACH, D., MÜLLER, T. & WOLF, M. (2005) A common core of secondary structure of the internal transcribed spacer 2 (ITS2) throughout the Eukaryota. *RNA,* 11**,** 361-364.

SCHWILK, D. & ACKERLY, D. D. (2005) Is there a cost to resprouting? Seedling growth rate and drought tolerance in sprouting and nonsprouting *Ceanothus* (Rhamnaceae). *American Journal of Botany,* 92**,** 404-410.

SHEPHERD, K. A., WAYCOTT, M. & CALLADINE, A. (2004) Radiation of the Australian *Salicornioideae* (Chenopodiaceae)-based on evidence from nuclear and chloroplast DNA sequences. *American Journal of Botany,* 91**,** 1387-1397.

SILVERTOWN, J. (2001) Plants stand still, but their genes don't: non-trivial consequences of the obvious. IN SILVERTOWN, J. & ANTONOVICS, J. (Eds.) *Integrating ecology and evolution in a spatial context*. London, Blackwell Science Ltd.

SILVERTOWN, J. & ANTONOVICS, J. (Eds.) (2001) *Integrating ecology and evolution in a spatial context,* Oxford, Blackwell Science Ltd.

SILVERTOWN, J., DODD, M., GOWING, D. & MOUNTFORD, J. O. (1999) Hydrologically defined niches reveal a basis for species richness in plant communities. *Nature,* 400**,** 61 - 63.

SILVERTOWN, J., MCCONWAY, K., GOWING, D., DODD, M., FAY, M. F., JOSEPH, J. A. & DOLPHIN, K. (2006) Absence of phylogenetic signal in the niche structure of meadow plant communities. *Proceedings of the Royal Society of London Series B,* 273**,** 39 - 44.

SPECHT, R. (1990) Chapter 16: Forested wetlands in Australia. IN LUGO, A. E., BRINSON, M. & BROWN, S. (Eds.) *Ecosystems of the world 15*. Amsterdam, Elsevier Science Publishers B.V.

SPIEGELHALTER, D., THOMAS, A., BEST, N. & LUNN, D. (2005) WinBUGS v.2.10.

SPILLER, D. A. & AGRAWAL, A. A. (2003) Intense disturbance enhances plant susceptibility to herbivory: natural and experimental evidence. *Ecology,* 84**,** 890-897.

STEPHENSON, A. & RIBATET, M. (2006) evdbayes: Bayesian Analysis in Extreme Value Theory. R package version 1.0-6. http://www.maths.lancs.ac.uk/~stephena/, http://www.lyon.cemagref.fr/hh/hydrologie/scientifiques/ribatet/hydrology-english.shtml.

STEPHENSON, A. & TAWN, J. (2004) Bayesian inference for extremes: accounting for the three extremal types. *Extremes,* 7**,** 291-307.

STOCKER, R. K. (1999) Mechanical harvesting of *Melaleuca quinquenervia* in Lake Okeechobee, Florida. *Ecological Engineering,* 12**,** 373-386.

STOREY, J. D. (2002) A direct approach to false discovery rates. *Journal of the Royal Statistical Society Series B,* 64**,** 479-498.

STOREY, J. D., TAYLOR, J. E. & SIEGMUND, D. (2004) Strong control, conservative point estimation, and simultaneous conservative consistency of false discovery rates: a unified approach. *Journal of the Royal Statistical Society Series B,* 66**,** 187-205.

STOREY, J. D. & TIBSHIRANI, R. (2003) Statistical significance for genome-wide studies. *Proceedings of the National Academy of Sciences USA,* 100**,** 9440-9445.

STOWE, K. A., MARQUIS, R. J., HOCHWENDER, C. G. & SIMMS, E. L. (2000) The evolutionary ecology of tolerance to consumer damage. *Annual Review of Ecology & Systematics,* 31**,** 565-595.

SUN, D. & DICKINSON, G. R. (1995) Survival and growth responses of a number of Australian tree species planted on a saline site in tropical north Australia. *Journal of Applied Ecology,* 322**,** 817-826.

SUN, D. & DICKINSON, G. R. (1997) Early growth of six native Australian tree species in windbreaks and their effect on potato growth in tropical northern Australia. *Forest Ecology and Management,* 95**,** 21-34.

SUZUKI, J. I., HERBEN, T. & MAKI, M. (2004) An under-appreciated difficulty: sampling of plant populations for analysis using molecular markers. *Evolutionary Ecology,* 18**,** 625 - 646.

SWOFFORD, D. L. (2002) *PAUP*: Phylogenetic Analysis Using Parsimony (* and Other Methods)*, Sinauer Associates, Sunderland, M.A.

SYTSMA, K. J., LITT, A., ZJHRA, M. L., PIRES, J. C., NEPOKROEFF, M., CONTI, E., WALKER, J. & WILSON, P. G. (2004) Clades, clocks and continents: historical and biogeographical analysis of Myrtaceae, Vochysiaceae, and relatives in the southern hemisphere. *International Journal of Plant Sciences,* 165(4 Suppl.)**,** S85-S105.

TABACCHI, E., CORRELL, D. L., HAUER, R., PINAY, G., PLANTY-TABACCHI, A. & WISSMAR, R. C. (1998) Development, maintenance and role of riparian vegetation in the river landscape. *Freshwater Biology,* 40**,** 497-516.

TABERLET, P., GIELLY, L., PATOU, G. & BOUVET, J. (1991).Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology,* 17**,** 1105-1109.

TELFORD, M. J., WISE, M. J. & GOWRI-SHANKAR, V. (2005) Consideration of RNA secondary structure significantly improves likelihood-based estimates of phylogeny: examples from the Bilateria. *Molecular Biology and Evolution,* 22**,** 1129-1136.

TEMPLETON, A. R. (2001) Using phylogeographic analyses of gene trees to test species status and processes. *Molecular Ecology,* 10**,** 779-791.

TERO, N., ASPI, J., SIIKAMAKI, P., JAKALANIEMI, A. & TUOMI, J. (2003) Genetic structure and gene flow in a metapopulation of an endangered plant species, *Silene tatarica*. *Molecular Ecology,* 12**,** 2073-2085.

THOMPSON, J. D., GIBSON, T. J., PLEWNIAK, F., JEANMOUGIN, F. & HIGGINS, D. G. (1997) The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research.,* 24**,** 4876-4882.

TIERNEY, D. A. (2004) Towards an understanding of population change for the long-lived resprouting tree *Angophora inopina* (Myrtaceae). *Australian Journal of Botany,* 52**,** 31-38.

TISCHENDORF, L. & FAHRIG, L. (2000) On the usage and measurement of landscape connectivity. *Oikos,* 90**,** 7-19.

TURNER, C. E., CENTER, T. D., BURROWS, D. W. & BUCKINGHAM, G. R. (1998) Ecology and management of *Melaleuca quinquenervia*, an invader of wetlands in Florida, U.S.A. *Wetlands Ecology and Management,* 5**,** 165-178.

VÄHÄ, J. P., ERKINARO, J., NIEMELÄ, E. & PRIMMER, C. R. (2007) Life-history and habitat features influence the within-river genetic structure of Atlantic salmon. *Molecular Ecology,* 16**,** 2638-2654.

VAN DER MOEZEL, P. G. & BELL, D. T. (1987) Comparative seedling salt tolerance of several *Eucalyptus* and *Melaleuca* species from Western Australia. *Australian Forest Research,* 17**,** 151-158.

VAN DER MOEZEL, P. G. & BELL, D. T. (1990) Saltland reclamation: selection of superior Australian tree genotypes for discharge sites. *Proceedings of the Ecological Society of Australia,* 16**,** 545-549.

VAN ECK, W. H. J. M., VAN DE STEEG, H. M., BLOM, C. W. P. M. & DE KROON, H. (2004) Is tolerance to summer flooding correlated with distribution patterns in river floodplains? A comparative study of 20 terrestrial grassland species. *Oikos,* 107**,** 393-405.

VAN, T. K., RAYACHHETRY, M. B. & CENTER, T. D. (2000) Estimating above-ground biomass of *Melaleuca quinquenervia* in Florida, USA. *Journal of Aquatic Plant Management,* 38**,** 62-67.

VARDON, M. J., BROCKLEHURST, P. S., WOINARSKI, J. C. Z., CUNNINGHAM, R. B., DONNELLY, C. F. & TIDEMANN, C. R. (2001) Seasonal habitat use by flying-foxes, *Pteropus alecto* and *P. scapulatus* (Megachiroptera), in monsoonal Australia. *Journal of Zoology (London),* 253**,** 523-535.

VEKEMANS, X. & HARDY, O. J. (2004) New insights from fine-scale spatial genetic structure analyses in plant populations. *Molecular Ecology,* 13**,** 921-935.

VENABLE, D. L. (1997) Bet-hedging in a guild of desert annuals. *Ecology,* 88**,** 1086-1090.

VERDAGUER, D. & OJEDA, F. (2002) Root starch storage and allocation patterns in seeder and resprouter seedlings of two Cape Erica (Ericaceae) species. *American Journal of Botany,* 89**,** 1189-1196.

VERHOEVEN, K. J. F., SIMONSEN, K. L. & MCINTYRE, L. M. (2005) Implementing false discovery rate control: increasing your power. *Oikos,* 108**,** 643-647.

VESK, P. A. (2006) Plant size and resprouting ability: trading tolerance and avoidance of damage? *Journal of Ecology,* 94**,** 1027-1034.

VESK, P. A., WARTON, D. I. & WESTOBY, M. (2004) Sprouting by semi-arid plants: testing a dichotomy and predictive traits. *Oikos,* 107**,** 72-89.

VESK, P. A. & WESTOBY, M. (2004) Sprouting ability across diverse disturbances and vegetation types worldwide. *Journal of Ecology,* 92**,** 310-320.

VIEIRA, D. L. M. & SCARIOT, A. (2006) Principles of natural regeneration of tropical dry forests for restoration. *Restoration Ecology,* 14**,** 11-20.

VUORISALO, T. O. & MUTIKAINEN, P. K. (1999) Chapter 1. Modularity and plant life histories. IN VUORISALO, T. O. & MUTIKAINEN, P. K. (Eds.) *Life history evolution in plants*. the Netherlands, Kluwer Academic Publishers.

WALTERS, M. B. & REICH, P. B. (2000) Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. *Ecology,* 81**,** 1887-1901.

WARD, J. V., TOCKNER, D. B., ARSCOTT, D. B. & CLARET, C. (2002) Riverine landscape diversity. *Freshwater Biology,* 47**,** 497-907.

WARTON, D. I., WRIGHT, I. J., FALSTER, D. S. & WESTOBY, M. (2006) Bivariate line-fitting methods for allometry. *Biological Review,* 81**,** 259-291.

WEINER, J. (2004) Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology, Evolution and Systematics,* 6**,** 207-215.

WESTOBY, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil,* 199**,** 213-227.

WESTOBY, M., JURADO, E. & LEISHMAN, M. (1992) Comparative evolutionary ecology of seed size. *Trends in Ecology and Evolution,* 7**,** 368-372.

WESTOBY, M., LEISHMAN, M. & LORD, J. (1996) Comparative ecology of seed size and dispersal. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences,* 351**,** 1309-1317.

WHELAN, R. J. (1995) *Ecology of fire,* Melbourne, Australia, Cambridge University Press.

WHITE, T. J., BRUNS, T., LEE, S. & TAYLOR, J. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. IN INNIS, M. A., GELFAND, D. H., SNINSKY, K. K. & WHITE, T. J. (Eds.) *PCR Protocols, A Guide to Methods and Applications*. San Diego, Academic Press Inc.

WHITHAM, T. G., YOUNG, W. P., MARTINSEN, G. D., GEHRING, C. A., SCHWEITZER, J. A., SHUSTER, S. M., WIMP, G., FISCHER, D. G., BAILEY, J. K., LINDROTH, R. L., WOOLBRIGHT, S. & KUSKE, C. R. (2003) Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology,* 84**,** 559-573.

WIDMER, A. (2002) A tight link between specialization and speciation. *Trends in Ecology and Evolution,* 17**,** 161.

WIENS, J. A. (1997) Metapopulation dynamics and landscape ecology. IN HANSKI, I. A. & GILPIN, M. E. (Eds.) *Metatpopulation biology: ecology, genetics and evolution*. San Diego, Academic Press, Inc.

WILBERG, M. J. & DREHER, B. P. (2004) GENECAP: a program for analysis of multilocus genotype data. *Molecular Ecology Notes,* 4**,** 783-785.

WILLIAMSON, G. B., COSTA, F. & VERA, C. V. M. (1999) Dispersal of Amazonian trees: hydrochory in *Swartzia polyphylla*. *Biotropica,* 31**,** 460-465.

WILSEY, B. J. & POLLEY, H. J. (2006) Aboveground productivity and root-shoot allocation differ between native and introduced grass species. *Oecologia,* 150**,** 300-309.

WILSON, G. A. & RANNALA, B. (2003) Bayesian Inference of recent migration rates using multilocus genotypes. *Genetics,* 163**,** 1177-1191.

WILSON, P. G., O'BRIEN, M. M., GADEK, P. A. & QUINN, C. J. (2001) Myrtaceae revisited: A reassessment of infrafamilial groups. *American Journal of Botany,* 88**,** 2013-2025.

WILSON, P. G., O'BRIEN, M. M., HESLEWOOD, M. M. & QUINN, C. J. (2005) Relationships within Myrtaceae *sensu lato* based on a *mat*K phylogeny. *Plant Systematics and Evolution,* 251**,** 3-19.

WINFIELD, M. & HUGHES, F. M. R. (2002) Variation in *Populus nigra* clones: implications for river restoration projects in the United Kingdom. *Wetlands,* 22**,** 33-48.

WOLFF, K., EL-AKKAD, S. & ABBOTT, R. J. (2003) Population substructure in *Alkanna orientalis* (Boraginaceae) in the Sinai Desert, in relation to its pollinator behaviour. *Molecular Ecology*, 6, 365-372.

WRIGHT, I. J. & WESTOBY, M. (2000) Cross-species relationships between seedling relative growth rate, nitrogen productivity and root vs leaf function in 28 Australian woody species. *Functional Ecology,* 14**,** 97-107.

WRIGHT, S. D., YONG, C. G., WICHMAN, S. R., DAWSON, J. W. & GARDNER, R. C. (2001) Stepping stones to Hawaii: a trans-equatorial dispersal pathway for *Metrosideros* (Myrtaceae) inferred from nrDNA (ITS plus ETS). *Journal of Biogeography,* 28**,** 769-774.

WRIGLEY, J. W. & FAGG, M. (1993) *Bottlebrushes, paperbarks and tea trees, and all other species in the Leptospermum alliance,* Pymble, NSW, Angus and Robertson.

YAMANOSHITA, T., MASUMORI, M., YAGI, H. & KOJIMA, K. (2005) Effects of flooding on downstream processes of glycolysis and fermentation in roots of *Melaleuca cajuputi* seedlings. *Journal of Forestry Research,* 10**,** 199-204.

YANG, R. C. (1998) Estimating hierarchical *F*-statistics. *Evolution,* 52**,** 950-956.

Appendices

(numbered according to chapter references)

Appendix 5A

Geographic distances between seven sampling locations in the Upper Burdekin River catchment, north-east Queensland, Australia. Matrix values represent Euclidean distances (kilometres) between the central sampling point of each site.

	KB	LUC	LD	GRE	BLU	CLA	BIG
KB		143.30	153.13	139.95	100.04	99.21	56.71
LUC			47.14	45.30	67.36	72.40	166.73
LD				13.23	55.20	58.02	160.03
GRE					42.14	45.18	147.35
BLU						5.22	105.63
CLA							102.18
BIG							

Appendix 6A

Summary list of Myrtaceae taxa and voucher specimens used to generate novel sequence data in this study. Voucher sources are plants grown from seed supplied by the Australian Tree Seed Centre, CSIRO, ACT, Australia (ATSC seed), Nindethana Seed Company, WA, Australia (Nind seed), herbarium samples provided by Lyn Craven, CSIRO, ACT, Australia (Leaf Herb Craven), and local collections (Leaf Own and Leaf JD).

genus	species	authority	seedlot	location		lat	long	alt (m)	viability/10g	parents	voucher source	GenBank accession
Asteromyrtus	*symphyocarpa*	(F. Muell.) Craven	18559	N OF KENNEDY RIVER	QLD	15°25'S	144°10'E	150	6600	5	ATSC seed	EF 041509
Callistemon	*pachyphyllus*	Cheel	20590	TUAN	QLD	25°49'S	152°53'E	23	59000	20	ATSC seed	
Callistemon	*viminalis*	(Sol. ex Gaertn.) G.Don	622	Mildura	VIC						Nind seed,	EF 041510
Calothamnus	*quadrifidus*	R.Br.	648	Esperance	WA						Nind seed, Oct 2002	EF 041511
Eucalyptus	*camaldulensis var. obtusa*		984		NT						Nind seed,	
Eucalyptus	*coolabah*		15076		QLD						ATSC seed	
Eucalyptus	*ravertiana*		1237		NT						Nind seed	
Eugenia	*reinwardtiana*	Candolle	eug	TOWNSV JCU		S19°19'43.1	E146°45'23.6	46			Leaf Own, 9/08/2005	
Lophostemon	*confertus*	(R.Br.) Peter G.Wilson & J.T.Waterh.	15598	MORETON ISLAND	QLD	27°04'S	153°23'E	5	2000	10	ATSC seed	
Melaleuca	*acacioides subsp. acacioides*	F.Muell.	20671	BULLA PLAIN	PNG	09°01'S	141°19'E	10	92000	5	ATSC seed	
Melaleuca	*arcana*	S.T. Blake	14866	NNE TOZERS GAP	QLD	12°43'S	143°12'E	100	43000	6	ATSC seed	
Melaleuca	*arcana*	S.T. Blake	14876	NW COOKTOWN	QLD	15°12'S	145°09'E	40	45500	10	ATSC seed	

genus	species	authority	seedlot	location		lat	long	alt (m)	viability/10g	parents	voucher source	GenBank accession
Melaleuca	*argentea*	W. Fitzgerald	17466	GEIKIE GORGE	WA	18°07'S	125°42'E	110	1200	4	ATSC seed	
Melaleuca	*argentea*	W. Fitzgerald	14904	W WROTHAM PARK	QLD	16°41'S	143°54'E	135	26500	10	ATSC seed	
Melaleuca	*cajuputi subsp. cajuputi*	Powell	18897	MATARANKA ROPER RIVER	NT	14°56'S	133°08'E	100	55000	5	ATSC seed	
Melaleuca	*cajuputi subsp. cajuputi*	Powell	19576	BEAGLE BAY	WA	16°58'S	122°40'E	10	39250	15	ATSC seed	
Melaleuca	*cajuputi subsp. cajuputi*	Powell	19538	WAI GEREN BURU ISLAND	INDO	03°23'S	126°55'E	70	39500	33	ATSC seed	
Melaleuca	*cajuputi subsp. cumingiana*	(Turcz.) Barlow	19862		INDO						Leaf Herb Craven	
Melaleuca	*cajuputi subsp. platyphylla*	Barlow	19217	ERAMANG RIVER	PNG	08°35'S	142°43'E	25	26000	5	ATSC seed	
Melaleuca	*cajuputi subsp. platyphylla*	Barlow	14878		QLD						Leaf Herb Craven	
Melaleuca	*citrolens*	Barlow	18561	S OF LAURA	QLD	15°34'S	144°27'E	150	0	3	ATSC seed	EF 041512
Melaleuca	*clarksonii*	Barlow	18686		QLD						Leaf Herb Craven	
Melaleuca	*cornucopiae*	Craven	10329		NT						Leaf Herb Craven	
Melaleuca	*deanei*	Lepschi Craven Brolby	945								Leaf Herb Craven	EF 041513
Melaleuca	*dealbata*	S.T. Blake	19357	BENSBACH WP	PNG	08°53'S	141°30'E	30	14000	5	ATSC seed	
Melaleuca	*dealbata*	S.T. Blake	18922	FLYING FOX CK KAPALGA	NT	12°40'S	132°19'E	30	51000	5	ATSC seed	

genus	species	authority	seedlot	location		lat	long	alt (m)	viability/10g	parents	voucher source	GenBank accession
Melaleuca	*dealbata*	S.T. Blake	18907	CAMBRIDGE GULF	WA	14°55'S	128°34'E	20	173000	3	ATSC seed	
Melaleuca	*dealbata*	S.T. Blake	15891	RIFLE CREEK	QLD	16°40'S	145°20'E	380	93000	5	ATSC seed	
Melaleuca	*decussata*	R.Br.	16740	20KM NE CAVEN DISH	VIC	37°25'S	142°12'E	230	29870	10	ATSC seed	
Melaleuca	*ferruginea*	Cowie	7335								Leaf Herb Craven	
Melaleuca	*fluviatilis*	Barlow	14899	SSE MUSGRAVE	QLD	15°02'S	143°39'E	55	9000	2	ATSC seed	
Melaleuca	*fluviatilis*	Barlow	18560	LAURA RIVER	QLD	15°35'S	144°27'E	150	0	5	ATSC seed	
Melaleuca	*glomerata*	F.Muell.	15335	80 MILE BEACH	WA	19°46'S	120°40'E	5	12000	10	ATSC seed	
Melaleuca	*lasiandra*	F.Muell.	18636	NO7 BORE BONKA BONKA	NT	18°43'S	134°04'E	290	131000	3	ATSC seed	
Melaleuca	*leucadendra*	(L.) L.	19220	BENSBACH	PNG	08°53'S	141°17'E	25	12800	5	ATSC seed	
Melaleuca	*leucadendra*	(L.) L.	13567	Mareeba	QLD	17°00'S	145°30'E	500	6200	3	ATSC seed	
Melaleuca	*leucadendra*	(L.) L.	19532	AMBON	INDO	03°44'S	128°14'E	75	21200	9	ATSC seed	
Melaleuca	*leucadendra*	(L.) L.	18914	KALUMBURU MISSION	WA	14°18'S	126°38'E	20	15900	5	ATSC seed	
Melaleuca	*leucadendra*	(L.) L.	20179	BUFFALO CREEK	NT	12°20'S	130°54'E	3	29000	5	ATSC seed	
Melaleuca	*leucadendra*	(L.) L.	GRE11.15	Burdekin R.	QLD	18.56.995	145.06.222	406	-	-	Leaf Own, 21/11/2003	
Melaleuca	*leucadendra*	(L.) L.	CLA21	Clarke R.	QLD	19.13.082	145.25.630	344	-	-	Leaf Own, 21/11/2004	
Melaleuca	*leucadendra*	(L.) L.	NM6	Burdekin R.	QLD	19.23556S	145.78910E	306.2	-	-	Leaf Own, 30/07/2004	
Melaleuca	*leucadendra*	(L.) L.	BRLIB	Burdekin R.	QLD	19.17076S	145.42809E	243	-	-	Leaf Own, 30/07/2005	
Melaleuca	*leucadendra*	(L.) L.	BIG3.4	Burdekin R.	QLD	19.50.411	146.08.498	246	-	-	Leaf Own, 5/11/2003	
Melaleuca	*leucadendra*	(L.) L.	KB1m61	Upper Keelbottom	QLD	19.22.432	146.21.437	331	-	-	Leaf Own,	

genus	species	authority	seedlot	location		lat	long	alt (m)	viability/10g	parents	voucher source	GenBank accession
				Ck.							8/12/2003	
Melaleuca	*linariifolia*	Sm.	19485	BULAHDELAH	NSW	32°24'S	152°16'E	10	52400	14	ATSC seed	
Melaleuca	*nervosa*	(Lindl.)Cheel	14879	NE HOMESTEAD	QLD	20°20'S	145°42'E	320	72500	10	ATSC seed	
Melaleuca	*nodosa*	(Lindl.)Cheel	17539	WOODGATE-GOODWOOD RD	QLD	25°08'S	152°30'E	20	36500	10	ATSC seed	
Melaleuca	*quinquenervia*	(Cav.) S.T.Blake	15869	ROKEBY NP	QLD	13°44'S	143°19'E	500	25500	5	ATSC seed	
Melaleuca	*quinquenervia*	(Cav.) S.T.Blake	19225	BIMEDEBUM	PNG	08°41'S	141°51'E	20	35000	5	ATSC seed	
Melaleuca	*quinquenervia*	(Cav.) S.T.Blake	19221	BENSBACH	PNG	08°53'S	141°17'E	25	37500	5	ATSC seed	
Melaleuca	*saligna*	Schauer	18557	N OF LAURA	QLD	15°29'S	144°16'E	150	27500	5	ATSC seed	
Melaleuca	*saligna*	Schauer	14871		QLD						Leaf Herb Craven	
Melaleuca	*sericea*	Byrnes	18904	E BAINES RIVER	NT	15°43'S	130°06'E	50	14000	5	ATSC seed	
Melaleuca	*stenostachya*	S.T. Blake	14148								Leaf Herb Craven	
Melaleuca	*trichostachya*	Lepschi and Slee	1089								Leaf Herb Craven	
Melaleuca	*triumphalis*	Craven, ex Ian Cowie	triumph		NT						Leaf Herb Craven	
Melaleuca	*uncinata*	R.Br.	14027	NW CURTIN SPRINGS	NT	24°59'S	131°31'E	400	6000	8	ATSC seed	
Melaleuca	*viridiflora*	Sol. Ex. Gaertn.	14152	WEIPA	QLD	12°31'S	141°48'E	10	14400	10	ATSC seed	
Melaleuca	*viridiflora*	Sol. Ex. Gaertn.	19545	KANTOR TANIMBAR	INDO	08°12'S	130°59'E	10	8000	5	ATSC seed	
Osbornia	*octodonta*	F.Muell.	Osbornia		QLD					-	Leaf BB,	

genus	species	authority	seedlot	location		lat	long	alt (m)	viability/10g	parents	voucher source	GenBank accession
											2005	
Tristaniopsis	*laurina*		2080		NSW						Nind. seed	EF 041514
Syzygium	*forte subsp. forte*	F.Muell. (B.Hyland)	Syz	Bramston Beach	QLD	17°21'00S	146°00'17E	2	-	-	Leaf JD, 18/05/2005	
Angophora	*floribunda*	Connors and Lepschi	739								Leaf Herb Craven	
Melaleuca	*pancheri*	Watt	96/037								Leaf Herb Craven	
Melaleuca	*styphelioides*	Lepschi and Mowatt	1469								Leaf Herb Craven	
Melaleuca	*ericifolia*	Brown and Pedersen	1								Leaf Herb Craven	
Xanthostemon	*chrysanthus*		xanth	TOWNSV Rosslea	QLD						Leaf JD, 2/09/2005	EF 041515

Appendix 6B

Sequence alignment data representing final concatenated data for 52 taxa and loci and spacer regions used in this study: (a) ITS1 and ITS2; (b) trnL; (c) rpL16. Missing data coded as "?".

ITS4—TCCTCCGCTTATTGATATGC
ITS16—CCGATTGAATGGTCCGGTGAAGTGCTCG
trnLF—ATTTGAACTGGTGACACGAG
trnLC—CGAAATCGGTAGACGCTACG
rpl16 71F—GCTATGCTTAGTGTGTGACTCGTTG
rpl16 R1661—CGTACCCATATTTTTCCACCACGAC
rpl16 CCRP—TCATAGCTTCCATCGTTCCCRTCG

(a)

Eucraver TCGAATCCTGCCCAGCAGAATGACCAGAGAATCGGTAACAAA-CTCAAT-GGGGACGGCGGGC--TCA-GCCCGACGTCCCTCTCGAC-----GCC-
GAGGATCAAGGCTCGGGCGCCTCAGGGCGCTCGG-CC-TTGTCCCCGGC-GGCAC-AACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-TGAACAA-GAGTGCGATGCTCCCGCCGCCCCATACAC-
GGTGCGCGCGCGGGACGCCATGCAATCTC-ATATT-AGTCATAAACATGGCGTTGCCCC--TAATCCC-TCCGCCCTTTCAACG-
GGGCGAGCGGGGACTTGGGCGCGTACGATGGCCTCCCGCGACGATCACGTCCCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-TCAGCACCACGACATTCGGTGGTTGA-T--TAGACCCC-AATGATC-
AATGTCGCGCGTGC--CGCT-CAT-CGCA-CGCTCGGCGAATCT-GCTCCTTACCAACGCGA

Euccoola TCGAATCCTGCCCAGCAGAATGACCAGAGAACCGGTAACAAA-CTCAAY-GGGGACGGCGGGC--TCA-GCCCGACGTCCCTCTCGAC-----GCC-
GAGGATCAAGGCTCGGGCGCCTCAGAGCGCTCGG-CC-TTGTCCCCGGC-GGCAC-AACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-TGAACAA-GAGTGCGATGCTCCCGCCGCCCCATACAC-
GGTGCGCGCGCGGGACGCCATGCAATCTC-ATATT-AGTCATAAACATGGCGTTGCCCC--TAATCCC-TCCGCCCTTTCAACG-
GGGCGAGCGGGGACTTGGGCGCGTACGATGGCCTCCCGCGACGATCACGTCCCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-TCAGCACCACGACATTCGGTGGTTGA-T--TAGACCCC-AATGATC-
AATGTCGCGCGTGC--CGCT-CAT-CGCA-CGCTCCGCGAATCT-GCTCCTTACCAACGCGA

Euccamal TCGAATCCTGCCCAGCAGAATGACCAGAGAACCGGTAACAAA-CTCAAC-GGGGACGGCGGGC--TCA-GCTCGACGTCCCTCTCGAC-----GTC-
GAGGATCGGGGCTCGGGYRCCTCAGGGCGCTCGG-CCTTTGTCCTCGGC-GGCGC-AACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-TTAACAA-GAGTGCGATGCTCCCGCCGCCCCATACAC-
GGTGCGCGCGCGGGATGCCATGCAATCTC-ATATT-AGTCATAAACATGGCGTTGCCCC--CAATCCCCTCCGCCCTTTGAACG-GGGCGAGC-
GGGACTCGGGCGCGTACGATGGCCTCCCGCGACGACCACGTCCCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-TCAGCACCACGACATTCGGTGGTTGA-T--TAGACCCC-AATGATC-
AATGTCGCGCGTGC--CGCT-CAT-CGCA-CGCTCCGCGAATCT-GCTCCTTACCAACGCGA

Ooctodon TCGAATCCTGCACAGCAGAACGACCAGAGAACCAGTAACAAAACTCGAT-GGAGGCGGTGGGC--TTC-GCTCAACGTCCTCCC-GAC-----GC--TTGGAT-TGCGCGGGGGCGCCTA-
GCGCGCTCGG-GC--CTTTCCCAGC-GGCAC-AATG-AACCCCGGCGCGGATTGCGCCAAGG-AACT-TGAACAA-
GAGTGCGGTGCTCCCGTCACCCCAAACATTGGCGTGTGCGCGGGATGCCATGCAATCTCC-TATT-ATTCATAAACATGGCGTTGCCCC--TAACCCC--TCGCC--TTGAATT-
GGGTGGGCCGGGACTTGGGTGCGTATGTTGGCCTCCCGTGACAACCTTGTCCCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-TTCGCACCACGACTTTCGGTGGTTGA-T--GAGACCCC-
AACGATCAAATGTCGCGGGTGC--CGCT-CATGCGC-GTGCTCCACGAATCC-ACTCTGTACCAACGCGA

Caloquad TTGTAGCCTGC-----AAAATGACCAGAGAACTAGTTACAAA-CTCGAC-GAGGGCGGTGGGC-TTTC-GCCCAACGTCCCTC--GAC-----GC--TGGGAT---CGCACGGGCGCCTA-TGGCGCCCGA-
GC--GTTTCTCGGC-GGAACTAACA-AACCCCGGCGCGGAATGCGCCAAGG-AACT-AAAACAA-GAGCGCGATGCTCCCATCACCCCAGACAT-GGTGCGTGCATGGGATGCCACGCAATCTC---ATT-
ACTTATAAACATGGCGTTGCCCC--TAGTCCC--TCGCCC-TGAA-TGTGGGCGGGA-GGAACTTGGGCGCGTAAGTTGGCCTCCCGTGACGATCTTGTCCCGGTTGGCTCAAAATCGAGCGTCGGAGCGA-
TTAGCACCACGACATTCGGTGGTTGA-T--GAGACCCC-AATGATC-AATGTCGCGCGTGC--CGCT-CGTGAGC-GCGCTCCGCGAATCT-ATTACTTACCAACGCGA

Cpachyph TCGAATCCTGCACAGCAGAATGACCAGAGAACTAGTAACAAA-CTCGAT-GGGGGCGGTGGGC--TTT-GCCCAACGTCCCAC--GAC-----GC--TTGGAT---CGCACGGGCGCCTA-
GTGCGCTCGG-GC--GTTTCTCGGC-GGCAATAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCATACAT-
GGTGCGTGCATGGGATGCCATGCAATCTCC-TATT-ACTTATAAACATGGCGTTGCCCC--TCATCCC--TCGCC--TTCAATTTGGGCGGGA-
GGAATTTGGGTGCGTAAGTTGGCCTCCCGTGACTACCTTGTCCCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-TTAGCACCACAACATTTGGTGGTTGATT---AGACCCC-AATGATC-AATGT--
TGTGTGT---GCT-CGCGCGC-GCGCTCTGCGAGTCT-TTTATTTACCAACGCGA

Cviminal TCGAATCCTGCACAGCAGAATGACCAGAGAACTAGTAACAAA-CTCGAT-GGGGGCGGTGGGC--TTC-GCTCAACGTCCCCC--GAC-----GC--TTGGAT---CGCGCGGGCGCCTA-
GTGCGCTCGG-GC--GTTTCTCGGC-GGCAATAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTACTTATAAACATGGCGTTGCCCC--TTATCCC--TCGCC--
TTGAATTTGGGCGGGGAGGAATTTGGGCGCGTAAGTTGGCCTCCCGTGACAACCTTGTCCCGGTTGGCCGAAAATCGAGCGTCGGAGCGA-
TTAGCACCACGACATTTGGTGGTTGATTAGAAGACCCC-AATGGTC-AATGTCGTGCGTGC-TCGCT-CGTGCGC-GCGCTCTGCGAATCT-TTTATTTACCAACGCGA

Mstyphel TCGAATCCTGCACAGCAGAATGACCAGAGAACTAGTAACAAA-CTCGAT-GGGGGCGGTGGGC--TTC-GCCTAACGTCCCCC--GAC-----GCC-TTGGAT---CGCACGAGTGCCTG-
GTGCGCTCGG-GC--GCTTCTCGGC-GGCACTAACGAAACCCCGGCGCGGAATGCGCCAAGG-AAAT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGATGCGATCCAATCTCA-TATT-ATTTATAAACATGGCGTTGCCCC--TAATCCC--TCGCCC-TGAA-TTTGGGCGGGA-
GGAACTTGGGCGCGTAAGTTGGCCTCCCGTGACTTTCTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-TTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-
AATGTCGCGTGTGTCTCGCT-CGTGCGT-GCGCTCCGCGAATCT-ATTATTTACCAACGCGA

Mpancher TCGAATCCTGCATAGCAGAATGACCAGAGAACTAGTAACAAA-CTCGAT-GGGGGCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-
GAGCGCTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACTCCAGACAT-
GGTGCGTGCATGGGATGCCATGCAATCTCC-TATT-ATTTATAAACATGGCGTTGCCCC--TAATCAC--TCGCCC-TTAA-TGTGGGCGGGA-
GGAACTTGGGCGCGTAAGTTGGCCTCCCGTGACGACTTTGTCCCGGTTGGCCCAAAATCGAGCGTCGGAGCGA--TAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-
AATGTCGCGTGTGC--CGCT-CGATCGC-GCGCTCTGCGAATCT-ATTATTTACCAACGCGA

Mcornuco TCGAATCCTGCACAGCAGAATGACCAGAGAACAAGTAACAAA-ATCGAT-GGGTGCGGTGGGC--TTC-GCCCAACCTCATCC--GAC-----GC--TTGGAT---CGCACGGGTGCCTA-
GTGCGCTCGA-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCGTCACCCCAGACAT-
GGTGTGTGTATGGGATGCCATGCAATCTCC-CATT-ATTTATAAACATGGCGTTGCCCC--TAATCCC--TCGCCC-TTAA-TGTGGGTGGGA-

GGAAATTGGGTGCGTAAGTTGGCCTCCCGTGATGACCTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCTA-TTAGCACCACGACATTCGGTGGTTGA-T----GACCCC-AATGATC-
AATGTCGCGTGTGC--CGCT-CGATTGC-GCGCTCTGCGAATCT-ATTATTTACCAACGCGA

Mdeanei TCGAATCCTGCACAGCAGAATGACCAGAGAACTAGTAACAAA-CTCGATGGGGGGGCGATGGGC--TTT-GCCCAATGTTCCCC--AAC-----GC--TGGGAT---CGCACGGGCGCCTT-
GTGTGCTCGG-GC-GGTTTCTCGGC-GGCAATAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGATGCCATGCAATCTCC-TATT-ACTTATAAACATGGCGTTGCCCC--TAACCCC--TCGCC--TTGAATTTGGGCAGGA-
GGAACTTGGGCGCGTAAGTTGGCCTCCCGTGACGCCATTGTCCCGGTTGGCCTAAAATCGAGCGTCGGAGCGA-TTAGCACCACGACATTTGGTGGTTGA-T--TAGACCCC-AATGATC-
AATGTCGCGTGTGC-TCGCT-CGTGCGC-GCGCTCTGTGAATCT-TCTATTTACCAACGCGA

Mericifo TCGAATCCTGCACAGCAGAACGACCAGAGAACCAGTAACAAA-CTCGAC-GGGGGCGGTGGGC---TT-GCCCAACGCCCCTC--GACGCTTAGC--TCGGAT---CGCACGGGCGCCTA-
GCGCGCTCGG-GC--GCTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGATGCCATGCAATCTCC-TATT-ACTTATAAACATGGCGTTGCCCC--TAATCCT--TCGCCC-TGAA-TTGGGGCGGGA-
GGAACTTGGGTGCGTAAGTTGGCCTCCCGTGACGATCTTGTCCCGGTTGGCCCAAAATCGAGCGTCGGAGCGAATTAGCACCACGACATTCGGTGGTTGA-T--TAGACCCC-AATGATC-
AATGTCGCGTGTGC--CGCT-CGTGCGC-GCGCTCCATGAATCT-ATTATTTACCAACGCGA

Mdecussa TCGAATCCTGCACAGCAGAACGACCAGAGAACCAGTAACAAA-CTCGAT-GGGGGCGGTGGGC---TT-GCCTAACGTCCCCC--GAC-----GC--TTGGAT---CGCACGGGTGCCTA-
GTGCGCTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGTGTGCATGGGATGCCATGCAATCTCC-TATT-ACTTATAAACATGGCGTTGCCCC--TACTCCC--TCGCCC-TGAA-TTTGGGCGAGA-
GGAACTTGGGTGCGTAAGTTGGCCTCCCGTGACAATCCCGTCCCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-TTAGCACCACGACATTCGGTGGTTGA-T--TAAACCCC-AATGATC--
ATGTCGCGTGTGC--CGCT-CC-------ATCTCCATGAATCT-ATTATTTACCAACGCGA

Mlinarii TCGAATCCTGCACAGCAGAACGACCAGAGAACTAGTAACAAA-CTCGAC-GGGGGCGGTGGGC---TC-GCCTAACGTCCCCC--GAC-----GC--TCGGAT---CGCGCGGGCGCCTA-
GCGCGCTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGATGCCATGCAATCTCC-TATT-ACTTATAAACATGGCGTTGCCCC--TAATCCC--TCGCAC-CGAA-TGCGGGCGGGA-
GGAACTTGGGCGCGTAAGTTGGCCTCCCGTGACGACCTCGTCCCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-TTAGCACCACGACATTCGGTGGTTGA-------ACCCC-AATGATC-
AATGTCGCGCGTGC--CGCT-CGTGCGC-GCGCTCCGCGAATCT-AATATTTACCAACGCGA

Mtrichos TCGAATCCTGCACAGCAGAACGACCAGAGAACTAGTAACAAA-CTCGAC-GGGGGCGGTGGGC---TC-GCCTAACGTCCCCC--GAC-----GC--TCGGAT---CGCGCGGGCGCCTA-
GCGCGCTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGCGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGACGCCATGCAATCTCC-TATT-ACTTATAAACATGGCGTTGCCCC--TAATCCC--TCGCAC-TGAA-TTCGGGCGGGA-
GGAACTTGGGCGCGTAAGTTGGCCTCCCGTGACGACCTCGTCCCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA----A---CCCC-AATGATC-
AATGTCGCGCGTGC--CGCT-CGTGCGC-GCGCTCCTCGAATCTAATATCTTACCAACGCGA

Macacioi TCGAATCCTGCACAGCAGAATGACTAGAGAACCAGTAACAAA-CTCGAT-GGGGGCGGTGGGC--TTT-GCCCAACGTCCCTT--GAC-----GCC-TTGGAT---CGCACGGGCACCTA-
GAGCGCTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGATGCCATGCAATCTCC-TATT-ATTTATAAACATGGCGTTGCCCC--TAATCCC--TCACCCCTTAA-CGCGGGCGGGA-
GGAACTTGGGCGCGTAAGTTGGCCTCCCGTGACTACCTTGTCCCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--GAGACCCC-AATGATC-
AATGTCTTGTGTGC--CGCT-CGAATGC-GCGCTCTCCGA-TCT-ATTATTTACCAACGCGA

Mcitrole TCGAATCCTGCACAGCAGAATGACCAGAGAACCAGTAACAAA-CTCGAT-GGGGGCGGTGGGC--TTT-GCCCAACGTCCCTT--GAC-----GCC-TTGGAT---CGCACGGGCGCCTA-
GAGCGCTCGG-GC--TTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGAYGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGATGCCATGCAATCTCC-TATT-ATTTATAAACATGGCGTTGCCCC--TAATCCC--TCGCCCCTTAA-CGCGGGCGGGA-
GGAACTTGGGCGCGTAAGTTGGCCTCCCGTGACTACCTTGTCCCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--GAGACCCC-AATGATC-
AATGTCTTGTGTGC--CGCT-CGAATGC-GCGCTCTCCGAATCT-ATTATTTACCAACGCGA

Mtriumph TCGAATCCTGCACAGCAGAATGACCAGAGAACCAGTAACAAA-TTCGAT-GGGGGTGGTGGGC--TTT-GCCCAATGTCCCTC--GAC-----GC--TTGGAT---CGCTCCGGCGCGTA-
GAGCGCTTGG-GC--GTTTCGCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCTATCACCCCAGACAT-
GGTGCGTGCATGGGATGCTATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TCGCC-TTTAT-CGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGACGAT-
TTGTCCCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTTGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CGATCGC-GCGCTCTGCGAATCT-
ATTATTTACCAACGCGA

McajcajindTCGAATCCTGCACGGCAGAATGACCAGAGAACTAGTAACAAA-CTCGAT-GAGGGCGGCGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TCGGAT---CGCTCGGGCGCCTA-
GAGCGCTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TTGCTC-TTAA-TGTGGGCGGGA-GGARTTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-
CTTGTCTTGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGGCATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CAATTGC-GCGCTCTGCGAATCT-
ATTATTTACCAACGCGA

Mcajcajwa TCGAATCCTGCACAGCAGAATGACCAGAGAACTAGTAACAAA-CTCGAT-GAGGGCGGCGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TCGGAT---CGCTCGGGCGCCTA-
GAGCGCTCGG-GC--GCTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TTGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-
CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGGCATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CAAGTGC-GCGCTCTGCGAATCT-
ATTATT----------

Mcajcajnt TCGAATCCTGCACGGCAGAATGACCAGAGAACTAGTAACAAA-CTCGAT-GAGGGCGGCGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TCGGAT---CGCTCGGGCGCCTA-
GAGCGCTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TTGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-
CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGGCATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CAATTGC-GCGCTCTGCGAATCT-
ATTATTTACCAACGCGA

Mcajplapng TCGAATCCTGCACAGCAGAATGACCAGAGAACTAGTAACAAA-CTCGAT-GAGGGCGGCGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-
GAGCGCTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TTGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-
CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCATGGCATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CAATTGC-GCGCTCTGCGAATCT-
ATTATT-ACCAACGCGA

Mcajplaqld TCGAATCCTGCACAGCAGAATGACCAGAGAACTAGTAACAAA-CTCGAT-GAGGGCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-
GAGCGCTCGG-GC--GTTTCCCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGTATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--GAATCAC--TTGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-

CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGTGTGTGC--CGCT-CAATCGC-GCGCTTTGCGAATCT-ATTATTTACCAACGCGA

Mcajcum TCGAATCCTGCACAGCAGAATGACCAGAGAACTAGTAACAAA-CTCGAT-GAGGGCGGCGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGTTT-------CTC-G-GC----------GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TTGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCATGGCATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CAATTGC-GCGCTCTGCGAATCT-ATTATTTACCAACGCGA

Mleucind TCGAATCCTGCACAGCAGAATGACCAGAGAACCAGTAACAAA-CTCGAT-GAGGGCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-GAGCACTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TCGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CAATCGT-GCGCTCTGCGAATCT-ATTATTTACCAACGCGA

Mleucpng TCGAATCCTGCACAGCAGAATGACCAGAGAACCAGTAACAAA-CTCGAT-GAGGGCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-GAGCACTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TCGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CAATCGT-GCGCTCTGCGAATCT-ATTATTTACCAACGCGA

Mleucnt TCGAATCCTGCACAGCAGAATGACCAGAGAACCAGTAACAAA-CTCGAT-GAGGGCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-GAGCACTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TCGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CAATCGT-GCGCTCTGCGAATCT-ATTATTTACCAACGCGA

Mleucmar TCGAATCCTGCACAGCAGAATGACCAGAGAACCAGTAACAAA-CTCGAT-GAGGGCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-GAGCACTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TCGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CAATCGT-ACGCTCTGCGAATCT-ATTATTTACCAACGCGA

Mleuckee TCGAATCCTGCACAGCAGAATGACCAGAGAACCAGTAACAAA-CTCGAT-GAGGGCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-GAGCACTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TCGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CAATCGT-ACGCTCTGCGAATCT-ATTATTTACCAACGCGA

Mleuccla TCGAATCCTGCACAGCAGAATGACCAGAGAACTAGTAACAAA-CTCGAT-GAGGGCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGAGCGCCTA-
GAGCACTCGA-GC--GTTTCTCG-C-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TCGCCT-CTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-
CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCATGTGC--CGCT-CAATCGC-
GCGCTCTACGAATCTTATTA-TTACC-ACGCGA

Mleucblu TCGAATCCTGCACAGCAGAATGACCAGAGAACTAGTAACAAA-CTCGAT-GAGGGCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-
GAGCACTCGA-GC--GTTTCTCG-C-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TCGCCT-CTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-
CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCATGTGC--CGCTTCAATCGC-
GCGCTCTACGAATCTTATTATTTACCAACGCGA

Mleucgre TCGAATCCTGCATAGCAGAATGACCAGAGAACTAGTAACAAA-CTTGAT-GAGGGCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-
GAGCACTCGG-GC--GTTTCTCG-C-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TCGCCT-CTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTTATGA-
CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCATGTGC--CGCT-CAATCGC-GCGCTCTACGAATCT-
ATTATTTACCAACGCGA

Mleucnew TCGAATCCTGCATAGCAGAATGACCAGAGAACTAGTAACAAA-CTYGAT-GAGGGCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGRGCGCCTA-
GAGCACTCGG-GC--GTTTCTCG-C-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TCGCCT-CTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-
CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCATGTGC--CGCT-CAATCGC-GCGCTCTACGAATCT---------
----

Mleucbig TCGAATCCTGCACAGCAGAATGACCAGAGAACCAGTAACAAA-CTCGAT-GGGGGCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-
GAGCGCTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGACGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGATGCCATGCAATCTSM-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--CCGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGACGA-
TTTGTCCCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CGATCGC-GCGCTCTGCGAATCT-
AGTATTTACCAACGCGA

Mviriqld TCGAATCCTGCACAGCAGAATGACCAGAGAACCAGTAACAAA-CTCGAT-GAGGGCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-
RAGCRCTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGYATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TCGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-
CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CAATCGC-TCGCTCTGCGA----------
-----

Mviriind TCGAATCCTGCACGGCAGAATGACCAGAGAACTAGTAACAAA-CTCGAT-GAGGGCGGCGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TCGGAT---CGCTCGGGCGCCTA-
GAGCGCTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TTGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-

CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGGCATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CAATTGC-GCGCTCTGCGAATCT-ATTATTTACCAACGCGA

Mquinpng1 TCGAATCCTGCACAGCAGAATGACCAGAGAACTAGTAACAAA-CTCGAT-GAGGGCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-GAGCGCTCGG-GC--GTTTCCCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-GGTGCGTGTATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--GAATCAC--TTGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGTGTGTGC--CGCT-CAATCGC-GCGCTTTGC----------

Mquinpng2 TCGAATCCTGCACAGCAGAATGACCAGAGAACTAGTAACAAA-CTCGAT-GAGGGCGGTGGGC--TTT-GCCCAATGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-GAGCGCTCGG-GC--GTTTCTCGGC-GGTATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-GGTGCGTGTATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TTGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CAATCGC-GCGCTCTGCGAATCT-ATTATTTACCAACGCGA

Mquinqld TCGAATCCTGCACAGCAGAATGACCAGAGAACTAGTAACAAA-CTCGAT-GAGGGCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-GAGCGCTCGG-GC--GTTTCCCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-GGTGCGTGTATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--KAATCAC--TTGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGTGTGTGC--CGCT-CAATCGC-GCGCTTTGCGAATCT-ATTATTTACCAACGCGA

Mdealqld TCGAATCCTGCATAGCAGAATGACCAGAGAACCAGTAACAAA-CTCAAT-GGGGGTGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-GAGCGCTTGG-GC--GTTTCTCGGCGGGAATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--CCGCCC-TTAA-TGTAGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGACGAT-TTGTCCCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CGATCGC-GCGCTCTGCGAATCT-ATTATTTACCAACGCGA

Mdealpng TCGAATCCTGCATAGCAGAATGACCAGAGAACCAGTAACAAA-CTCAAT-GGGGGTGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-GAGCGCTTGG-GC--GTTTCTCGGCGGGAATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-GGTGCATGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--CCGCCC-TTAA-TGTAGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGACGAT-TTGTCCCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CGATCGC-GCGCTTTGCGAATCT-ATTA-TTACCAACGCGA

Mdealwa TCGAATCCTGCACAGCAGAATGACCAGAGAACCAGTAACAAA-CTCAAT-GGGGGTGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-GAGCGCTTGG-GC--GTTTCTCGGCGGGAATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--CCGCCC-TTAA-TGTAGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGACGAT-TTGTCCCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGCC-CGCT-CGATCGC-GCGCTCTGCGAATCT-ATTATTTACCAACGCGA

Mstenost TCGAATCCTGCACAGCAGAATGACCAGAGAACTAGTAACAAA-CTCGAT-GAGGGCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-
GAGCGCTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TTGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-
CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CAATCGC-GCGCTCTGCGAATCT-
ATTATTTACCAACGCGA

Msaligna1 TCGAATCCTGCACAGCAGAATGACCAGAGAACTAGTAACAAA-CTCGAT-GAGGGCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-
GAGCGCTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGTATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TTGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-
CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CAATCGC-GCGCTCTGCGAATCT-
ATTATTTACCAACGCGA

Marcana1 TCGAATCCTGCACAGCAGAATGACCAGAGAACTAGTAACAAA-CTCGAT-GAGGGCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-
GAGCGCTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGTATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TTGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-
CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CAATCGC-GCGCTCTGCGAATCT-
ATTATTTACCAACGCGA

Margqld TCGATTCCTGCACAGCAGAATGACCAGAGAACCAGTAACAAATCTCGAT-GGGGGCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-
GAGCGCTTGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGGAAACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--CCGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGACGA-
TTTGTCCCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CGATCGC-GCGCTCTGCGAATCT-
ATTATTTACCAACGCGA

Margwa TCGAATCCTGCACAGCAGAATGACCAGAGAACCAGTAACAAATCTCGAT-GGGGGCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-
GAGCGCTTGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGGAAACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--CCGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGACGA-
TTTGTCCCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CGATCGC-GCGCTCTGCGAATCT-
ATTATTTACCAACGCGA

Mferrugi TCGAATCCTGCACAGCAGAATGACCAGAGAACTAGTAACAAA-CTCGAT-GAGGGCGGTGGGC--CTT-GCCCAACATCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-
GAGCACTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-
GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TCGCCC-TTAA-TGTGGGCGAGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-
CTTGTCTCGGTTGGCCTAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-ATTGTCGCGTGTGC--CGCT-CAATCGC-GCGCTCTGCGAATCT-
ATTATTTACCAACGCGA

Mclarkso TCGAATCCTGCACAGCAGAATGACCAGAGAACTAGTAACAAA-CTCGAY-GAGGGCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-
GAGCGCTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCRTCACCCCAGACAT-

GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--TTGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGATGA-CTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCGCGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGT--CGCT-CAATTGC-GCGCTCTGCGAATCT-ATTATTTACCAACGCGA

Mnervosa TCGAATCCTGCAYAGCAGAATGACCAGAGAACCAGTAACAAA-CTCGAT-GRGGGCGRTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTYGGGCGYCTW-GAGCGCTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGAYGCTCCCATCACCCCAGACAT-GGTGCGTGCATGGGATGCCATGCAATCTCC-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--YCGCCC-TTAA-TGTGAGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGAYGA-YTTGTCYCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCAYGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CRATCGC-GCGCTCTGCGAATCT-AKTA-TTACCAACGCGA

Mfluviat1 TCGAATCCTGCACAGCAGAATGACCAGAGAACCAGTAATAAA-CTCGAT-GGGGCCGGTGGGC--TTT-GCCCAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGCGCCTA-GAGCGCTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACCCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGACGCTCCCATCACCCCAGACAT-GGTGCGTGCATGGGATGCCATGCAATCTCA-TATTTATTTATAAACATGGCGTTGCCCC--TAATCAC--CCACCC-TTAA-TGTGGGCGGGA-GGAATTTGGGCGCGTAAGTTGGCCTCCCGTGACGA-TTTGTCTCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGC--CGCT-CGATCGC-GCGCTCTGCGAATCT-ATTATTTACCAACGCGA

Mlasiand TCGAATCCTGCACAGCAGAATGACCAGAGAACCAGTAACAAA-CTCGAT-GGGGGCGGTGGGC--TTT-GCCTAACGTCCCTC--GAC-----GC--TTGGAT---CGCTCGGGTGCCTA-GAGCGCTCGG-GC--GTTTCTCGGC-GGCATTAACG-AACTCCGGCGCGGAATGCGCCAAGG-AACT-CAAACAA-GAGTGCGATGCTCCCATCACCCCAGACAT-GGTGTGTGCATGGGATG-TATGCAATCTCC-TATT-ATTTATAAACATGGCGTTGCCCC--AAATCAC--TCGCCC-TTAA-TGTGGGCGGGA-GGAATTTGGGTGCGTAAGTTGGCCTCCCGTGACGACTTTGTCCCGGTTGGCCCAAAATCGAGCGTCGGAGCGA-CTAGCACCACGACATTCGGTGGTTGA-T--AAGACCCC-AATGATC-AATGTCGCGTGTGT--CGCT-CGATCGC-ACGCTTTGCGAATCT-ATTATTTACCAACGCGA

(b)

Eucraver CCCGACCATT CCTTACACAT CATCCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTAGAA AAAGTCTTAT CCAGACTCCA GAATTTTTTT TATTTT---C
AAACA----- -GA-ATAGGA TAAATCGTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTCTAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA ATCAGTTCTT CAAAAGATTT ATCAGACCAC GG-----AGT AAATGATTTA ATCAATGAAT
ATTCGATTCT TTCTTCAACT TAGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT TCGCGTCGTC ATTAATCATT TGAGATAGTA TTCAGTACGT ATACGTATAT ACATAGGTTT
ATCCTTTCCC TTTCTCGAGT TTCGAGAAAA A-G------A TTCC-TTTAC CAACGCAACG TGGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTATC CTATCCTTTT TTTATTCTCG
CTT-----TA TGAA------ CCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Euccoola CCCGACCATT CCTTACACAT CATCCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTAGAA AAAGTCTTAT CCAGACTCCA GAATTTTTTT TATTTT---C
AACA------ -GA-ATAGGA TAAATCGTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTCTAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA ATCAGTTCTT CAAAAGATTT ATCAGACCAC GG-----AGT AAATGATTTA ATCAATGAAT
ATTCGATTCT TTCTTCAACT TAGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT TCGCGTCGTC ATTAATCATT TGAGATAGTA TTCAGTACGT ATACGTATAT ACATAGGTTT
ATCCTTTCCC TTTCTCGAGT TTCGAGAAAA A-G------A TTCC-TTTAC CAACGCAACG TGGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTATC CTATCCTTTT TTTATTCTCG
CTT-----TA TGAA------ CCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Euccamal CCCGACCATT CCTTACACAT CATCCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTAGAA AAAGTCTTAT CCAGACTCCA GAATTTTTTT TATTTT---C
AACA------ -GA-ATAGGA TAAATCGTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTCTAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA ATCAGTTCTT CAAAAGATTT ATCAGACCAC GG-----AGT AAATGATTTA ATCAATGAAT
ATTCGATTCT TTCTTCAACT TAGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT TCGCGTCGTC ATTAATCATT TGAGATAGTA TTCAGTACGT ATACGTATAT ACATAGGTTT
ATCCTTTCCC TTTCTCGAGT TTCGAGAAAA A-G------A TTCC-TTTAC CAACGCAACG TGGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTATC CTATCCTTTT TTTATTCTCG
CTT-----TA TGAA------ CCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Ooctodon CCCGACCATT CCTTACACAT CATCCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTAGAA AAAGTC---- -CAGGCCCCA GAATTTTTTG GACTTTTT-C
AAAAA----- -GA-ATAGGA TAAATCGTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTATAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA ATCAGTTCTT CAAAAGATTT CTCAGACCAT GG-----AGT AAATGATTTA ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT TCGTGTCGTC ATTAATCATT TGAGATAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G------A TTCC-TTTAC CAACGCAACG TGGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTATC CTATCCTTTT TTTATTCTCG
CTTCGCTTTA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Caloquad CCCGACCATT CCTTACACAT CATCCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCGGGTCCCA GAATTTTTTG GATTTTTT-
C AAAAAGAAAA AGA-ATAGGA TAAGTCCTTA AGTTAAGGGG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTATAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTCAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT TCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G------A TTCC-TTTAC CAACGCAACG CCGTCAACTC CATTTGTTAG AACAGCTTCC ATTGAGTCTC TGCACCTATC CTATCCTTTT TTGATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Cpachyph ?????????? ?????????? ?????????? ?????????G ACTTGGTTCT ATGTCAATTA AAAAGATGAA AGGGGTATAA AAAGTCTTAT ACAGGCCCCA GAATTTTTTT TCTTTTTT-C AAAAA----- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTATAAA TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTCAGTTTTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATGAATGAAT ATTCGATTCT TTCTTCAACT TCGAATTGAT TTGATTCACA AAAATTCTTT CCT------C ATATAAAAAT TCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ATATAGGGTT ATCCTTTCCC TTTCTCGAGT TTCGAGAAAA AA-------A TTCC-TTTAC CAACGCAACG TGGTCAACTC CATTTGTTCG AACAGCTCCC ATTGAGTCTC TGCACCTATC CTATCC-TTT TTTATTCTCG CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTTGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Cviminal CCCGACCATT CCTTACATAT CATCCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGATGAA AGGGGTATAA AAAGTCTTAT ACAGGCCCCA GAATTTTTTT TCTTTTTT-C AAAAA----- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTATAAA TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTCAGTTTTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATGAATGAAT ATTCGATTCT TTCTTCAACT TCGAATTGAT TTGATTCACA AAAATTCTTT CCT------C ATATAAAAAT TCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ATATAGGGTT ATCCTTTCCC TTTCTCGAGT TTCGAGAAAA AA-------A TTCC-TTTAC CAACGCAACG TGGTCAACTC CATTTGTTCG AACAGCTCCC ATTGAGTCTC TGCACCTATC CTATCC-TTT TTTATTCTCG CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTTGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mstyphel CCCGACCATT CCTTACACAT CATCCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTT--C AAAAA----- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTATAAA TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTCAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT TCGCGTCGTC ATTA------ TATTATAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT ATCCTTT--- ---CTCGAGT TTCGATAAAA A-G------A TTCC-TTTAC CAACGCAACG TGGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTATC CTATCCTTTT TTTATTCTCG CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mpancher CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTCAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCC-TTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTATC CTATCCTTTT TTGATTCTCG CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mcornuco CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTCAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GTGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCC-TTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mdeanei CCCGACCATT CCTTACACAT CATCCTCATT TTACTAGAGG ACTTGGTTCT ATGTCAATTA AAAAGATGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGATC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTATAAA TTTCATTGTT GTCAGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTCAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT TCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT

ATCCTTTCCC TTTCTCGAGT TTCGAGAAAA A-G------A TTCC-TTTAC CAACGCAACG TGGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTATC CTATCCTTTT TTTATTCTCG
CTT-----TA TGAATATGAA GCCTTATTAT TTTG-----T TGGTTTTTGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mericifo CCCGACCATT TCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGATGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG
GATTTTTTTC AAA------- -GA-CTAGGA TAAATCCTTA AGTTAAGGAG TAAAATGATC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC
TTACTATAAA TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTCAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC
ATCAATGAAT ATTTAATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT TAGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT
ACATAGGGTT ATCCTTTCCC TTTCTCGAGT TTCGAGAAAA A-G------A TTCC-TTTCC CAACGCAACG TGGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTATC CTATCCTTTT
TTTATTCTCG CTT-----TA TGAA------ GACTTATTGT TTTG-----T TGGTTTTTGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mdecussa CCCGACCATT TCTTACACAT CATTCTCATT TTACTAGATG ACTTAGTTCT ATGTCAATTA AAAAGATGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-C
AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGATC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTATAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTCAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT TCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ATATAGGGTT
ATCCTTTCCC TTTCTCGA-- -----GAAAA A-GAAAAAGA TTCC-TTTAC CAACGCAACG TGGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTATC CTATCCTTTT TTTATTCT-G
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTTGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mlinarii CCCGACCATT CCTTACACAT CATCTTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGATGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTATAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTCAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATAGAAAAAT TCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTAGAGAAAA A-G------A TTCC-TTTAC CAACGCAACG TGGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTATC CTATCCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTTGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mtrichos CCCGACCATT CCTTACACAT CATCCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGATGAA AGGGGTATCA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTATAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTCAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT TCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTAGAGAAAA A-G------A TTCC-TTTAC CAACGCAACG TGGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTATC CTATCCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTTGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Macacioi CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCC-TTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

```
Mcitrole    CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCC-TTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mtriumph  CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCC-TTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

McajcajindCCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

McajcajwaCCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCC-TTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mcajcajnt  CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTGTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mcajplapng              CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG
GATTTTTT-C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC
TTACTAGAAA TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC
ATCAATGAAT ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT
```

ACATAGGGTT ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----
CCTTTT TTTATTCTCG CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mcajplaqld CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG
GATTTTTT-C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC
TTACTAGAAA TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC
ATCAATGAAT ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT
ACATAGGGTT ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----
CCTTTT TTTATTCTCG CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mcajcum CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mleucind CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mleucpng CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mleucnt CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mleucmar CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mleuckee ?????????? ?????????? ???TCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-C AAA-------GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTA-TTCCA GGGTTTCTCT GAA

Mleuccla ?????????? ?????????? ?????????? ??ACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCC-TTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTA-TTCCA GG-TTTCTCT GA?

Mleucblu ?????????T CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCC-TTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mleucgre CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCC-TTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mleucnew CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT

ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCC-TTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mleucbig CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mviriqld CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mviriind CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mquinpng1 CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG
GATTTTTT-C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC
TTACTAGAAA TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC
ATCAATGAAT ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT
ACATAGGGTT ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----
CCTTTT TTTATTCTCG CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mquinpng2 CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG
GATTTTTT-C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC
TTACTAGAAA TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC
ATCAATGAAT ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT
ACATAGGGTT ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----
CCTTTT TTTATTCTCG CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mquinqld CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mdealqld ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????CGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-C AAA------- -GA-ATAGGA
TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA TTTCATTGTT GTCGGTATTG
ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT ATTCGATTCT TTCTTCAACT
TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT ATCCTTTCCC TTTCTCGAGT
TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG CTT-----TA TGAA------
GCCTTATTGT TTTG-----T TGGTTTTCGT AAA-CAGGAT TTGGCTCAGG ATTGCCCATC TTTAA????? ?????????? ???

Mdealpng CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mdealwa CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mstenost CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Msaligna1 CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT

ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Marcana1 CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Margqld CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCC-TTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Margwa CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCC-TTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mferrugi CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCC-TTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mclarkso CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAG GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mnervosa CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCC-TTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mfluviat1 CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CACGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCC-TTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

Mlasiand CCCGACCATT CCTTACACAT CATTCTCATT TTACTAGATG ACTTGGTTCT ATGTCAATTA AAAAGACGAA AGGGGTATAA AAAGTCTTAT CCAGGCCCCA GAATTTTTTG GATTTTTT-
C AAA------- -GA-ATAGGA TAAATCCTTA AGTTAAGGAG TCAAATGGTC CTTTTTTGGG GATAGAGGGA CTTGAACCCT CATGATTTTT AAAGTCGACG GATTTTCCTC TTACTAGAAA
TTTCATTGTT GTCGGTATTG ACATGTAGAA TGGGACTCTA TCTTTATTCT CGTCCGATTA GTGAGTTCTT CAAAAGATTT ATCAGACCAT GG-----AGT AAATGATTTC ATCAATGAAT
ATTCGATTCT TTCTTCAACT TCGAATTGAT T-----CACA ACAATTCTTT CCT------C ATATAAAAAT GCGCGTCGTC ATTA------ -----TAGTA TTCAGTACGT ATACGTATGT ACATAGGGTT
ATCCTTTCCC TTTCTCGAGT TTCGATAAAA A-G-AAAAGA TTCCCTTTAC CAACGCAACG TCGTCAACTC CATTTGTTAG AACAGCTCCC ATTGAGTCTC TGCACCTAT- ----CCTTTT TTTATTCTCG
CTT-----TA TGAA------ GCCTTATTGT TTTG-----T TGGTTTTCGT AAAACAGGAT TTGGCTCAGG ATTGCCCATC TTTAATTCCA GGGTTTCTCT GAA

(c)

Eucraver TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT ATGTTGTTTT
CGAAATCTGG TTCTTTTAGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTACTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCATCGC GAATGAAACG ATTCGAATTT GAG-
AATTTT ATGAAAATAT ACGGAATCAT GGATTCTTTG AGATTTCATC TAATCTATTA GAAATTTCTA TATCTTGTTT GGATATATAC TT---AAA-- ---------- ---CATGTAT TT-TTTTTTT CTAGATAATT
ATTTCTATTT CTAGATAGGG AGATAATGGG GTTTTTTT-C TAACGAATCT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCGAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCTACCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCGTCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TTTTAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----CTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CATATATT-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAACCTTTCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTTA- ---TTTTTTT ---
----TCT TTATGTAAGA AAGATTTCAG TTGCTACAAT GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGTTATAT AGTTATTAGT
TCAC-AGT-A GGGGTCTGTC CA

Euccoola TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT ATGTTGTTTT
CGAAATCTGG TTCTTTTAGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTACTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCATCGC GAATGAAACG ATTCGAATTT GAT-
AATTTT ATGAAAATAT ACGGAATCAT GGATTCTTTG AGATTTCATC TAATCTATTA GAAATTTCTA TATCTTGTTT GGATATATAC TT---AAA-- ---------- ---CATGTAT TT-TTTTTTT CTAGATAATT
ATTTCTATTT CTAGATAGGG AGATAATGGG GTTTTTTT-C TAACGAATCT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCGAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACCCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCTACCT
AATGAATTAT TAGGATTC-A TTTTTCAATA TAATCTTACG TATTCATAGG TTCCATCGTT CCCGTCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TTTTAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----CTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CATATATT-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAACCTTTCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTTA- ---TTTTTTT ---
----TCT TTATGTAAGA AAGATTTCAG TTGCTACAAT GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGTTATAT AGTTATTAGT
TCAC-AGT-A GGGGTCTGTC CA

Euccamal TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT ATGTTGTTTT
CGAAATCTGG TTCTTTTAGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTACTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCATCGC GAATGAAACG ATTCGAATTT GAG-
AATTTT ATGAAAATAT ACTGAATCAT GGATTCTTTG AGATTTCATC TAATCTATTA GAAATTTCTA TATCTTGTTT GGATATATAC TT---AAA-- ---------- ---CATGTAT TT-TTTTTTT CTAGATAATT
ATTTCTATTT CTAGATAGGG AGATAATGGG GTTTTTTT-C TAACGAATCT TTATTTTGTT TTGCCTTTGA ----TCATAT TATCATATTG GATCGAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCGGG TTCGTTCCGC CATCCTACCT
AAGGAATTAT TAGGATTC-A TTTTTCAATA TAATCTTACG TATTCATAGG TTCCATCGTT CCCGTCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TTTTAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----CTTAT GGATCAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC CTAAACCTTA CATATATT-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAACCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT ---
--TTTGT TTATGTAAGA AAGATTTCAG TTGCTACAAT GATATGACCA ATATATCATA TCTTGACGGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGTTATAT AGTTATTAGT
TCAC-AGT-A GGGGTCTGTC CA

Ooctodon TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT ATGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTACTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TCG-

AATTTT ATGAAAATAT ACTGAATCAT GGATTCTTTG AGATTTCATC TAATCTATTA GAAATTTCTA TATCTTGTTT GGATATATAC TT-------- ---------- ---CA----- ---------- CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC ---------A TAACGAATCT TTATTTTGTT TTGCCTTTGA ----TCATAT TATCATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -CTAATAAAA
ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCACCT AATGAATTAT
TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA TTTGTTCTTG AGTCAA-
TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT GAGATGACTC
ATAAACCTTA CATATATTTG GAATCCTATA TCATTGATAT TCTTTT--CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCCGATTGA- ---TTTTTTT TTTGTTTATT
TTATGCAAGA AAAATTTCAG TTGCTACAAT GATATGACCA ATAGATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGTTCTAT AGTTATTATT TCAC-
AGTTA GGGGTCGGTC CA

Caloquad TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCAAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTG-
AATTTT ATGAAAATAT ACTGAATCGT GGATTCTTTG AAATTTCATC TAATCTTTTA GAAATTTCTA TAGATTGTTT GGATATCTAT TT---AAA-- ---------- ---CATGTAT TT---TTTTT CTAGATAATT
ATTT------ CTAGATAAT- -------GTC GTTTTTTT-A TAACGAATCT TTATTTTGTT TTGCCTTTGA ----TCATAT TATCATATTG TATCAAACAA GATTGAGTAA T--------- ---------- -CTAATAAAA
ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCACCT AATGAATTAT
TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA TTTTTTATTG AGTCAA-
TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT GAGATGACTC
CTAAACCTTA CATATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT ----------
TTGTGCAAGA AAAATTTCAG TTGCTACAAT GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-A
GGGGTCTGCC CA

Cpachyph TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCTATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTACTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
AATTTT ATGAAAATAT ACTGAATCAT GGATTCTTTG AAATTTCATC TAATCTCTTA GAAATTTCTA TAGATTCTTT GGATATATAT TT---AAA-- ---------- ---CATGTAT TT--TTTTTT CTAGATAATT
ATTTCTATTT CTAGATAAT- -------GTC GTTTTTTT-A TAACGAATCT TTATTTTGTT TTGGCTTTGA ----TCATAT TATCATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -CTAATAAAA
ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAACTCATG AATTCYCGGA ATAAATGAAT TGGTCCCKGG TTCGTTCCGC CATCCCACCT AATGAATTAT
TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA TTTGTTCTTG AGTCAA-
TTT TCTCAGTCTT TATTGACTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCC GTATTGATGC TTTATTACAT TGCCTTTTAT GAGATGACTC
ATAAACCTTA CATATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT ----------
TTGTGCAAGA AAAATTTCAG TTGCTACAAT GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAT-AGT-A
GGGGTCTGTC CC

Cviminal TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCTATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTACTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
AATTTT ATGAAAATAT ACTGAATCAT GGATTCTTTG AAATTTCATC TAATCTCTTA GAAATTTCTA TAGATTCTTT GGATATATAT TT---AAA-- ---------- ---CATGTAT TT--TTTTTT CTAGATAATT
ATTTCTATTT CTAGATAAT- -------GTC GTTTTTTT-A TAACGAATCT TTATTTTGTT TTGGCTTTGA ----TCATAT TATCATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -CTAATAAAA
ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAACTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCACCT AATGAATTAT
TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA TTTGTTCTTG AGTCAA-
TTT TCTCAGTCTT TATTGACTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCC GTATTGATGC TTTATTACAT TGCCTTTTAT GAGATGACTC
ATAAACCTTA CATATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT ----------

TTGTGCAAGA AAAATTTCAG TTGCTACAAT GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAT-AGT-A
GGGGTCTGTC CC

Mstyphel TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTCCC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTGTTT CTCAATTCCA TCTCTACTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTG-
AATTTT ATGAAAATAT ACTGAATCAT GGATTCTTTG AAATGGAATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATATAT TTATTAAA-- ---------- ---CATGTAT TT-------- ---------- -TTT---
TTT CTAGATAAT- -------GTC GTTTTTTT-A TAACGAATCT TTATTTTGTT TTGCCTTTGA ----TCATAT TATCATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -CTAATAAAA
ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCCGG TTCGTTCCGC CATCCCACCT AATGAATTAT
TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA TTTGTTCTTG AGTCAA-
TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GAATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT GAGATGACTC
ATAAACCTTA CATATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT ---------- -
TGTGCAAGA AAAATTTCAG TTGCTACAAT GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-ATT-A
GGGGTCTGTC CA

Mpancher TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT GGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATATAT TT---AAA-- ---------- ---CATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTTT-A TAACGAATCT TTATTTTGTT TTGCCTTTGA ----TCATAT TATCATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCACCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCCGATTTA- ---TTTTTTT ---
------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATCTATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-A
GGGATCTGTC CA

Mcornuco TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT GGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATATAT TT---AAA-- ---------- ---CATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATCT TTATTTTGTT TTGCCTTTGA ----TCATAT TATCATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCACCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAT GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-A
GGGATCTGTC CA

Mdeanei TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTACTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
AATTTT ATGAAAATAT ACTGAATCAT GGATTCTTTG AAATTTCATC TAATCTCTTA GAAATTTCTA TAGATTGTTT GGATATATAT TT---AAA-- ---------- ---CATGTAT TT---TTTTT CTAGATAATT

ATTTCTATTT CTAGATAAT- -------GTC GTTTTTTT-A TAACGAATCT TTATTTTGTT TTGCCTTTGA ----TCATAT TATCATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -CTAATAAAA
ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCACCT AATGAATTAT
TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA TTTGTTCTTG AGTCAA-
TTT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA ATCTAGTTAT GGATGAATCC GTATTGATGC TTTATTACAC TGCCTTTTAT GAGATGACTC
ATAAACCTTA CATATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT ----------
TTGTGCAAGA AAAATTTCAG TTGCTACAAT GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-A
GGGGTCTGTC CA

Mericifo ?????CTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA CGAAATCTGG
TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTACTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-CATTTT
ATGAAAATAT ACTGAATCAT GGATTCTTTG AAATGTCATC TAATCTCTTA GAAATTTCTA TAGATTGTTT GGATATATAT TT---AAA-- ---------- ---CATGTAT TT----TTTT CTAGATAATG
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTTT-A TAACGAATCT TTATTTTGTT TTGCCTTTGA ----TCATAT TATCATATTG TATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCACCT
AATGAATTAT TAGGATTCTA TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TTT TCTCAGTCTT TATTGGCTCG AGGCTCTT-- TTTTTTTTT- -ATGA????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??

Mdecussa TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCTTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTATTT CTCAATTCCA TCTCTACTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT
TTTTCATTTT ATGAAAATAT ACTGAATCAT GGATTCTTTG AAATTTCATC TAATCTCTTA GAAATTTCTA TAGATTGTTT AGATATATAT TT---AAACA ATATATATTT AAACATGTTT TT----TTTT
CTAGAAAATT ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATCT TTATTTTGTT TTGCCTTTGA ----TCATAT TATCATATTG GATCAAACAA GATTGAGTAA T--------- --------
--- -CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCACCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TTT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCC GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CATATATG-G GAATCCTATA TCATTGATAT TCTTTATTCT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT -
--------- -TGTGCAAGA AAAATTTCAG TTGCTACAAT GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCACCAGT-
A GGGGTCTGTC CA

Mlinarii TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAAGAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTACTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTG TTT-
CATTTT ATGAAAATAT ACTGAATCAT GGATTCTTTG AAATTTCATC TAATCTCTTA GAAATTTCTA TAGATTGTTT GGATATATAT TT---AAA-- ---------- ---CATGTAT TT-TTTTTTT CCCGATAATT
ATTTATATTT CTAGATAAT- -------GTC TTTTTTTT-A TAACGAATCT TTATTTTGTT TTGCCTTTGA ----TCATAT TATCATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -CTAATAAAA
ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCAGG AATTCCCGGA ATAAATGAAT TGGTCCCGGG TTCGTTCCGC CATCCCACCT AAGGAATTTT
TAGAATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA TTTGTTCTTG AGTCAA-
TTT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCC GTATTGATGC TTTATTACAC TGTCTTTTAT GAGATCACTC
ATAAACCTTA CATTTATG-G GAATCCTATA TCATTGATAT TATTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT -----TTTTT
TGGGGCAAAA AAAATT???? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??

Mtrichos TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTACTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
AATTTT ATGAAAATAT ACTGAATCAT GGATTCTTTG AAATGGAATC TAATCTCTTA GAAATTTCTA TAGATTGTTT GGATATATAT TT---AAA-- ---------- ---CATGTAT TTTTTTTTTT
CTCGATAATT ATTTCTATTT CTAGATAATG AGATAATGTC TTTTTTTTTA TAACGAACCT TTATTTTGTT TTGCCTTTGA ----TCATAT TATCATATTG GATTAAACAA GATTGAGTAA T--------- ------
---- -CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCCCATG AATTCTCGGA ATAAATGAAT TGGCCCCTGG TTCGTTCCGC CATCCCACCT
AATGAATTTT TAGAATTC-A TTTATCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA --GGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATAAAA
TTTGTTCTTG AGTCAA-TTT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATAGA -----GTTAT GGATGAATCC GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CATATATG-G AAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------T TTGGGCAAGA AAAATTTAAG TTGCTACAAT GATATGACCA ATATATCATA TCTTGACGGC TTT-TTTGTA TCCAGATAAG GGGAAACGAT GAGTTAGTTA TTAGT----- ---------- TCAC-
AGT-A GGGGTCTGTC CA

Macacioi TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT GGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATATAT TT---AAA-- ---------- ---CATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATCT TTATTTTGTT TTGCCTTT-- -ATATCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCACCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCCTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mcitrole TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT GGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATATAT TT---AAA-- ---------- ---CATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATCT TTATTTTGTT TTGCCTTT-- -ATATCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCACCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCACCAGT-
A GGGATCTGTC CA

Mtriumph TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATTTATTA GAAATTTCTA TAGATTGTTT GGATATCTAT TT---AAA-- ---------- ---CATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCACCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA

TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------T TTGGGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACGGC TTT-TTTGTA TCCAGATAAG GGGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-
AGT-A GGGATCTGTC CA

McajcajindTTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

McajcajwaTTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATTTATTA GAAATTTCTA TAGATTGTTT GGATATCTAT TT---AAA-- ---------- ---CATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCACCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------T TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACGGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mcajcajnt TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAG AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGGCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mcajplapng TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mcajplaqld TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCAWTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT -
--------- TTGTGCAAGA AAAATTTTAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mcajcum TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mleucind TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA

TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mleucpng TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mleucnt TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAG AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mleucmar TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAG AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGGCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACYC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCACCAGT-
A GGGATCTGTC CA

Mleuckee TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAG AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGGCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mleuccla TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATTTATTA GAAATTTCTA TAGATTGTTT GGATATCTAT TT---AAA-- ---------- ---CATGTAT TT--TTTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCACCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------T TTGGGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACGGC TTT-TTTGTA TCCAGATAAG GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mleucblu TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATTTATTA GAAATTTCTA TAGATTGTTT GGATATCTAT TT---AAA-- ---------- ---CATGTAT TT--TTTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCACCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------T TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACGGC TTT-TTTGTA TCCAGATAAG GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mleucgre TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATTTATTA GAAATTTCTA TAGATTGTTT GGATATCTAT TT---AAA-- ---------- ---CATGTAT TT--TTTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCACCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA

TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------T TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACGGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mleucnew TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATTTATTA GAAATTTCTA TAGATTGTTT GGATATCTAT TT---AAA-- ---------- ---CATGTAT TT--TTTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCACCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------T TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACGGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mleucbig TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAG AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGGCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mviriqld TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACYC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mviriind TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mquinpng1 TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mquinpng2 TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAA GAGTTGGTTA TTAGT----- ---------- TCACCAGT-
A GGGATCTGTC CA

Mquinqld TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA

TTTTTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mdealqld TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAG AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mdealpng TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAG AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCACCAGT-
A GGGATCTGTC CA

Mdealwa TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAG AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mstenost TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Msaligna1 TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Marcana1 TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCGATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCACCAGT-
A GGGATCTGTC CA

Margqld TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATTTATTA GAAATTTCTA TAGATTGTTT GGATATCTAT TT---AAA-- ---------- ---CATGTAT TT--TTTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCACCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA

TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------T TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACGGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Margwa TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATTTATTA GAAATTTCTA TAGATTGTTT GGATATCTAT TT---AAA-- ---------- ---CATGTAT TT--TTTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATT AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCACCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -GGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------T TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACGGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mferrugi TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATTTATTA GAAATTTCTA TAGATTGTTT GGATATCTAT TT---AAA-- ---------- ---CATGTAT TT--TTTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCACCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------T TTGGGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTKGACGGC TTT-TTKGTA TCCAGATAAG GGGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-
AGW-A GGGATCTGTC CA

Mclarkso TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------- TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACTGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mnervosa TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATTTATTA GAAATTTCTA TAGATTGTTT GGATATCTAT TT---AAA-- ---------- ---CATGTAT TT--TTTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCACCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------T TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACGGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mfluviat1 TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATTTATTA GAAATTTCTA TAGATTGTTT GGATATCTAT TT---AAA-- ---------- ---CATGTAT TT--TTTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCACCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------T TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACAGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA

Mlasiand TTTGTCTAGA TGTGATCCAA GCGGGTTCAA GTGCCTGAAG AGCATATTTA CCGAAACAAA TACGATTACC TCGATAAGAT ATTCCTTTCA TTCTTCCTCT GTGTTGTTTA
CGAAATCTGG TTCTTTTGGG GTTATAGTTG ATGGTTCTTT CTCAATTCCA TCTCTATTAC AGAACCGGAC ATGAGAGTTT CTTCTCATCC GGCTCCTCGC GAATGAAACG ATTCGAATTT TTT-
CATTTT ATGAAAATAT ACTGAATCAT AGATTCTTTG AAATTTCATC TAATCTATTA GAAATTTCTA TAGATTGTTT GGATATCGAT TT---AAA-- ---------- ---TATGTAT TT---TTTTT CTAGATAATT
ATTTCTATTT CTAGATAATG AGATAATGTC GTTTTTT--A TAACGAATTT TTATTTTGTT TTGCCTTTGA ----TCATAT TATTATATTG GATCAAACAA GATTGAGTAA T--------- ---------- -
CTAATAAAA ACCTTCGCGG GCGAATATTT ACTCTTTCAA TATCTATTTT AGTTGTAGGG TTAGCTCATG AATTCTCGGA ATAAATGAAT TGGTCCCTGG TTCGTTCCGC CATCCCCCCT
AATGAATTAT TAGGATTC-A TTTTTCAATA GAATCTTACG TATTCATAGG TTCCATCGTT CCCATCGCTT CGC-AATTAA -TGGTTAGGT TTGAATTCTA CAATGGAGCC CCTCATGAAA
TTTGTTCTTG AGTCAA-TCT TCTCAGTCTT TATTGGCTCG AGGCTCTTGA TTTTTTT--C TATGAA--TA GATTCATATA -----GTTAT GGATGAATCA GTATTGATGC TTTATTACAC TGCCTTTTAT
GAGATGACTC ATAAACCTTA CACATATG-G GAATCCTATA TCATTGATAT TCTTTTT-CT TTCTTTCTCT CAATCTTCCC TTTATCTGCA TACTTTTTTT -ATATCATAA TCAGATTGA- ---TTTTTTT --
-------T TTGTGCAAGA AAAATTTCAG TTGCTACAAC GATATGACCA ATATATCATA TCTTGACGGC TTT-TTTGTA TCCAGATAAT GTGAAACGAT GAGTTGGTTA TTAGT----- ---------- TCAC-AGT-
A GGGATCTGTC CA