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VULNERABILITY OF NORTH QUEENSLAND RAINFOREST PLANTS TO PREDISPERSAL SEED PREDATION BY INSECTS

Thesis submitted by

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for the degree of Doctor of Philosophy

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ABSTRACT

Seed predation by animals is one of the major causes of death for seeds in tropical rainforests. By reducing seed availability in tropical rainforests seed predation may affect the recruitment of new plants, as has been shown in other types of ecosystems. Seed predation may therefore be one of the factors that determines the species composition of tropical rainforests. The purpose of this thesis was to determine what factors were associated with the vulnerability of rainforest plants to seed predation, what types of species were most vulnerable to seed predation and hence what types of species were most likely to be limited in abundance by seed predation. This study focussed on predispersal seed predation by insects in the tropical rainforests of north Queensland, on the Atherton Tablelands.

The presence and intensity of insect predispersal seed predation (IPSP) on the seed crops of rainforest plants was assessed and associations between the presence and intensity of IPSP, and species and site characteristics were tested.

Five factors were found to be associated with variations in IPSP:

1) Plants that produced fruit with a hard, thick pericarp layer (fruit wall) were less likely to be attacked by IPSPs than those with a thin hard pericarp or no hard pericarp at all.

2) The total fruit pericarp thickness was also inversely related to the likelihood that any seeds within were attacked. This relationship was caused by the confounding effects of hard pericarp thickness, which is positively correlated with total pericarp thickness.

3) Differences in the intensity of IPSP found among plants of different families suggest that the vulnerability of plants to IPSP was also associated with phylogeny. Plants belonging to the Lauraceae had particularly low intensities of IPSP while plants belonging to the Euphorbiaceae and the Sapindaceae had particularly high intensities of IPSP.

4) Native species of plant were more likely to be attacked by IPSP than exotic species. This was not due to any confounding phylogenetic differences.

5) There were indications that shade dwelling species of plant were less likely to be attacked by IPSPs than species that grew in well lit conditions. However, this association may be due to confounding differences in growth form.

Native species that grew in high light conditions and had soft and/or thin fruit pericarp layers were considered to be more vulnerable to IPSP than species that were exotic, grew in low light conditions and that had thick hard seed pericarp layers. Hence seed availability and in turn possibly seedling recruitment, was more likely to be limited by IPSP in the former species, particularly species in the Euphorbiaceae and the Sapindaceae.

The recruitment of plants is also affected by many other factors, hence the varying effect of IPSP on the recruitment of different species will be modified. The possible effects of IPSP on seed availability, and in turn recruitment, are discussed within the context of these other modifying factors, in particular - seed longevity and post-dispersal seed predation.

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STATEMENT OF SOURCES DECLARATION

I declare that this thesis is my own 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.

10/3/2000

Peter Alexander Juniper

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CHAPTER 1: INTRODUCTION

The relative abundances of plant species in a rainforest dfines its composition as a community. The abundance of any particular species depends on the production, development and survival of plants through the whole life cycle (Harper 1977). However, processes that affect the earlier phases of the life cycle, such as the seed phase, often underpin the abundance of later phases. This is because mortality rates tend to be highest during the seed phase (Schupp 1988, 1990, Sork 1987, Howe et al. 1985, Alvarez-Buylla and Martinez-Ramos 1992, Osunkoya 1992). During this phase, interspecific differences in mortality rates and seed availability, may have a significant influence on the relative abundance of species observed in the forest.

Studies of recruitment over spatial scales ranging from that of the individual plant to plant populations support the idea that seed availability can be important to the abundance of adult rainforest plants. Seed rain tends to be highest beneath the parent plant (Fleming and Heithaus 1981, Harper 1977, Howe et al. 1985, Sinha and Davidar 1992). Consequently, seed availability can lead to locally high densities or aggregations of adults at small spatial scales (Okuda et al. 1997, Lieberman and Lieberman 1994). At the landscape scale, positive correlations have been found between seed survival and adult abundance (Putz et al. 1990, Smith 1987, 1988 and Smith et al. 1989).

Seeds in tropical rainforests often die by predation. For some species, very high proportions of each plant's seed crop can be killed by seed predators (eg.

Cunningham 1997, De Steven 1981, De Steven and Putz 1984, Forget et al. 1999, Grieg 1993, Howe et al. 1985, Janzen 1975b, Janzen and Wilson 1977, Osunkoya 1992, Sork 1987). In other types of ecosystem seed predation has been shown to affect seed availability and hence the dynamics of plant populations (Baker and Normano 1975, Borchert and Jain 1978, Brown and Heske 1990, Davidson et al. 1984 and 1985, Greig-Smith and Sagar 1981, Inouye et al. 1980, Klinkhamer et al. 1988, Louda 1982a, 1982b, Putz et al. 1990, Risch and Carroll 1986) and plant communities (Baker and Normano 1975, Brown and Heske 1990, Davidson 1993, Davidson et al. 1984 and 1985, Inouye et al. 1980, Risch and Carrol 1986). Seed predation may also have similar effects on plant population and community dynamics in tropical rainforests.

1.1 Seed predation and the composition of tropical rainforest plant communities

Seed predation in tropical rainforests has received much attention because it has been hypothesised to help maintain the often high tree species diversity of these communities, by suppressing potentially dominant species. However, almost all the attention that has been given to this hypothesis has come from studies of postdispersal seed predation.

Post dispersal seed predation has been hypothesised to regulate the population densities of tree species in tropical rainforests by increasing in intensity as population density increases. Thus, recruitment for potentially dominating species is lowered. This hypothesis, termed the Janzen-Connell model (Clark and Clark 1984), was first proposed by Janzen (1970) and may be summarised as follows. The intensity with which a dispersed seed crop is predated increases toward the parent tree. This is because the activity or searching efficiency of seed predators increases towards the parent, in response to either distance to the parent tree *per se* or to the density of seeds which increases towards the tree. These two types of seed predator response are termed 'distance dependent seed predation' and 'density dependent seed predation', respectively. Because the seeds that have been dispersed some distance from the parent plant are more likely to escape predation, new recruits tend to be well dispersed. This leads to low population densities for each species and allows a correspondingly higher packing density among species and hence a higher forest diversity.

Although the Janzen-Connell model has been instrumental in raising the awareness of the possible importance of plant-seed predator interactions to the local plant species diversity of tropical rainforests, it has mixed theoretical and empirical support. Firstly, the even spacing of trees predicted in the Janzen-Connell model cannot be produced by the minimum distance effect alone (Hubbell 1980), is insufficient in itself to explain the maintenance of the tree diversity observed in tropical forests (Hubbell 1980) and is not actually found in some tropical rainforests. The distribution of adult conspecifics is often random or clumped (Ashton 1988, Hubbell 1979, 1980 and Webb et al. 1972). Moreover adult conspecifics generally occur at densities lower than that predicted by the model (Hubbell and Foster 1992). Secondly, distant dependent and density dependent seed predation is not, as was assumed, universal among tropical rainforest tree species (Forget 1992b, Schupp 1988a, Wilson and Janzen 1972, Terborgh et al. 1993).

Theoretically, predispersal seed predation may also suppress potentially dominant plant species in tropical rainforests through some density dependent process. For example, predispersal seed predators may inhibit population growth in plant species by increasing their activity or local population density in response to an increase on local plant density. This density dependent process has had some support from studies that have shown how the more isolated a plant is from conspecifics the lower its intensity of seed loss by predispersal predators (Chung and Waller 1986, Vandermeer 1974), but other studies have also shown the reverse trend (Auspurger 1981a, De Steven 1983). Overall, there is little evidence to support the idea that predispersal seed predation may, through dependent processes, suppress some potentially dominant plant species in tropical, let alone act in a generalized manner across species analogous to the Janzen-Connell model.

If seed predation, both prior to seed dispersal and after seed dispersal, can affect the composition of tropical plant communities, this is more likely to occur by affecting the recruitment of some plant species more than others, rather than through a generalized effect across all species. The significance of differential effects of seed predation on plant community composition has been demonstrated, but once again this is by studies of postdispersal seed predation, rather than predispersal seed predation.

Almost all of the studies of the differential effects of postdispersal seed predation have been conducted in desert ecosystems (eg. Brown and Heske 1990, Davidson et al. 1984 and 1985 and Inouye et al. 1980), however, there is also an example from tropical rainforest (Putz et al. 1990). The loss of mammalian seed predators from the tropical rainforest on the islets of Lake Gatun in the Panama Canal has reduced post-dispersal seed predation for large-seeded tree species that are present. Apparently, as a consequence, the recruitment rates of these species have increased and led to their dominance in these communities. By inference, the postdispersal seed predation that continues on the mainland suppresses the population growth of these potentially dominating species and helps to support the species diversity in mainland communities.

The possible effect of differential seed predation on plant community composition has not yet been tested for in any plant community, let alone, specifically tropical rainforest. However, there is study showing differences of predispersal seed predation intensity between co-occuring tropical rainforest species (Grieg 1993). Although much limited, the existing support for differential predispersal seed predation in tropical rainforests does leave open the possibility that predispersal seed predation may affect tropical rainforest composition by affecting the recruitment of some plant species more than others.

For a full understanding of the effects of seed predation on the composition of tropical rainforest plant communities it is therefore necessary to know what species are most likely to be restricted by seed predation in terms of offspring recruitment. This is dependent on the degree by which seed predators lower the availability of their seeds. However seedling recruitment in tropical rainforests may also be affected by other factors, other than seed availability, such as leaf litter depth (Molofsky and

Augspurger 1992), herbivory (Green et al 1997, Nadolny 1999, Osunkoya et al 1992), light availability (Alvarez-Buylla and Martinez-Ramos 1992, Nadolny 1999, Vazquez-Yanes and Orozco Segovia 1993, Whitmore 1996) and water availability (Vazquez-Yanes and Orozco Segovia 1993). The effect of seed predation on seedling recruitment must therefore be viewed within the context of these other factors.

1.2 General aim of thesis

The aim of this thesis was to study seed predation in the tropical rainforest of North Queensland and to determine what species were most vulnerable to seed predation. This was done with a view to finding out how seed predation might affect the species composition of the rainforest plant community. This study has focussed on the insect predispersal seed predation (IPSP) which can considerably reduce the size of a rainforest plant's viable seed crop (Cunningham 1997, De Steven 1981, Forget et al. 1999, Grieg 1993, Janzen 1975b, Janzen and Wilson 1977). IPSP has yet to be studied at the community level anywhere and has not been studied at all in Australian rainforests.

1.3 Structure of thesis

Chapter 2 reviews what is known about the factors that may affect levels of IPSP in plants and draws attention to shortfalls in our understanding of the field. Following this review are the specific aims of the thesis.

Chapter 3 provides a geographical and ecological context to the thesis with an overview of the study region and its rainforests.

Chapters 4 to 6 are experimental chapters. The first experimental chapter investigates community level patterns in the vulnerability of plants to IPSP. The second and third experimental chapters test for relationships between IPSP and the specific factors; host plant resource availability and host indigeneity.

Finally Chapter 7 summarises the factors associated with the vulnerability of plants to IPSP in the Atherton Tablelands tropical rainforests and discusses what significance this may have for the plant species composition of these communities.

CHAPTER 2: LITERATURE REVIEW OF THE FACTORS THAT AFFECT PREDISPERSAL SEED PREDATION BY INSECTS

Abstract

This review defines seed predation and outlines its general significance to seed performance, plant population dynamics and plant evolution. Predispersal seed by insects predation is then defined and the factors that affect insect predispersal seed predation are described. This last section leads into the general aims of the thesis. The degree by which insect predispersal seed predators lower seed availability can be affected by many ecological factors, and as a result, tends to be highly variable across space, time and phylogeny. Because there are so many factors potentially involved, and insect predispersal seed predation is often affected by a number of interacting factors, this review classifies these factors according to whether they; 1) affect seed predation directly or not, 2) affect the abundance and exploitability of seeds potentially available to seed predators, or the abundance and activity of the seed predators themselves, and 3) cause variations in seed predation over time and space, or between plant species. Of the many factors that may possibly affect insect predispersal seed predation, few of these have been studied in depth, and few studies have compared the significance of different factors simultaneously across a number of plant species. It is therefore not yet possible to generalize on what types of plant are most vulnerable to insect predispersal seed predation. To do this, studies are required that compare the effect of different factors on insect predispersal seed predation across species.

2.1 Introduction

Seed predation can be important to the dynamics of plant populations and communities because it kills seeds, lowers seed availability and reduce plant recruitment (Crawley 1989a, 1992, Davidson 1993, Ehrlen 1996, Louda 1982a). The effect of seed predation on seed availability is, however, highly variable across space, time and phylogeny. To understand the significance of seed predation to plant populations and communities it is necessary to understand the nature of this variation.

The degree by which seed predators lower seed availability is dependent on the chance a plant is attacked by seed predators, the proportion of the seed crop that is damaged and the extent of damage done to attacked seeds. These measures of seed predation are affected by many different ecological factors. This review summarises what is known about these ecological factors, with a focus on those that affect predispersal seed predation by insects. This review begins by defining seed predation and outlines its general significance to seed performance, plant population dynamics and plant evolution. The main component of the review then deals with predispersal seed predation by insects. Here predispersal seed predation by insects is defined and the factors that affect insect predispersal seed predation are described. This last section leads into the general aims of the thesis.

2.1.1 What is seed predation?

Seed predation is the process during which all or part of the vital tissue of a plant seed is destroyed by an animal (seed predator) directly causing death. The vital tissues of a seed are those necessary to for seed viability: the embryo, endosperm, cotyledons and the seed coat. Damage to other tissues associated with the seed (the fruit wall and receptacle) does not constitute seed predation. These other tissues may allow for seed development and maturation, protect the seeds from other potential causes of death or aid in seed dispersal, but their destruction cannot cause death directly. Two examples illustrate this.

Firstly, a seed within a fruit may die because it was infected by fungi that were introduced by a pulp-feeding insect. Although the damage done to the fruit by the insect led to the death of the seed, seed mortality was not the direct result of damage to vital seed tissue. The insect cannot therefore be called a seed predator. Secondly, an animal may chew the wings off a seed and destroy its potential for dispersal. As a result the seed may fall into the shade of its parent, fail to successfully establish and die. Again, in this case the seed did not die from predation as the animal had not directly killed the seed by damaging vital tissue. Instead the seed may have died from the exhaustion of its energy reserves.

2.1.2 What are seed predators?

Seed predators are animals that ingest all or part of a seeds vital tissue, directly causing death. Although other types organisms can destroy seed tissue they are not commonly referred to as seed predators. For example, when fungi and bacteria destroy vital seed tissue they are referred to as pathogens rather than seed predators (eg. Augspurger 1990).

There are many different types of seed predator animals. They may be classified according to their taxonomy, the degree to which they can damage individual seeds or seed crops, or their effects on seed performance. Seed predators may also be classified according to why they damage seeds or their mode of attack. By classifying seed predators according to their mode of attack they may be ordered along a continuum that shows how intimately their life-history is associated with host seed/s. This continuum ranges from insects that live within a single seed to vertebrates that may not necessarily eat seeds themselves but damage them while extracting insects for food (Table 2.1).

Seed predators may initially be classified as endophages, which live part of their life within one or more host seeds or as exophages, that live wholly outside any seeds. Endophagous seed predators are insects which are totally reliant on seed tissue as a food source during their larval phase. Those species most intimately associated with their host spend their larval and pupal phase within a single seed, while some live within a number of successive seeds (within the one fruit) as they eat the tissue, moving from one seed to another. Other insect species do not actually live in the host seed but still remain within the one fruit. These insect species inhabit either the space available between the seeds and the fruit wall or a space that they have created themselves by eating into the fruit wall. Not all endophagous insects remain wholly within the one fruit, however. Some moth larvae, for example, may move from one fruit to another as each fruit is exhausted of its seeds.

Table 2.1. A partial list of the types of seed predators that occur. The seed predators are arranged according to their mode of attack, with example references.

Seed predator type	Reference
Endophagous animals	
- living within 1 seed (within 1 fruit)	
- Beetles	(Center and Johnson 1974, Cipollini 1991, Debouzie and Pallen 1987, Hopkins 1984, New 1983, Ricca et al. 1996, Szentesi and Jermy 1995 Wright 1983)
- Wasps	(Chung and Waller 1986, Green and Palmbald 1975, Janzen 1979, Louda 1982b, Nalepa and Grissell 1993, Nalepa and Piper 1994, Weiblen et al. 1995)
- living within >1 seed by moving between seeds within 1 fruit	
- Beetles - *Bruchids*	(Center and Johnson 1974)
- *Curculionids*	(Auld 1983, De Steven 1983)
- Flies	(Solbreck and Sillen-Tulberg 1986a)
- Moths	(De Steven 1981a)
- living outside seeds whilst remaining within 1 fruit	
- Flies	(Zimmerman 1980)
- Beetles - *Bruchidae*	(Janzen 1975a)
- *Curculionidae*	(Auld and Myerscough 1986)
- Wasps	(Louda 1982b)
- Moths	(Auld and Myerscough 1986, Inouye and Taylor 1979, Van Den Burg 1980a)
- living outside seeds, within >1 fruit by moving between fruit	
- Moths	(Green and Palmbald 1975)
Exophagous animals - living outside seeds and fruit	
- Sap sucking bugs	(Davidar 1987, Greig 1993, Ralph 1977, Sauer and Feir 1973, Slater 1972, Solbreck and Sillen-Tulberg 1990)
- Animals that eat whole seeds	
- Birds - *chickadees*	(Haftorn 1974)
- *jays*	(Ligon 1978, Nilsson 1985)

- *parrots*	(Coates-Estrada et al. 1993, Higgins 1979, Saunders 1980, Scott and Black 1981)
- *pigeons*	(Crome 1975, Frith et al. 1976, Willson 1983)
- *rooks*	(Purchas 1980)
- *others*	(Smith and Aldous 1947, Vander Wall 1990)
- Crabs	(Brown and Fielder 1991, O'Dowd and Lake 1991 Smith et al. 1989)
- Insects - *Grasshoppers*	(Auld and Myerscough 1986, Cunningham 1997)
- *Ants*	(Andersen 1987, Byrne and Levey 1993, Davison 1982, Davidson et al. 1985, Risch and Carroll 1986).
- *Beetles*	(Alcock 1976, Thompson 1985)
- Slugs and snails	(Duggan 1985, Godnan 1983)
- Mammals - *Rodents - agoutis*	(Forget 1992a, 1993)
- *rats, mice*	(Blate et al. 1998, Borchert and Jain 1978, Brown and Heske 1990, Howard and Evans 1961, Janzen 1971c, Osunkoya 1994, Terborgh et al. 1993)
- *squirrels*	(Elliot 1974, Heaney and Thorington 1978, Semel and Andersen 1988, Sinha and Davidar 1992)
- *chipmonks*	(Kawamichi 1980, Shaffer 1980)
- *Carnivores - red fox*	(Herrera 1989a)
- *badger*	(Herrera 1989a)
- *marten*	(Herrera 1989a)
- Ungulates - *peccary*	(Bodmer 1991)
- *cattle*	(Gardner et al. 1993, Hauser 1994)
- *sheep*	(Russi et al. 1992)
- *tapir*	(Janzen 1981b)
- *elephant*	(Lamprey et al. 1974, Miller and Coe 1993)
- *giraffe*	(Miller 1994)
- *kudu*	(Miller 1994)
- *duiker*	(Miller and Coe)
- *gazelle*	(Lamprey et al. 1974)
- Primates	(Oates et al. 1990)

Exophagous seed predators do not spend any part of their life within a seed or a fruit and are much more diverse than endophagous seed predators. Exophagous seed predators include vertebrates as well as invertebrates.

There is no clear boundary between exophagous animals that use ingest seed tissue as a source of food and animals that ingest seed tissue in the process of exploiting other food sources. This is because amongst these animals there is a gradual change in the significance of seeds to their diet. At one extreme are bugs (Hemiptera) that draw sap from seeds as a food source, or animals that eat and digest whole seeds, such as rodents, ants and pigeons (see Table 2.1). At the other extreme are animals that ingest seeds because they eat them along with a main diet of leaves and fruit. For example, seeds may be broken and/or digested by mammals that eat foliage (Gardener et al. 1993, Quinn et al. 1994, Russi et al. 1992) or fruit (Bodmer 1991, Hauser 1994, Herrera 1989a, Lamprey et al. 1974, Miller and Coe 1993). For some of these animals the nutritional gain from these seeds may be negligible.

Even though an animal may kills seeds by ingesting seed tissue, hence earning the name "seed predator", this doe not imply that every seed that may be attacked will be killed. For example, some large seeds may survive partial damage by insect seed predators, whilst other seeds in that same attacked seed crop are killed (Crome and Irvine 1986, Hopkins and Graham 1987). As another example, large mammals, such as sheep, that ingest seeds and kill them through digestion may not necessarily kill all ingested seeds, others may pass through the animal and subsequently germinate (eg. Russi et al 1992).

2.1.3 The effects of seed predation on seed performance

Seed predation can have a variety of direct and indirect effects on seed performance. These effects can either alter the performance of those seeds initially damaged by seed predators (seed-level effects) or alter the performance of the seeds remaining in a seed crop that has been attacked (crop-level effects). Some effects are detrimental to seed performance while other effects may be beneficial. Detrimental effects are the increased probability of death for a seed and the decreased probability of dispersal, while beneficial effects are the increased probability of seed survival and germination, and the dispersal of seeds (Fig. 2.1).

Seed-level effects

Seed mortality

Most seeds attacked by seed predators are killed outright because the embryo is damaged and unable to function. If the embryo survives immediate damage to the seed, death may still ocurr through water loss, because the storage tissue supporting the embryo is consumed (Moore 1972, Southgate 1979) or because conducting tissue is damaged interfering with the transport of resources to the embryo (Moore 1972). Where seeds have been attacked by hemipteran seed predators they may also die because of the toxic effects of remaining saliva (Nuorteva 1954 in Janzen 1972).

Not all seeds that are attacked by seed predators are directly killed. Large seeds appear most likely to survive any initial damage caused by seed predators (Crome and Irvine 1986, Hopkins and Graham 1987, Forget 1992a). This may be because they contain more tissue and the embryo is therefore less likely to be consumed (unless

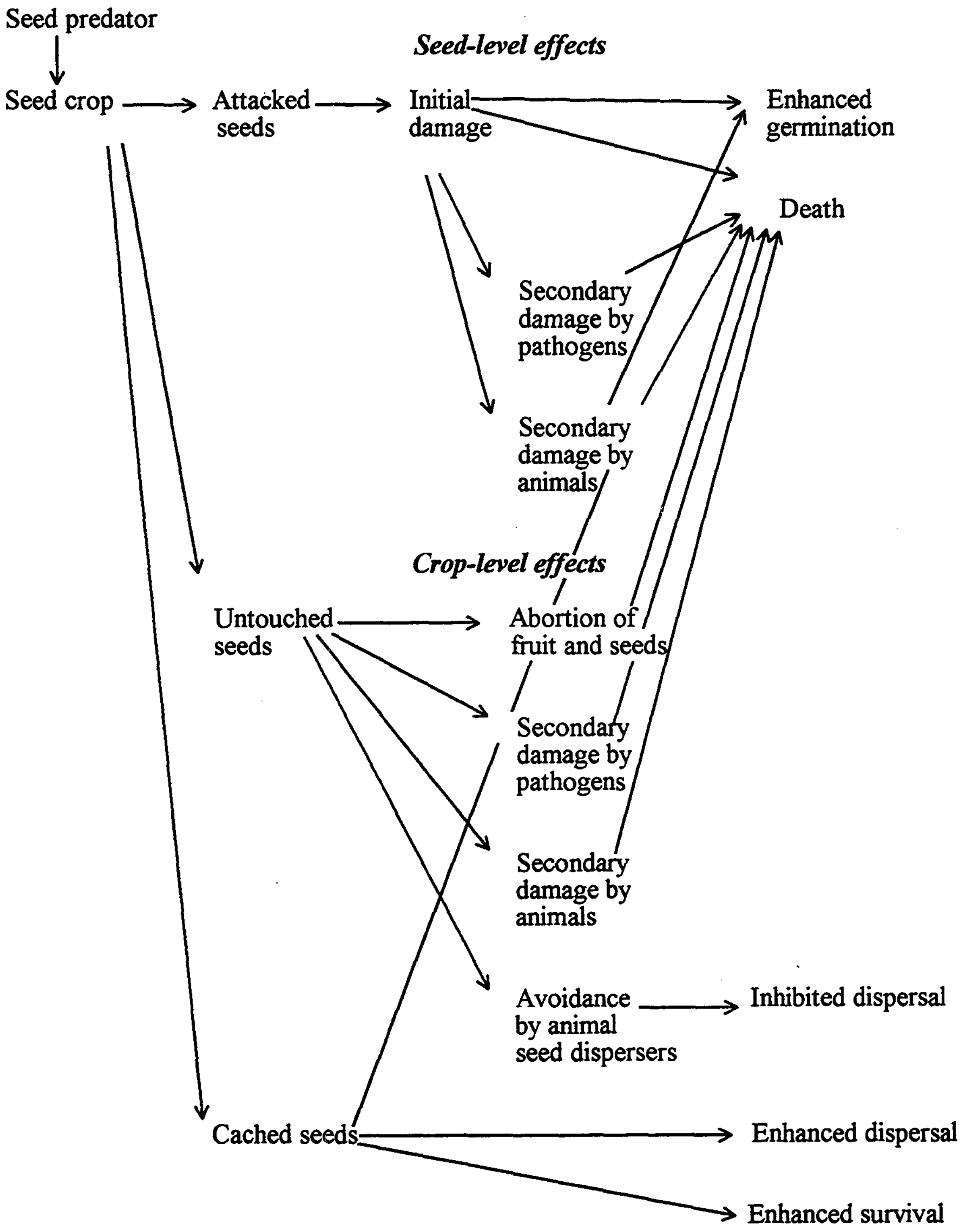

Figure 2.1. The possible fate for a seed from a seed crop attacked by seed predators showing both seed-level and crop-level effects on seed performance.

especially sought out be seed predators (Crawley 1989a, Fox 1982) or because there is more likely to be enough storage material remaining in the seed to support an intact embryo.

If a seed does survive the direct effects of tissue damage caused by a seed predator it may die later through secondary effects involving other organisms. For instance, when a seed has been attacked by an insect secondary damage may be caused by the invasion of pathogens, such as bacteria or fungi (Janzen 1971c), or by rodents and birds seeking the insect itself for food (Crome and Irvine 1986, Janzen 1971c, see also Weckerly et al. 1989). Seeds that would otherwise have survived an attack by an insect seed predator may also subsequently die by digestion in large seed eating animals. This effect has been suggested to kill *Acacia albida* seeds (Hauser 1994). Ungulates eat the pods of this species and disperse the seeds which are protected from digestion by their hard seed coats. However when the seeds have been attacked by bruchid beetles and their seed coats are damaged by the exit holes of emerging adult beetles they may be more liable to digestion than dispersal.

Seed germination

Although the most important effect seed predators have on seeds is to kill them, thus preventing germination, some seeds may survive an attack by a seed predator with a subsequently improved chance of germination. This may occur because the seed coat surrounding the seed has been broken, allowing the seed to absorb water more easily. This may be why the germination of seeds has been accelerated after attack by rodents (Mc Adoo et al. 1983, Reynolds and Glendening 1949). Seed predation by bruchid beetles may have the same effect on germination speed. For example, the hard seed coats of *Acacia tortilis* seeds become perforated when the adult beetles emerge from their host seeds, after having developed as larvae and metamorphosed within the seed. The emergence holes that are cut by the beetles can allow water to enter the seed. Amongst the seeds that have been attacked but are still viable these emergence holes can initiate germination. According to Halevy (1974) this process may occur even when the seeds are ingested by ungulates and subsequently deposited in dung. How important this process is to the germination ecology of *A. tortilis* is unknown, however, as those seeds that have been attacked are also more vulnerable to being completely digested (Coe and Coe 1987, Miller 1994).

Crop-level effects

Seed mortality

Seed predation may not only kill seeds through direct damage but also lead to the indirect death of other intact seeds that would have otherwise survived. Intact seeds within a fruit may die because the predation of other seeds has allowed secondary invasion by pathogens (Janzen 1971c) or insects (Janzen and Wilson 1977). Intact seeds may also die as fruit are torn apart by birds extracting insects from those seeds that were initially attacked (Scott and Black 1981). The animals that attack previously damaged seeds or the intact seeds accompanying them can be considered to be secondary seed predators. This is because their presence has been initiated by other, primary seed predators.

Seed predation may also lead to the indirect death of intact seeds through the response of the host plant. If a seed is damaged the host plant may abort the infested fruit which contains it (Boucher and Sork 1979, Stephenson 1981). If there are other developing seeds within that fruit they would also be lost.

Seed dispersal

Seed predators can aid or hinder seed dispersal. Seed predators can aid dispersal by dispersing the seeds themselves. This occurs when seeds are harvested by seed eating animals but for some reason are not actually eaten. Seeds collected by ants escape predation if they are lost or discarded en route to the nest (Kaspari 1993, Kelrick et al. 1986), or remain in abandoned caches by itinerant species (Drake 1981, Culver and Beattie 1978). Rodents and birds also cache seeds (Smith and Reichman 1984, Vander Wall 1990). A proportion of these stored seeds may not be eaten if there is a surplus of seeds within the animal's territory (Jensen 1985, Vander Wall and Balda 1977) or the animal fails to recover all buried seeds.

Seed predators can hinder seed dispersal by discouraging frugivory by birds. This is because birds are less likely to eat fruit with seeds that have been attacked by insect seed predators than uninfested fruit (Borowicz 1988, Jordano 1987, Knight 1987, Valburg 1992). Consequently any intact seeds within an infested fruit are less likely to be dispersed. Birds may also avoid fruit infested by seed predators because the fruit may have been secondarily infected by microbes which may make them distasteful (Borowicz 1988). Infested fruit may also be ignored by birds because they do not develop their normal ripe colour and hence are unattractive (Krischik et al 1989). This effect of fruit colour may be a response of the plant to seed/fruit damage or as suggested by Krischik et al. (1989) is induced by the seed predators themselves to avoid accidental consumption by birds. This latter explanation is supported by Herrera (1984a) who suggests that the consumption of seed predator insects by birds may exert a strong election pressure for avoidance mechanisms. Fruit attacked by insects are not always avoided by frugivores however. Valburg (1992) found that bush tanagers (neotropical birds) responded to attacked fruit differently according to host species.

Seed survival

The chances of survival for seeds may, under certain circumstances, be increased as an indirect effect of seed predation. This can occur when seeds have been harvested by seed predator animals and stored as food reserves, but for some reason have not actually been eaten. Seeds buried by scatter hoarding rodents may be protected from frost damage (Jensen 1985), dehydration (Borchert et al. 1989, Forget 1990, Jensen 1985), predation by insects (Forget 1990 and 1991, Forget and Milleron 1991, Janzen 1971c, Smythe 1989) or predation by other vertebrates (Borchert et al. 1989).

Seed germination

Scatter hoarding by rodents may not only increase the chances of survival for any seeds that are not ultimately eaten, but may also increase their chances of germination. This can occur when the seeds are cached at microsites that are favourable to germination rather than quiescence and storage (Borchert et al. 1989, Culver and

Beattie 1978, Forget 1992b, Reichman 1979, Stapanian and Smith 1986, Tomback 1986).

2.1.4 What is predispersal seed predation?

Seeds are potentially vulnerable to predation at any time - from fertilisation to germination (Fig. 2.2). To study seed ecology it can be usefull to partition the seed phase of the plant life at the time of seed dispersal, which occurs when the seed moves from the parent plant by the action of gravity, wind, animal activity and other agents (van der Pijl 1982). Predispersal seed predation thus occurs between the time of fertilisation and seed dispersal. During this time the seed may be developing, or having matured, it may be independent of the parent and still awaiting dispersal. Note, however, that interactions between a predispersal seed predator and its host plant may not be limited to this particular period of time only. For example, insects that consume seeds may also have consumed unpollinated flowers from the same plant (Louda 1983, Solbreck and Sillen-Tulberg 1986a), may have hatched from eggs laid in flowers before pollination (Fig. 2.2) (eg. Augspurger 1981, Duggan 1985, Zimmerman 1980) or may metamorphose and emerge from seeds after their dispersal from the parent plant (Boucher and Sork 1979, De Steven 1981a, Ernst et al. 1989, Nalepa and Piper 1994).

According to Crawley (1992) insects are the dominant type of predispersal seed predator, whereas the post-dispersal seed predator fauna is dominated by mammals, as well as some types of insect (ants and beetles). Although these differences in fauna

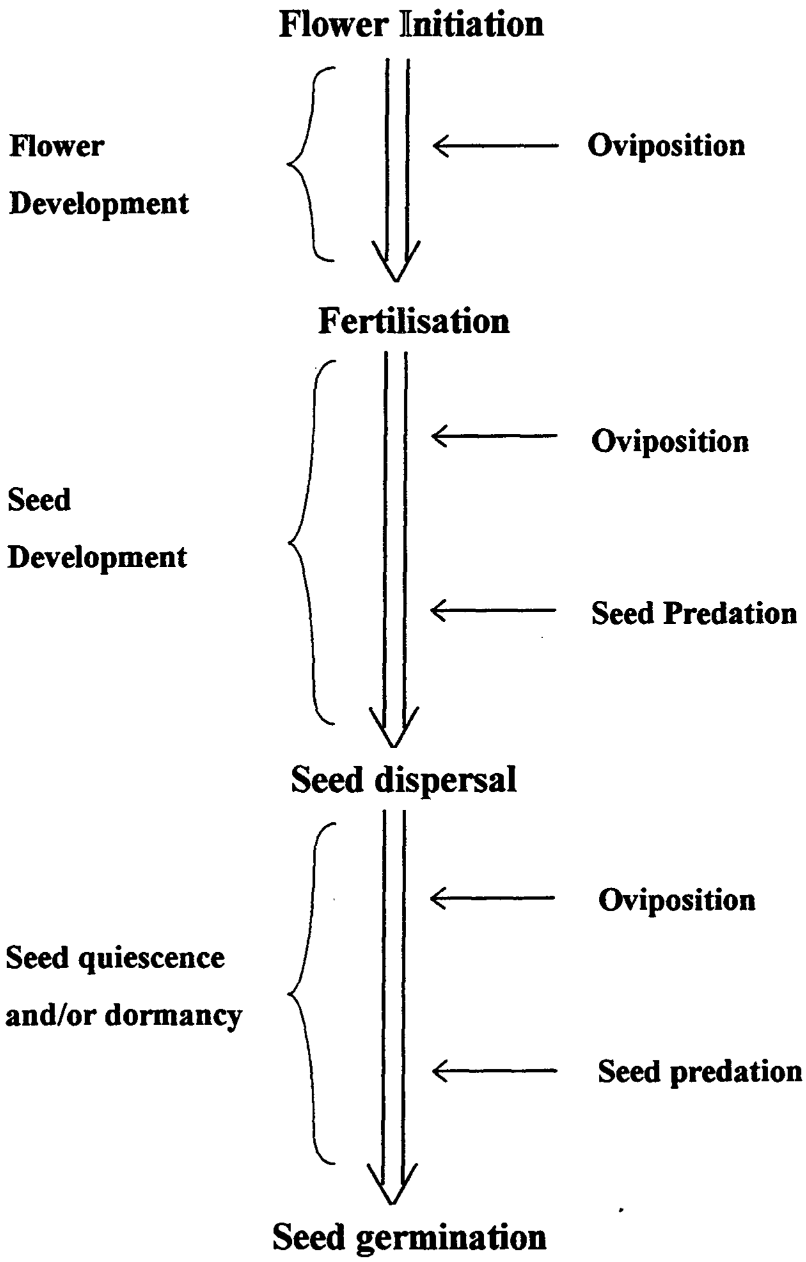

Figure 2.2. A seed may be consumed by a seed predator at any stage between fertilisation and germination. The fate of a seed may however be determined even earlier if the eggs of insect seed predators are laid in flowers before pollination.

may be due in part to the selective attention of ecologists, they are supported by the few studies that have included both the pre- and postdispersal seed predators of a plant species (Table 2.2).

Table 2.2. Intensities of pre- and postdispersal seed predation, taken for the same host species.

Host plant	Predispersal		Postdispersal		Reference
	Animal	% seed loss	Animal	% seed loss	
Ceriops tagal	insects	8.2	crabs	1.6	Robertson et al. (1990)
Fagus silvatica	moth	7	rodents	5	Nielsen (1977)
Carya glabra	beetle	47.7	squirrels	79.5	Sork and Boucher (197
Cirsium canescens	insects	61	small vertebrates	90.5	Louda et al. (1990)
Juniperus virginiana	finches	3.1	rodents	3.5	Holthuijzen et al. (1987)
	insects	1			

2.2 Factors affecting predispersal seed predation by insects

2.2.1 Defining factors which affect insect predispersal seed predation

There are many factors which influence predispersal seed predation by insects. In the broadest sense these factors may be considered to be environmental or biological substances, processes or characteristics whose presence can affect seed predation. Defining a factor is further complicated because factors are rarely independent. Hence predispersal seed predation by insects may vary because of the effects of a chain of successively more distant factors. For example, seasonal variations in the intensity of seed crop destruction for *Costus woodsonii* (Zingiberaceae) by insect seed predators (Schemske 1980) may be caused by a complex of three or possibly four interacting factors (Fig. 2.3).

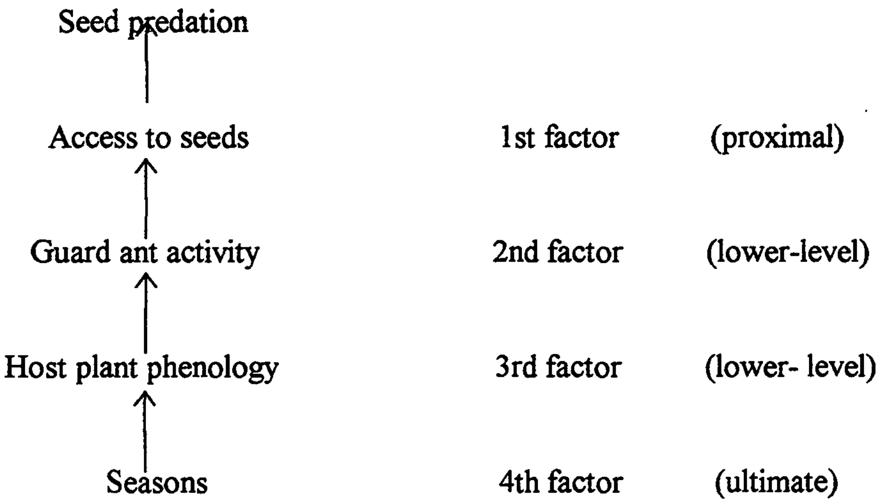

Figure 2.3. The chain of successively more distal factors that may underlie variations in seed predation intensities for *Costus woodsonii* in Schemske (1980).

The intensity of seed crop predation for *C. woodsonii* was found to be reduced by the activity of two species of guard ants, *Campanotus planatus* and *Wasmannia auropunctata* (Schemske 1980). These ants appeared to have a symbiotic relationship with *Costus woodsonii* - while they are attracted to the nectaries of this plant, they also repel seed predator *Euxesta* flies which lay their eggs amongst the flowers. The activity of these ants may thus be regarded as a factor affecting seed predation for *C. woodsonii*. The effectiveness of this symbiotic relationship at limiting predispersal seed predation by insects is dependent on the seasons as another factor. This is because lower intensities of predispersal seed predation were recorded for plants during the dry season than the wet season. This variation occurs because during the dry season the dominant species of ant on the plant was *C. planatus*, which is more effective at repelling ants than *W. auropunctata*. These interactions between the host plant, its seed predator and the guard ants may be further complicated by confounding seasonal differences in flower production.

The seasonal differences in the ants attending the plants may have been a response to host phenology. If this was the case then seed predation in these plants was affected by a chain of four interdependent factors (Fig. 2.3). The factor most closely connected with the variations of seed predation intensity over time was whether or not seed predators were able to get access to the flowers for oviposition. This first factor is called the proximal factor. This access was dependent on a second factor - the presence and activity of the guard ants. This second factor is a lower-level factor. If host phenology was important then this would be another lower-level factor, while seasonal variations in weather or insolation, which entrain the phenology of the host plant could be considered as the ultimate factor.

To provide structure to this review the factors that affect predispersal seed predation by insects will be discussed below according to their possible level of action. The proximal factors that affect predispersal seed predation by insects will be dealt with first, followed by the factors acting at lower and ultimate levels. The lower-level and ultimate factors will be dealt with together. As most studies of the factors that affect predispersal seed predation by insects are correlative, little is known about the mechanisms behind these correlations and often the position of these factors in any chain of effect is speculative.

Describing the factors that affect insect predispersal seed predation in terms of linear interations and how directly they can affect seed predation may appear to over-simplify and over-order the processes involved. However, some degree of ordering is necessary to describe how these factors may interact in a manner that is readable. The system of order used may partly be an arbitrary construct, but it is based on what is known about these factors.

2.2.2 The factors that affect insect predispersal seed predation

Proximal factors

Predispersal seed predation by insects can vary across space, time and phylogeny. This variation is dependent on proximal factors and how their affects vary across space, time and phylogeny. The proximal factors describe the abundance and exploitability of seeds potentially available to seed predators, and the abundance and activity of the seed predators themselves. They are:

a) Seed availability

b) Seed exploitability

c) Seed predator abundance and activity

Seed availability can affect predispersal seed predation by insects by affecting the relative supply of seeds versus demand by seed predators. If, for example, a plant population has a very high level of seed production one year, the abundance of seeds may overwhelm the demand of the local seed predator population. The relative intensity of seed crop predation for this particular year would then be much lower than the intensity expected if the availability of seeds was low, provided that insect numbers were constant between years.

Seed exploitability can affect predispersal seed predation by insects by determining whether or not seed predators can actually access and consume any available seeds. For example, the seeds of a plant are affectively inaccessible if they are surrounded by a hard pericarp that potential seed predators cannot penetrate. Seeds may also have a lower chance of being attacked by insects because, despite being accessible, they may be too small to be inhabited by them.

Seed predator abundance and activity can determine the predator demand for seeds. Thus high intensities of seed crop predation may be expected for a plant if it fruits at a time when there are many active seed predators. If, however, the potential seed predators are inactive at this particular time, during their pupal phase for example, then the intensity of seed crop predation would be low (Augspurger 1981).

Lower level factors

In contrast to proximal factors, lower-level factors are much more varied (Table 2.4), but they may be grouped into three categories:

- temporally related factors
- spatially related factors
- static attributes

Each of these will be discussed in detail below.

Table 2.4. Lower level factors and ultimate factors that may account for variations in the effects of proximal factors and hence predispersal seed predation by insects [1,2].

Lower-level factors	Ultimate factors	Proximal factors		
		Seed availability	Seed exploitability	Predator activity and abundance
Temporally related factors				
Variable successive seed crop size	Weather conditions	●		
Variable successive seed crop size	Pollination success	●		
Synchronised seeding	Weather conditions	●		
Fruiting time vs predator activity	Weather conditions	●		
Length of predispersal period		●		
	Bush fire			●
Seed development time	Elevation gradient		●	
Abundance of seed predators	Bush fire			●
	Water availability			●
Ant symbiont activity	Seasonal weather conditions?		●	
Spatially related factors				
Local host abundance	Disturbance/regeneration conditions?	●		
Host plant size	Disturbance/regeneration conditions?	●		
Vegetation cover	Disturbance/regeneration conditions?			●
	Animal seed dispersers			
Abundance of seed predators	Distribution of seed dispersers			●
Host plant responses?	Climate			●

Table 2.4. Continued…

Lower-level factors	Ultimate factors	Proximal factors		
		Seed availability	Seed exploitability	Predator activity and abundance
Host plant responses?	Water availability			•
Seed/fruit toxin content	"		•	
Host plant responses?	Proximity to water			•
Host plant responses?	Bush fire			•
Seed/fruit toxin content	Water availability		•	
------------------------------------	Host indigeneity		•	
Static plant attributes				
Infructescence/capitulum size	Resource availability?	•		
Fruit seediness	Resource availability?		•	
Seed size	Resource availability?		•	
Seed shape	Resource availability?		•	
Fruit surface texture	Resource availability?		•	
Hard pericarp	Resource availability?		•	
Pericarp resin layers	Resource availability?		•	
Toxic seed coat/ pericarp	Resource availability?		•	
Toxins in seeds	Resource availability?		•	
Symbiont guard ants	Resource availability?		•	

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[1] For a more detailed table with references see Table 2.5.

[2] Only those factors that have been correlated with variations in IPSP levels are included here.

Temporally related factors

Temporally related factors affect predispersal seed predation by determining seed availability, in particular, the year to year production of seed and the timing of seed availability in relation to seed predator activity.

Year to year production of seed

The year to year production of seed can be important because if production within a given area fluctuates, the local seed predator population will have to follow the level of resources. When the size of the local predator population is small but local seed production is high, the demand for seeds by predators may be overwhelmed. Under these conditions relatively low intensities of seed crop predation would be expected. Conversely during years of low seed production the predator population may be starved for seeds, in which case relatively high intensities of seed crop predation would be expected

Solbreck and Sillen-Tulberg (1986a) present one of the more detailed examples of this effect. They studied irregular seed production in patches of the perennial herb *Vincetoxicum hirundinaria* (Asclepiadaceae) and its effect on local populations of the seed predator fly *Euphranta connexa* (Tephritidae). During years of unfavourable weather, seed production in patches of this herb was low and only able to provide resources for a small population of flies per patch. When this occurred almost all the seeds were attacked by fly larvae and intensities of seed crop predation were very high. Although fly populations were able to grow in response to increases of seed production this did not occur at a sufficient rate to keep up with levels of seed production during favourable years. During these years the flies in the patches of *Vincetoxicum hirundinaria* were overwhelmed with seeds and intensities of seed crop predation were low. Overall fluctuations of seed availability keep intensities of crop predation lower than would otherwise occur if seed production was constant from year to year. In summary, fluctuations in intensities of seed crop predation were caused by fluctuations in seed availability (the proximal factor), in response ultimately to growth conditions affected by the weather (a lower level factor).

Synchronised year to year production of seed

This inverse relationship between the intensity of seed crop predation and the level of local seed production may select for synchronised seed production in plants, both within species and across species. This is because those plants that fruit outside the time of greatest seed availability (when the majority of plants are fruiting) will suffer greater intensities of seed crop predation, and therefore have a lower biological fitness. Conversely plants that fruit with the majority of the population (for whatever reason) will have lower intensities of seed crop predation, higher seed survival and a higher biological fitness. As seed predation pressure selects for plants that fruit in synchrony, the time span across which fruiting occurs through a population could therefore be expected to shorten, over evolutionary time (Janzen 1971a, 1974).

Synchronous seed production may occur from every 2 to 10 or more years, through one or more related species in a region. This is loosely known as masting (but see Herrera et al. 1998) and may lower intensities of seed crop predation, not only by saturating the local seed predator demand as originally suggested by Janzen (1971a, 1974) but by decreasing population densities of predators during periods when seed supply is low (Augspurger 1981b). This is why years of high seed production have been correlated with years of low seed predation intensity (Nilsson and Wastljung 1987, Shibata et al. 1998, Silvertown 1980). The plants that mast tend to be trees that mature late, are long-lived and produce large, non-toxic seeds (Janzen 1971a, Waller 1979). Masting species include pines (Reukema 1982), oaks (Sork et al. 1993), dipterocarps (Ashton 1988, Ashton et al. 1988, Toy 1991, Janzen 1978), podocarps (Norton and Kelly 1988), beeches (Jensen 1985, Nilsson 1985) and laurels (West 1986 in Norton and Kelly 1988, Wheelright 1986). Small seeded species which mast include *Carpinus sp*. (Shibata et al. 1998) and *Hamamelis sp.* (De Steven 1981b).

Synchronous seed production *per se*, without major fluctuations from year to year, can also reduce predispersal seed predation by insects (Augspuger 1981b, 1982, De Steven 1981b). For example Augspurger (1981b) found lower intensities of seed crop predation for *Hybanthus prunifolius* (Violaceae) shrubs when they flowered and fruited in synchrony with the rest of the local population than for shrubs that flowered and fruited out of synchrony (Augspurger 1981b). This was because when seeds were available to seed predators at the sites where seeding was synchronous the quantities of seed available were much greater than at the other sites where only a few plants seeded at a time. At the 'synchronous sites' seed availability exceeded local demand by seed predators whereas at the asynchronous sites this did not occur.

Although tracing the pathway of interacting factors from predispersal seed predation by insects to irregular seed production and variable weather conditions is relatively simple, explaining masting and fruiting synchrony in these terms is more complex. Masting has been correlated with environmental conditions that can affect plant growth, such as air temperature and water availability (Ashton et al. 1988, Sork et al. 1993, Norton and Kelly 1988) but it does not appear to be a simple and direct response to these factors. Masting involves some evolved internal control as well. This is because resource use actually switches from vegetative growth to seed production during a mast season (Norton and Kelly 1988). Moreover regional masting among a number of dipterocarp species occurs despite their staggered flowering times (Toy 1991). Masting thus appears to be an evolved feature.

The factors that ultimately affect predispersal seed predation by insects via masting may be those that had selected for this particular phenological pattern in the past. These factors are variable growth conditions (Janzen 1978, Silvertown 1980, Waller 1993) and seed predation (Janzen 1971a, 1974). Resource availability may also be important, possibly explaining why masting is a characteristic of dipterocarps from low fertility soils. Janzen (1974) suggests that this is because the animal biomass (ie. seed predator biomass) of tropical forests on infertile soils is lower than that of tropical forests on fertile soils. It may therefore be easier to overwhelm the lower numbers of seed predators in the tropical forests of poorer soils than that of tropical forests in richer soils.

Other factors may also have contributed to the evolution masting. For example masting may have evolved as a result of past selection for increasing resource efficiency during flower and fruit production (Waller 1979). For tropical oaks at least, masting may partly be a result of selection for large seed size and the storage of resources between seed crops (Sork 1993). For wind pollinated or outcrossing species masting may be a by-product of synchronous flowering that improves pollination efficiency (Nilsson and Wastljung 1987, Norton and Kelly 1988, Shibata et al. 1998, Smith et al. 1990, Sork 1993).

Synchrony of seed production and seed predator activity

The relationship between seed production and seed predator activity in time can also affect predispersal seed predation by insects. Janzen (1969) had suggested plants that fruit when insect seed predators are active, either at their egg laying phase or larval phase, would be expected to have higher intensities of seed crop predation than plants that fruit when seed predators are inactive. This has been supported in findings by Augspurger (1981a), English-Loeb and Karban (1992), Jordano et al. (1990) and Knight (1987).

A study by Jordano et al. (1990) serves as an example of how synchrony between seed predator activity and host plant phenology can affect predispersal seed predation by insects. This example involves interactions between the timing of egg laying by the butterfly *Tomares ballus* (Lycaenidae), flowering time and seed loss for the host plant *Astralgalus lusitanicus* (Fabaceae), and seasonal habitat conditions. The seed crops of

A. lusitanicus plants on a south facing slope were found to have higher intensities of predation than those of plants on a north facing patch. These differences in seed predation appear to be caused by differences in the timing of egg laying by the seed predator. Whilst flowering occurred at the same time across the patches, *T. ballus* had laid eggs on host flowers in the south facing patch earlier than on plants in the north facing patch. Consequently egg laying was more closely synchronised with flowering in the south facing patch than the north facing patch.

Spatially related factors

Spatially related factors are responsible for variation in seed predation over space. This variation occurs because the effects of these factors vary over space. Spatially related factors are the most diverse of the three different classes of factor that can affect predispersal seed predation by insects. The way in which these factors affect predispersal seed predation by insects is poorly understood as only a few of the pathways of interaction between spatially related factors and the insects have been confirmed (Jordano et al. 1990, Louda et al. 1987, Herrera 1989b). Consequently, the significance of many spatially related factors is speculative.

Despite the limited understanding of how spatially related factors may affect predispersal seed predation by insects, there appears to be two possible mechanisms (Fig. 2.4):

1) A pathway of effect from an ultimate factor to predispersal seed predation by insects may involve a single spatially related factor. This one factor may directly affect

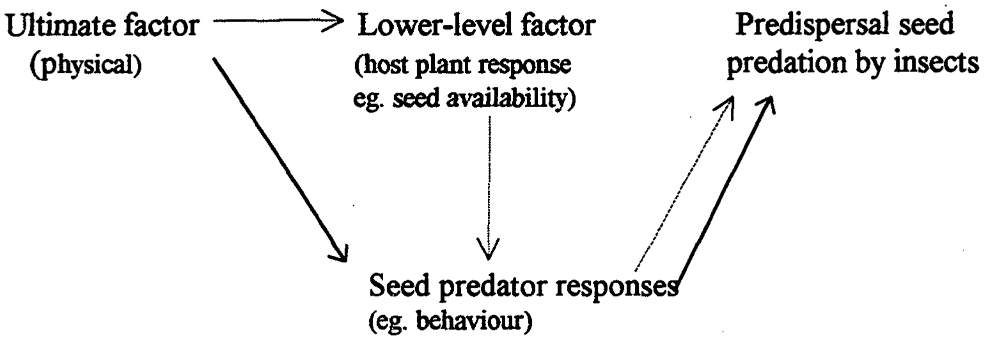


Figure 2.4. The two pathways by which spatially related factors appear to affect predispersal seed predation by insects. ——— indicates the most direct pathway where seed predation is affected by the action of a single factor on seed predators. ——— indicates where seed predation is affected by the action of two factors on seed predators. In this case one factor affects an aspect of seed availability which in turn affects seed predators and seed predation.

the seed predators, hence their demand for seeds and as a result, the intensity of seed predation for a plant. As only one factor is involved it can be considered as the ultimate factor.

2) The alternative pathway of effect from an ultimate factor to predispersal seed predation by insects involves two spatially related factors. In this case the ultimate factor affects the seed predators via the effects of a lower-level factor. It is this lower-level factor that affects the seed predators and determines what the demand for seeds is and hence intensities of seed predation.

Spatially related factors include conditions of disturbance and regeneration (Chung and Waller 1986, Sauer and Feir 1973, Silander 1978, Vandermeer 1974), resource availability (Janzen 1975a, Jordano et al. 1990, Knight 1987, Louda et al. 1987, Moore 1978b), climatic and weather conditions (Herrera 1984b, Inouye and Taylor 1979, Kelly et al. 1992, Louda 1982a, b, White 1975) and seed dispersal (Augspurger 1981a, Herrera 1989b). These factors may directly affect the behaviour or population dynamics of seed predators and hence predispersal seed predation by insects. Alternatively they may operate via lower-level spatially related factors such as host plant abundance (eg. Chung and Waller 1986, Sauer and Feir 1973, Silander 1978, Vandermeer 1974), microhabitat conditions (Jordano et al. 1990) or host plant toxin concentration (Louda et al. 1987).

Our understanding of the influence of spatially related factors is limited but three examples of the way in which some of these factors may affect predispersal seed predation by insects are given below. Two examples are given for pathways involving a single spatially related factor; one pathway affects seed predator population dynamics while the other affects seed predator behaviour. The third example is for a pathway of effect involving two spatially related factors which affect seed predation via effects on predator behaviour.

Example 1: One spatially related factor and seed predator population dynamics

This example shows how a variation in the presence of seed dispersers over space can cause a variation in intensities of predispersal seed predation by insects in space

(Fig. 2.5). Herrera (1989b) studied seed predation in the plant *Guazuma ulmifolia* (Sterculiaceae) and found that plants growing where horses and cattle were present had lower intensities of seed crop predation by bruchid beetles than plants that grew where these animals were absent. This is because the bruchid beetles pupate after their larval phase in the core of the host fruit. At this stage in their life history they are often killed when cattle and horses, the only known dispersers of *G. ulmifolia* seeds, eat the fruit. Enough seed predators are killed in this manner to limit predator population densities and intensities of seed crop predation. Thus cattle and horses, as a component of *G. ulmifolia's* environment act as an ultimate factor affecting seed predation intensities by affecting the population dynamics of the seed predators.

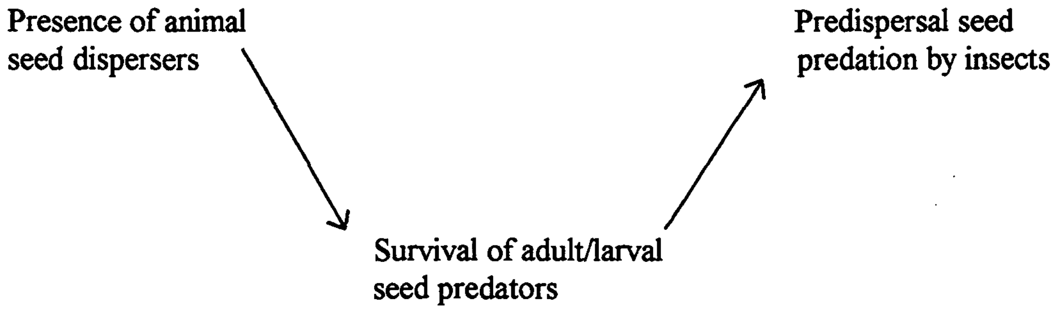


Figure 2.5. The pathway summarising the effect of animal dispersers on predispersal seed predation by insects in *Guazuma ulmifolia* (Herrera 1989b).

Example 2: One spatially related factor and seed predator behaviour

This example shows why, in the study by Jordano et al. (1990), there was a negative correlation between intensities of seed crop predation for *Astragalus lusitanicus* (Fabaceae) and the successional phase of its habitat. This correlation occurred because the seed predator *Tomares ballus* (Lycaenidae) oviposited on plants that were exposed to sunlight, in preference to hosts that had become shaded by other plants. As a result, host plants growing in earlier successional vegetation, where their exposure to sunlight was greater, tended to have higher intensities of seed crop predation than plants growing in later successional habitats where they were more likely to be shaded. In summary the oviposition behaviour of the seed predators was affected by the successional phase of their habitat, which in turn affected their abundance on host plants and the degree to which they destroyed the hosts seed crops (Fig. 2.6).

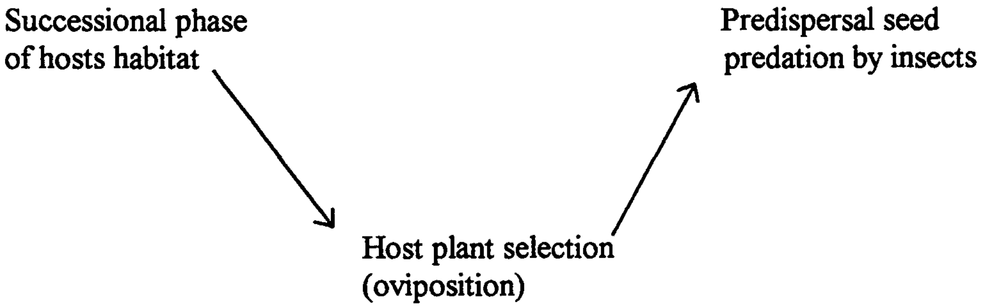


Figure 2.6. The pathway summarising the effect of habitat successional phase on predispersal seed predation by insects in *Astragalus lusitanicus* (Jordano et al. 1990).

Example 3: Two spatially related factors and seed predator behaviour

This example shows how the spacing of host plants, possibly determined by disturbance and establishment conditions, can affect seed predator behaviour and hence predispersal seed predation by insects (Fig. 2.7). Vandermeer (1974) studied seed predation in the plant *Calliandra grandiflora* (Mimosaceae) and found that there

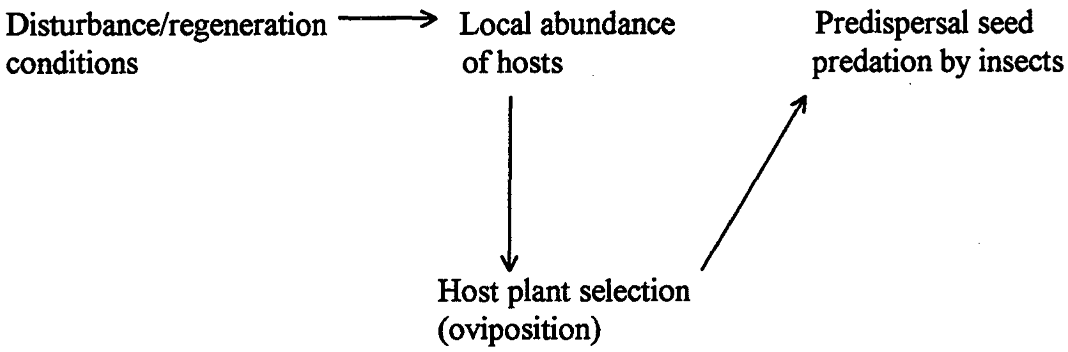


Figure 2.7. The pathway summarising the effect of disturbance/regeneration conditions on predispersal seed predation by insects in *Calliandra grandiflora* (Vandermeer 1974).

was an inverse relationship between the spatial isolation of conspecifics and intensities of seed crop predation caused by an unidentified lepidopteran.

The intensity of seed crop predation for *C. grandiflora* may ultimately be affected by disturbance and establishment conditions as the species grows in forest regrowth with a clumped distribution. The actual spacing of these plants may be considered as the next important factor as it was this that was correlated with the intensity of seed crop predation. Vandermeer (1974) does not suggest why this correlation occurred, however the more isolated plants may have been less easily found by the seed predators and hence had less seed predation. Similar responses by seed predators to the spacing of host plants have been documented elsewhere (De Steven 1983, Ralph 1977, Silander 1978). If in this example the seed predators do respond to host spacing *per se*, then host plant distribution had affected seed predation via behavioural responses in the seed predators.

Static plant attributes

Static plant attributes appear to affect predispersal seed predation by insects by acting as lower-level factors that affect seed exploitability. Most static plant attributes are morphological characteristics of fruit and seeds, but they also refer to associations between host plants and symbiotic guard ants. Static plant attributes may affect predispersal seed predation by insects by:

- acting as a protective barrier around seeds,
- limiting the resources within a seed that are available to a seed predator,
- reducing the edibility of those resources that are available.

Protective barriers around seeds

Barriers may protect seeds from predation by insects by either hindering oviposition or by preventing larvae or adults from entering seeds. Oviposition may be hindered by the surface characteristics of seeds and fruit in a number of ways. Firstly, spiny or hairy surfaces on seeds and fruit can deter oviposition (Fernandez and Talekar 1990, Raina 1971). This may be why varieties of *Xanthium strumarium* that produce fruit covered in short burrs had higher intensities of seed crop predation than long-burred varieties (Hare 1980). This may also be why the smooth legume *Astragalus cibarius* was attacked by chalcid wasps where as its sympatric congeneric *A. utahensis*, which produces hairy pods, was not (Green and Palmbald 1975). Secondly eggs may not remain attached to a seed if it has a very smooth coat (Bridwell 1918, 1920 in Janzen 1969). Thirdly, if eggs are successfully laid on a seed they may be detached later. Bridwell (1918, 1920 in Janzen 1969) suggested that this was the function of the exfoliating surface on the pods of some legume species. Swelling surfaces, the exuding of gum or the further growth of surface tissue can also detach eggs (Bridwell 1918, 1920 in Janzen 1969, Scott 1982, Szentesi and Jermy 1995).

Oviposition may also be hindered, not as a direct result of the host plant itself but by symbiotically associated guard ants (Inouye and Taylor 1979, Keeler 1981, Schemske 1980). These ants are attracted to their host plant by floral nectaries and will attack any insects that come to the flowers and developing fruit. By doing this, any seed predators that may try to lay eggs on the host will be deterred (Inouye and Taylor 1979, Keeler 1981, Schemske 1980).

If the eggs of an insect seed predator are successfully laid on a host, the larvae that hatched may still be prevented from entering the seed. This may be because the seed is surrounded by hard tissue that they are unable to penetrate (Ironside 1974, Janzen 1977, Nwanze and Horber 1976, Podoler and Applebaum 1968). Resinous or albuminous material surrounding the seeds of some legume species has also been suggested to prevent entry (Bridwell 1919 in Southgate 1979, Hinckley 1960 in Janzen 1969).

Even if the layers of tissue surrounding the seeds are penetrable they may still hinder seed predation if they are toxic. This appears to by why the larvae of *Callosobruchus maculatus* (Bruchidae) died cutting through the seed coats of some non-host legume species (Janzen 1977) and why the legume *Cercidium floridum* was more resistant to predation by the bruchid *Stator limbatus* than the sympatric *C. microphyllum* (Siemens et al. 1992). The identity of the compounds active in these examples is not known. Lignin, which is very toxic to *Acanthoscelides obtectus* (Bruchidae), has, however, been isolated from the seed coats of another legume - *Phaseolus vulgaris* (Stamopoulos 1988 in Huignard et al. 1990).

Availability of resources for seed predators within seeds

For insect seed predators that live within a single fruit the size and number of seeds available determine the quantity of resources available. This can affect larval development, survival and adult fecundity (Herrera 1984b, Knight 1987, Mitchell 1975, Moegenburg 1996, Nalepa and Grissell 1993, Russell 1962, Wilson 1988). Because the quantity of resources available within a seed is important, seed predators may have a preference for attacking larger seeds or larger, seedier fruit. This may explain why higher seed predation intensities have been reported for the larger seeds of a plant (Moegenburg 1996), the more seedy fruit of a plant (Herrera 1984b, Knight 1987) or larger seeded varieties and species (Chung and Waller 1986, Fernandez and Talekar 1990, Russel 1962, Szentesi and Jermy 1995).

Seed shape also appears to be able to affect predispersal seed predation by insects. Bridwell (1918 in Center and Johnson 1974) suggests that plant species with flat seeds are less likely to be attacked than species with more spherical seeds because they cannot provide enough space for a maturing insect. This appears to be why legumes with more spherical seeds have a greater chance of being attacked by bruchid beetles than those with flattened seeds (Szentesi and Jermy 1995).

Edibility of resources within seeds

Although a plant may have large, easily accessible seeds it may still only lose low numbers of seeds to predispersal insect seed predators if its seeds are toxic and inedible. Janzen (1969) suggested that legume seeds may have secondary compounds in them that are toxic to seed predators which may function as deterrents. As deterrents they may reduce predispersal seed predation by insects for a plant species by limiting the potential number of seed predator species that are able to consume its seeds. A considerable amount of work has since been done on secondary compounds in seeds and many have been found to be toxic to seed predator insects (eg. Bell 1984, Janzen et al. 1976, Janzen et al. 1977, Janzen et al. 1986, Southgate 1979). However their exact functions are difficult to determine. Some compounds may have been selected for by past seed predation pressure but they may also have additional or alternative functions such as nitrogen storage (Murray 1984b) or as allelopathogens (Wilson and Bell 1978). Moreover the effect of toxic compounds in seeds on insect seed predators under natural conditions has yet to be clearly demonstrated.

Although static plant attributes are generally genotypic and therefore fixed in ecological time (as opposed to evolutionary time) it is useful to consider them as lower-level factors rather than ultimate factors. This is because the ecological pressures that select for static plant attributes may. These last factors can therefore be considered as ultimate factors.

One ultimate factor that underlies the significance of intermediate static plant attributes may be host plant resource availability. Evidence supporting the significance of host plant resource availability comes mainly from herbivory studies (Herms and Mattson 1992, Loehe 1996). These studies indicate that plant species adapted to sites lacking in soil nutrients or sunlight, for example, invest more resources in the production of traits that inhibit herbivory than species adapted to resource rich sites. If resource availability is an important factor in the selection of traits that decrease herbivory in plants then it may also be important to the selection of traits that decrease seed predation levels. This was originally suggested by Janzen (1974) and has the support of Louda et al. (1987) who found correlations between water availability, glucosinolate concentration and intensities of seed crop predation within a single host species. The part resource availability may play in interactions that underlie variations in predispersal seed predation by insects is summarised in Fig. 2.8.

2.3 Discussion and conclusions

2.3.1 The current state of knowledge on the factors that affect predispersal seed predation by insects

The factors that have been associated with variations in predispersal seed predation by insects describe characteristics of both the biotic and abiotic components of

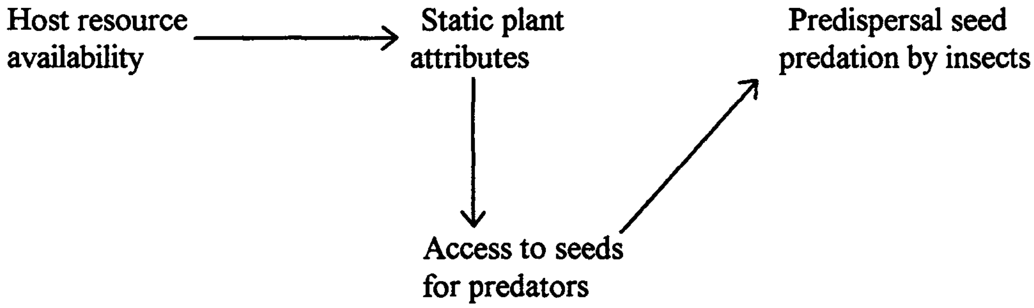


Figure 2.8. Pathway summarising the how resource availability may affect predispersal seed predation by insects.

ecosystems across a wide range of spatial and temporal scales, and taxonomic levels. This indicates that there is a diversity of factors that may affect predispersal seed predation by insects in plants. However it is premature to draw generalisations from the current literature on what characteristics lend plants a greater vulnerability to seed predation. This is because:

1) The actual significance of many of the factors that have either been suggested to affect predispersal seed predation by insects or that have been associated with variations in predispersal seed predation by insects is poorly understood.

2) The effects of different factors on predispersal seed predation by insects has rarely been compared as most studies have focussed on one or a few factors.

3) The effect of any one factor on predispersal seed predation by insects has rarely been compared across species. Most studies have focussed on single plant species.

1) *The actual significance of factors to predispersal seed predation by insects*

Many of the factors that have been associated with variations in predispersal seed predation by insects cannot, in any strict sense, be considered as true factors because they have not actually been demonstrated to affect predispersal seed predation by insects. Most of the factors in Table 2.5 (24 of 30) have been correlated with variations in predispersal seed predation by insects. However only 14 of these have some confirmation as true factors with an underlying mechanism. Without an underlying mechanism to provide a clear understanding of how a factor might affect seed predation, its exact significance is in doubt. Without such an understanding a factor thought to affect predispersal seed predation by insects may:

- not act alone as thought but interact with other unidentified factors.
- not actually affect predispersal seed predation by insects but be mistaken for another confounding factor.
- may affect predispersal seed predation by insects independently rather than through interactions involving other factors.

2) *The comparative effects of different factors to predispersal seed predation by insects*

Predispersal seed predation of a plant by insects may be affected by a range of factors of varying importance. The absolute significance of a factor must be considered in relation to the effects of other possible factors. For example, a factor

Table 2.5. A list of the factors that have either been suggested to affect IPSP levels, have been correlated with variations in IPSP levels or have been shown to affect IPSP with support for an underlying mechanism ^{1}. Following the references, the third column marks those references that suggest a particular factors may affect IPSP levels. The fourth column marks those references that have found a correlation between a particular factor and IPSP levels, fifth column marks those that support a particular underlying mechanism, the sixth column enumerates the number of plant species included in each study.

Factor	Reference	Suggested as a factor	Correlated factor	Explanatory mechanism	No. sp in study
Temporally related factors					
Variable successive seed crop size					
- affected by - flower production, pollination success	De Steven (1981b)		●	●	1
- fruit initiation	De Steven (1983)		●	●	1
- flower production, pollination success	Nilsson and Wastljung (1987)		●	●	1
- variable weather conditions	Solbreck and Sillen-Tulberg (1986a)		●	●	1
	Auld (1991)	●			6
	Janzen (1969)	●			-
	Shibata et al. (1998)		●		4
Synchronised seeding					
- affected by - rainfall variation	Augspurger (1981b)		●	●	1
- rainfall variation	Augspurger (1982)		●	●	1
- flower production	De Steven (1981b)		●	●	1
	Janzen (1969)	●			-
	Shibata et al. (1998)		●		4
Fruiting time vs predator activity					
- affected by	Augspurger (1981a)	●	●		1
	Bertness et al. (1987)	●			
	Evans et al. (1989)		●		1
- seasonal changes in local microclimate	Jordano et al. (1990)		●	●	1
- seasonality of local water availability	Knight (1987)		●	●	1
	Janzen (1969)	●			-

Table 2.5. Continued...

Parameter	References	Suggested as a factor	Correlated parameter	Explanatory mechanism	No. sp in study
Synchrony of fruiting and predator parasite activity	Janzen (1969)	●			-
Abundance of seed predators					
- affected by - fire	Auld and O'Connell (1989)	●			1
- seasonal water availability	Derr (1980)		●	●	1
Time of fruiting within the year	Spence (1990)	●			9
Length of predispersal period					
	Janzen (1969)	●			-
Seed development time					
	Andersen (1988)		●		1 *
- affected by - an elevation gradient	Herrera (1984)	●			1
	Janzen (1969)	●			-
	Prevett (1966)	●			-
	Scott (1982)		●		6
Activity of defensive ant symbionts					
- affected by - wet/dry seasons	Schemske (1980)		●		1
Spatially related factors					
Complex elevation gradient	Kelly et al. (1992)		●		5 **
	Louda (1982a, b)		●		1
	Herrera (1984)	●			1
	Inouye and Taylor (1979)		●		1
	Molau et al (1989)	●			1
	White (1975)	●			5 **

Table 2.5. Continued…

Parameter	References	Suggested as a factor	Correlated parameter	Explanatory mechanism	No. sp in study
Vegetation cover					
- affected by - disturbance/regeneration conditions	Jordano et al. (1990)		●	●	1
Water availability	Janzen (1975a)		●		1
	Jordano et al. (1990)		●	●	
	Knight (1987)		●		1
	Louda et al. (1987)		●	●	1
Proximity to water	Moore (1978 b)		●		1
Seed predator abundance					
- affected by - fire	Auld and O'Connell (1989)	●			2
Isolation from conspecifics					
- affected by - seed dispersal patterns?	Augspurger (1981)		●		1
	De Steven (1983)		●		1
- disturbance/regeneration conditions	Chung and Waller (1986)		●		1
	Janzen (1970)	●			-
	Leroi et al. (1990)		●		1
- disturbance/regeneration conditions?	Sauer and Feir (1973)		●		1
- disturbance/regeneration conditions?	Silander (1978)		●		1
- disturbance/regeneration conditions	Vandermeer (1974)		●		1
- habitat availability	Wolf et al (1999)		●		1
Host plant size	Nilsson and Wastljung (1987)		●		1
	Sauer and Feir (1973)		●		1
Distribution of seed dispersers	Herrera (1989)		●	●	1
Host plant indigeneity	Moore (1978a)		●		1

Table 2.5. Continued…

Parameter	References	Suggested as a factor	Correlated parameter	Explanatory mechanism	No. sp in study
Static' plant attributes					
Seed size					
- affected by - parent plant canopy density?	Moegenburg (1996)	●			-
	Bridwell (1918)	●			-
	Ernst et al. (1989)	●			1
	Janzen (1969)	●			-
	Russel (1962)	●			-
	Szentesi and Jermy (1995)		●	●	110
Seed shape	Bridwell (1918)	●			-
	Szentesi and Jermy (1995)		●	●	110
Fruit surface texture	Bridwell (1918) [2]	●			-
	Center and Johnson (1974)	●			-
	Green and Palmbald (1975)		●		2
	Hare (1980)		●		1
	Raina (1971)	●			1
	Stamopoulos and Huignard (1980) [3]		●		1
Hard pericarp layer	El-Sawaf (1956)		●	●	1
	Davidar (1987)		●	●	2
	Janzen (1977)	●		●	63
	Nwanze and Horber (1976)		●	●	1
	Podoler and Applebaum (1968)		●	●	1
	Scott (1982)		●	●	6

Table 2.5. Continued…

Parameter	References	Suggested as a factor	Correlated parameter	Explanatory mechanism	No. sp in study
Resin barriers in pericarp	Bridwell (1919)[2]	●			-
	Bridwell (1920)[2]	●			-
	Hinckley (1960)[2]	?	?		-
	Scott (1989)	●			6
Toxic seed coat/pericarp	Brett (1946)[4]	?	?		-
	Janzen (1969)	●			-
	Janzen (1977)		●	●	63
	Siemens et al (1992)		●	●	2
Toxins in seeds					
- affected by - water availability	Louda et al. (1987)		●		1
- water availability	Moore (1978b)		●		1
	Janzen (1977)		●	●	63
Infructescence/capitulum size	Chung and Waller (1986)		●		1
	Fenner (1985)		●		1
	Molau et al (1989)		●		1
Fruit seediness	Chidumayo (1997)			●	2
	Herrera (1984)		●	●	1
	Knight (1987)		●	●	1
Symbiotic protection by guard ants	Inouye and Taylor (1979)		●	●	1
	Keeler (1981)[5]		●	●	1
	Schemske (1980)[5]		●	●	1

Table 2.5. Continued…

Parameter	References	Suggested as a factor	Correlated parameter	Explanatory mechanism	No. sp in study
Abortive response to seed damage	Janzen (1969)	●			-
"Host quality"	Debouzie and Pallen (1987)		●		1

[1] With some exceptions this table does not include the literature dealing with predispersal seed predator species and stored seed products.

[2] in Janzen (1969)

[3] in Huignard et al. (1990)

[4] in Center and Johnson (1974)

[5] in Wilson 1983

* Correlation recorded for 1 of 4 species studied

** Associations between factors and seed predation were not compared between these species.

may appear to be important because when its effects are removed the intensity of seed crop predation for a plant drops by, say, 80%. However if the intensity of seed crop predation drops by a similar degree when the effects of other factors are removed, this first factor would not appear to be quite so important. In this case the first factor is just one of a number of equally important factors that contribute to seed mortality on the host plant.

Comparative studies are necessary to determine the relative importance of different factors to predispersal seed predation by insects. Most of the studies of factors that may affect predispersal seed predation by insects focus on just a single factor or a few factors; eg. 15 of 38 studies were concerned with 2 or more factors while only seven have dealt with four or more factors simultaneously (Table 2.5).

3) *The comparative effect of factors on predispersal seed predation by insects across species*

How factors vary in their effects on predispersal seed predation by insects from species to species is unknown. Most studies of the factors that may affect predispersal seed predation by insects have focussed on single host species and are not directly comparable as they differ in their ecological context and methodology. Only 5 of 38 studies have dealt with relationships between predispersal seed predation by insects and one factor across four or more species from the same plant community. Without this knowledge it is not possible to make generalisations on what species within a community are most vulnerable to predispersal seed predation by insects.

2.3.2 Further study necessary for the factors that may affect predispersal seed predation by insects

To increase understanding in this field, both in-depth and broad-scale studies are necessary. Specifically, there is a need for:

- more comprehensive studies of factors that may affect predispersal seed predation by insects to confirm their significance and understand what the underlying mechanisms are.

- studies that compare the effects of different factors on predispersal seed predation by insects in plants and that examine variation in factors from species to species. To provide predictive hypotheses on the importance of different factors regarding seed predation and seed survival and hence to plant community composition, any variations in the significance of factors to predispersal seed predation by insects should be related to plant functional types.

- research into the ultimate factors that underlie the importance of lower-level and proximal factors. This may help to uncover broadscale patterns in the significance of different factors to predispersal seed predation by insects. For example, if resource availability is a major determinant of the presence of static plant attributes that act as defences against seed predators, then studying resource availability may identify community-level patterns in plant defences.

A knowledge of the factors that affect predispersal seed predation by insects in single species of plant may be useful for understanding:

- how to maximise seed survival for rare and threatened plant species.

- how the effectiveness of seed predator biocontrol agents may vary according to particular conditions.

- how to maximise seed yield and minimise fruit damage in agricultural crops.

A knowledge of the factors that affect predispersal seed predation by insects across many species of plants may be useful for:

- identifying what types of plants are most likely to possess particular traits, such as chemical defences in seeds.

- understanding what types of plants within a community are most likely to be attacked by seed predators and have high intensities of seed crop predation.

- understanding what types of plants are most likely to be suppressed, in terms of population density, by predispersal seed predation by insects and how this may affect the composition of plant communities.

CHAPTER 3: A DESCRIPTION OF THE STUDY REGION AND ITS RAINFORESTS

Abstract

This study was conducted in the Atherton Tableland region of northeast Queensland's wet tropics. This region is a dominated by a plateau of 700 to 800m altitude with a lot of surrounding higher, more variable terrain. The region has a subtropical climate, with a mean annual rainfall that varies from approximately 1500mm to over 3000mm, most of which falls early in the year. The geology of the region is complex, the major rock types are either basalt, low grade metamorphics or granite and rhyolite. Primary tropical rainforest is the most extensive of the natural vegetation types in the region, even though on the Atherton Tableland proper it has been mostly cleared for crops and pasture. The structure, function and floristics of this rainforest is variable, depending on with varying soil and climatic conditions (Webb 1968, Webb at el. 1984, Tracey 1982). The most common type of rainforest however is Complex Notophyll Vine Forest, which in turn can be differentiated into subtypes according to floristics (Tracey 1982). The structure and floristics of the Atherton Tablelands rainforest also varies according to anthropogenic factors. Human activity has altered much of rainforest through disturbance, the deflection of post-disturbance plant successions and the introduction of exotic plant species.

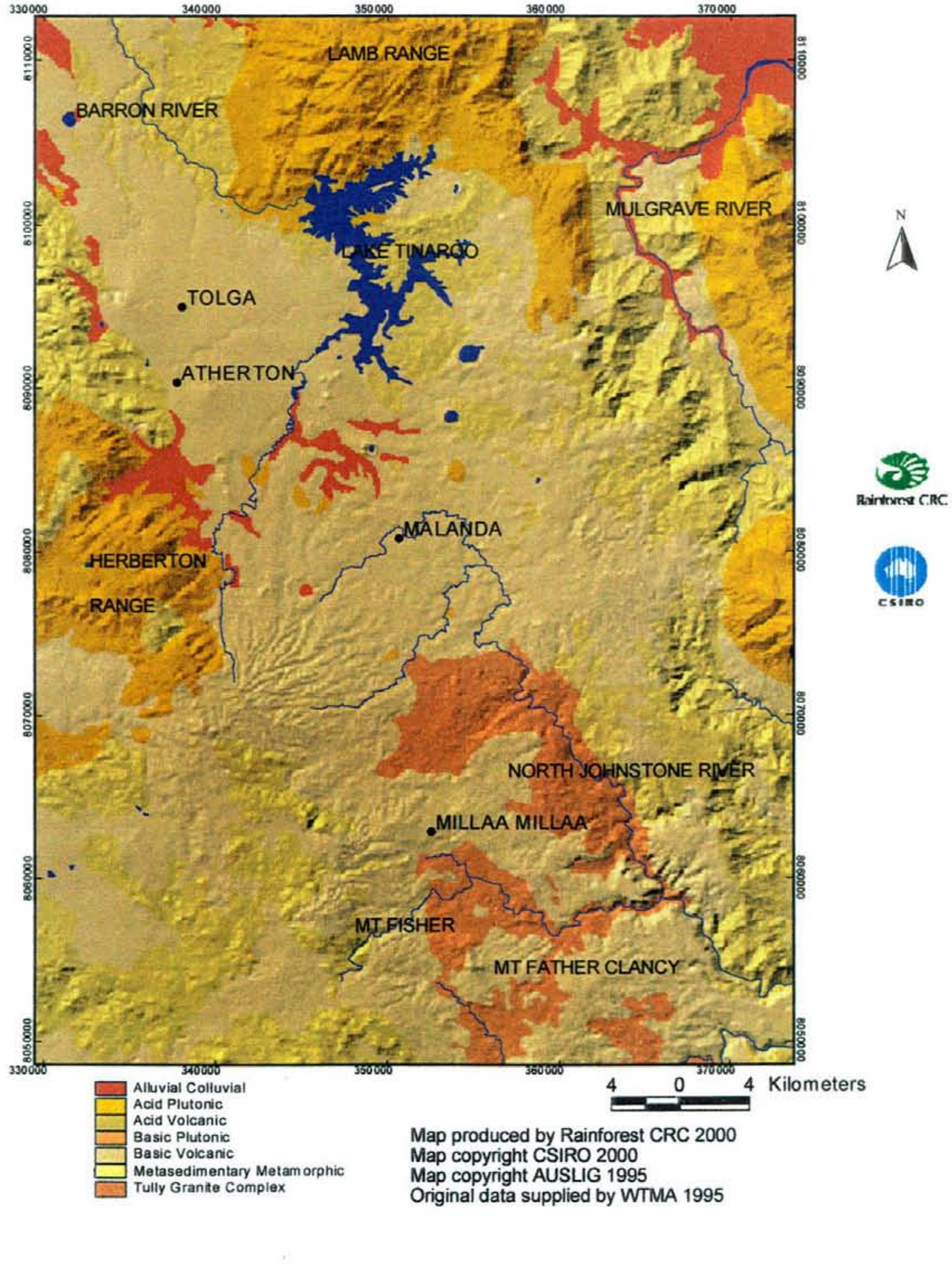
3.1 Physical geography and vegetation of the Atherton Tableland

This study was conducted in the Atherton Tableland region of northeast Queensland. The Atherton Tableland proper is an undulating plateau 700 to 800m in altitude, bounded by higher mountain ranges in the north and west, an escarpment and deep valleys to the east and two prominent mountains; Mt Fisher and Mt Father Clancy, to the south (Fig. 3.1). Both the Atherton Tableland proper and the adjacent lower slopes of the northern and eastern bounding ranges were included in the study region as they were considered to be within the one bioclimatic zone.

The study region is favourable for the study of tropical rainforest for the following reasons:

- it contains an extensive area of tropical rainforest currently protected under World Heritage listing.
- research can be conducted with the support of local research bodies and universities, in particular CSIRO's Tropical Forest Research Center.
- the flora and fauna of the region is well documented.
- although within the one bioclimatic zone, there is a range of tropical rainforest subformations and considerable floral diversity due to variation in soil type, local climate and the effects of anthropogenic disturbance (Tracey 1982).

Figure 3.1 Physical geography and geology of the Atherton Tableland region.



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Original data supplied by WTMA 1995

3.1.1 Climate

Although geographically tropical (Lat 17° 15') the Atherton Tableland region has a subtropical climate with a mean annual temperature of 22° C (Nix 1991) and occasional frosts. Rain is seasonal with about 70% falling between December and April during the "wet season" (Bureau of Meteorology 1971). This rain generally falls in association with a surface low pressure trough over northern Australia. Some rain is also associated with the westerly winds characteristic of the true South-east Asian monsoonal system that strengthens further north, but the Atherton Tablelands region itself is borderline monsoonal (Gentilli 1972, Jackson 1977). From April to July light rain falls from the orographic ascent of the south-east trade winds. This is then followed by a "dry season" of little rain until December.

The climate and rainfall in the region is quite heterogenous because of the varied topography in the region. Mean annual rainfall tends to increase from Atherton in the west (1426mm) to over 3000mm towards the Russell River and Johnston Rivers in the south east (Bureau of Meteorology 1971). The orographic effect towards the east and south also increases cloud cover bringing additional condensation and reducing insolation.

3.1.2 Geology and soils

The soils of the Atherton Tableland region vary primarily according to parent rock composition, which is dominated by either basalt, low grade metamorphics or granite and rhyolite (Fig. 3.1). Basalt is the most extensive parent material, laid down during Pliocene and Holocene lava flows (Stephenson et al. 1980). This gives the Atherton

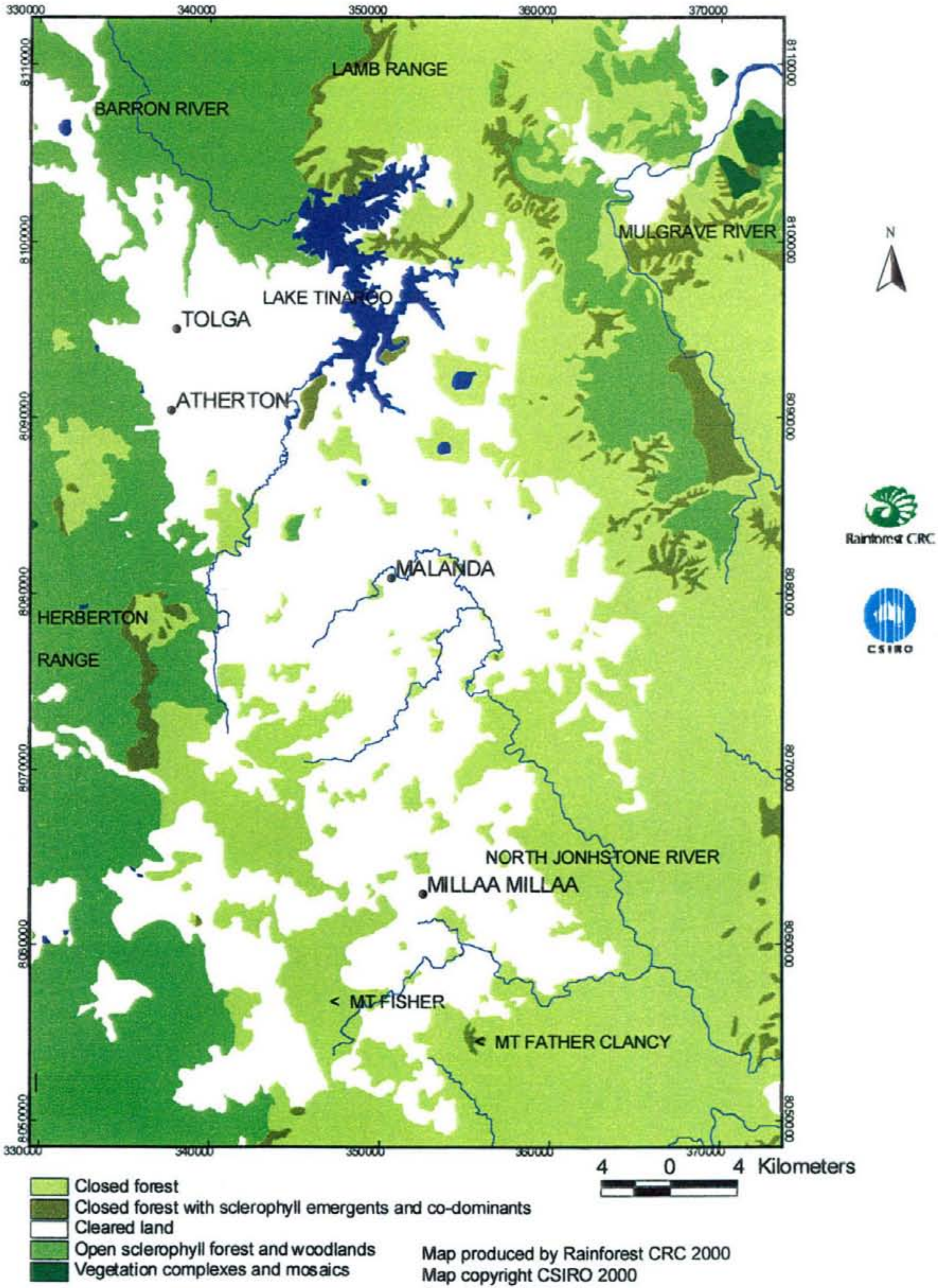
Tableland proper its gentle topography. This basalt lies on the metasedimentary/metamorphic Hodgkinson formation that lies exposed towards the north and east of the region (Arnold and Fawckner 1980). The Lamb and Herberton Ranges to the north and west of the Atherton Tableland are built primarily of Permian granitoids although similarly aged acid volcanics (rhyolite) contribute to the Herberton Ranges towards the north-west (Oversby et al. 1980).

The most fertile soils in the region are derived from basalt. These soils vary from deep and well developed on the oldest parent materials, to shallow and poorly developed on the youngest lava and scoria, but are characteristically high in exchangeable cations and particularly high in extractable phosphorus (Laffan 1988). The granitic and low grade metamorphic derived soils are lower in phosphorus and extractable cations, and the metamorphics are particularly low in calcium (Laffan 1988). In addition to parent rock composition soil fertility is also affected by climate. For any one soil type, fertility tends to decrease towards the southeast where greater leaching occurs under the higher rainfall.

3.2 The rainforest of the Atherton Tableland

Primary tropical rainforest is the most extensive of the natural vegetation types in the Atherton Tableland region, even though on the Atherton Tableland proper most of it has been cleared for crops and pasture (Fig. 3.2). Some rainforest fragments do remain on the plateau and other localised areas previously under pasture now support regenerating closed secondary rainforest. The peripheral slopes of the region have retained their primary rainforest and this continues into extensive surrounding areas.

Figure 3.2 Major vegetation types of the Atherton Tableland region.



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Original data supplied by WTMA 1995
Map based on vegetation maps prepared by
J.G.Tracey and L.J.Webb (1975)

3.2.1 Rainforest Structure and Floristics -The Influence of Climatic and Edaphic Factors

In the Atherton Tableland region there are number of different types of tropical rainforest. These types, classified by Webb (1959), differ in their structure, function and floristics in association with varying soil and climatic conditions (Fig. 3.3) (Webb 1968, Webb at el. 1984, Tracey 1982). The major differences among the rainforest types of the Atherton Tableland region are:

- a decrease in the leaf size distribution with a decrease in soil fertility and altitude.
- an additional decrease in life form diversity with an ascent in altitude.
- an increase in the number of deciduous species with a decrease in rainfall.

The most common type of rainforest on the Atherton Tablelands is Complex Notophyll Vine Forest, which in turn can be differentiated into subtypes according to floristics. These subtypes share a complex forest structure and diversity of plant life forms, a dominant canopy leaf length of 7.5 to 12.5 cm and support woody lianas (Tracy 1982).

3.2.2 Rainforest Structure and Floristics -The Influence of Anthropogenic Factors

Anthropogenic factors are also of major importance to the structure and floristics of the rainforest on the Atherton Tablelands. Human activity can alter forest structure and floristics through disturbance (the destruction of plant biomass (Grime 1979)), the deflection of post-disturbance plant successions and the introduction of exotic plant species.

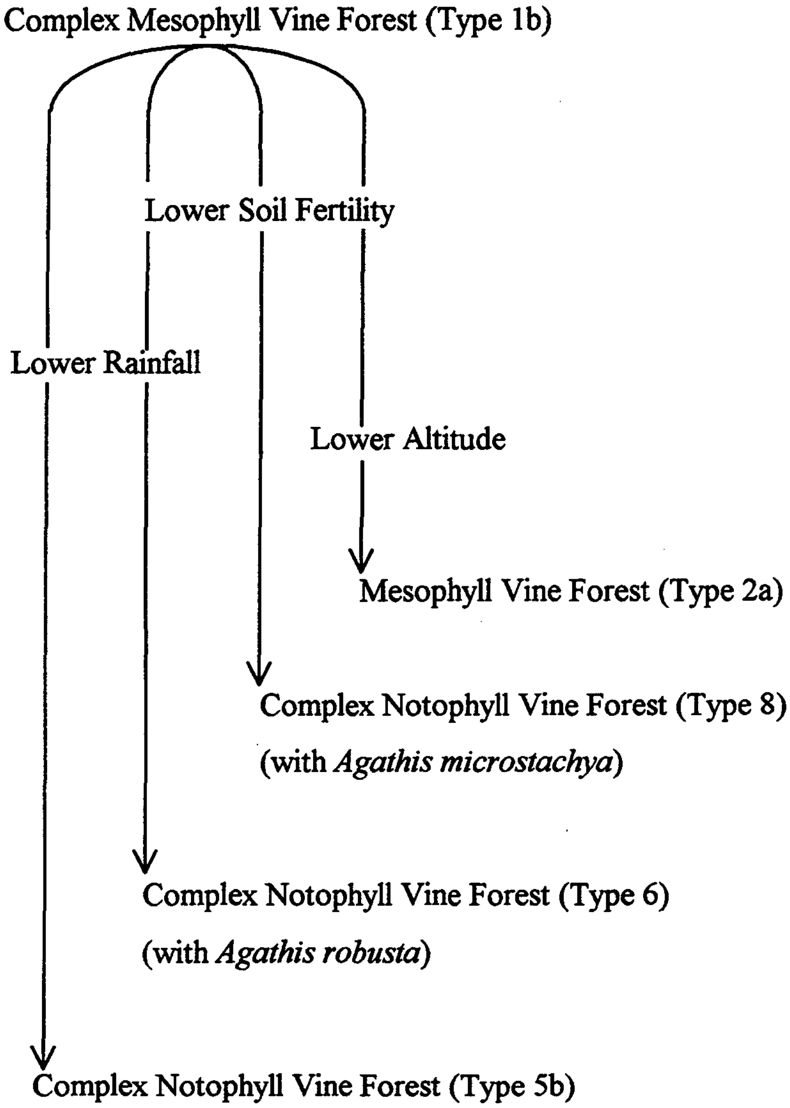

Figure 3.3. Environmental gradients and relationships of the rainforest types found in the Atherton Tableland region. Note: this scheme omits the rainforests of the cloudy wet highlands in the surrounding ranges and those with emergent *Eucalyptus sp.* as these were not included in the study. (Adapted from Tracey 1982).

Selective logging carried out in nearly all the region's rainforest after World War 2 (Andrew Graham, pers. comm.), removed many of the larger trees and appears to have initiated the growth of a denser forest understorey. However the exact effect of logging on the region's forests is impossible to determine as the documentation of this logging is poor and there is very little intact forest left with which to compare.

The effects of intense and widespread disturbance to the rainforest, by clearance for agriculture for example, are obviously more dramatic than selective logging. In the absence of further disturbance pasture will support a succession of plant species that can be seen to lead, under 'ideal' conditions, back towards the original dynamic and heterogenous primary rainforest. This is termed a 'reconstructive' succession (Hopkins 1981, 1990).

During a secondary rainforest succession typical for the Atherton Tableland an abandoned pasture will be replaced by an 'early secondary phase' of predominantly small short lived trees, shrubs and scramblers. This succession may be prevented from further progression towards the original rainforest by a number of different factors. Subsequent disturbance by fire prevents succession (Hopkins and Graham 1984a), leading to grassland that is even more fire prone (Hopkins 1981). Alternatively, in the absence of the succession may be inhibited by the domination of the exotic scrambler *Lantana camara* (Webb et al. 1972) or by the native short-lived tree species *Acacia aulacocarpa* characteristic of early forest successions on low fertility soils (Hopkins et al. 1996). If allowed to progress over a late secondary phase (as happens for example after *Acacia aulacocarpa* senesces) longer lived trees establish and the forest gains species, biomass and structural complexity.

Exotic plant species are an added component to the rainforest of the Atherton Tableland and are generally associated with some degree of forest disturbance. Many exotic species are found in the soil seed bank (Hopkins and Graham 1983, 1984a and b) and are a major component of early secondary rainforest succession (Humphries and Stanton 1992, Webb et al. 1972). Some exotic species may accelerate succession, eg. by acting as foci for seed dispersal (Willson and Crome 1989) or by providing microclimates that facilitate seed germination (Aide and Cavalier 1994). Other exotic species such as grasses or *Lantana camara* may, as previously stated, inhibit succession. In addition to occupying rainforest through their establishment during forest succession, exotic species may also encroach relatively undisturbed forest from edges that are themselves disturbed, for example by climbing over the canopy as vines (Humphries and Stanton 1992). By smothering the canopy, some exotic vine species are capable of eventually dominating the rainforest, converting it to a much simplified climax community (Floyd 1989, Stockard et al. 1985).

CHAPTER 4: A SURVEY OF INSECT PREDISPERSAL SEED PREDATION IN NORTH QUEENSLAND TROPICAL RAINFOREST: RELATIONSHIPS BETWEEN VULNERABILITY TO SEED PREDATION, AND PLANT AND HABITAT CHARACTERISTICS

Abstract

Many different factors have been demonstrated or suggested to affect the vulnerability of plants to insect predispersal seed predation but little is known of their comparative significance across species at the community level. This study compared associations between IPSP and 14 parameters, as possible factors, across a broad range of species in a tropical rainforest community. The factors were the attributes of plants and their habitat. Seeds were collected from 211 plants, each representing a different species. 41% of the plants were attacked by seed predators (predominantly Coleopterans and Lepidopterans). Hard pericarp thickness, total pericarp thickness and plant indigeneity were significant predictors of probability of attack by predispersal seed predators, while intensity of the attack was significantly associated with only plant family. Plants with seeds surrounded by a thick hard pericarp layer were less likely to be attacked by seed predators than those with a thin layer or no layer at all. Total pericarp thickness was also negatively associated with likelihood of attack. This was because total pericarp thickness positively associated with hard pericarp thickness. Plants also had a lower chance of being attacked if they were exotic. The vulnerability of IPSP may also have been independently associated with family-level taxonomic affiliation as Euphorbiaceous and Lauraceous plants differed significantly in their intensity of IPSP.

4.1 Introduction

Seed predation is a well documented cause of seed mortality for many plants in tropical rainforests, often occurring at high intensities (eg Crome and Irvine 1986, Cunningham 1997, Grieg 1993, Osunkoya 1994). By reducing seed availability seed predation has been found to limit seedling recruitment in tropical rainforests (De Steven and Putz 1984, Schupp 1990, Sork 1987) and appears to be capable of altering community composition by limiting the abundance of potentially dominating tree species (Putz et al. 1990, see also Asquith et al. 1997, Davidson 1993, Louda 1989). As a common cause of seed mortality in tropical rainforests, seed predation may be of general importance to the plant species composition of these communities.

To determine how seed predation might affect the species composition of tropical rainforest it is necessary to know what plant species are most likely to lose seeds to seed predators. This can be done by determining what factors affect seed predation for these species. The purpose of this study was to measure seed predation in a tropical rainforest, and determine what factors might be affecting seed predation and hence what species are most vulnerable to attack. This study focussed on IPSP in the tropical rainforest of north Queensland. IPSP has rarely been studied at the community level and has not been studied in Australian rainforests.

4.1.1 What factors can affect insect predispersal seed predation?

Seed predation may be affected by a broad variety of factors, judging by the number of correlations that have been found between measures of seed predation and possible factors of influence (Table 4.1). These factors can be categorised into three non-

Table 4.1. The numbers of studies that have dealt with factors that may affect insect predispersal seed predation. The first column enumerates the studies that have found correlations between a factor and variations in insect predispersal seed predation. The second column enumerates the studies that have investigated possible effects of one or more factors on seed predation for over two plant species, while the third column enumerates similar studies conducted at the community level.

	Number of studies*		
	showing correlations	comparing > 2 species	studying communities
Temporally related factors			
Variable successive seed crop size	6	2	1
Synchronised fruiting	5	1	1
Synchrony of fruiting time vs predator activity	3	1	0
Abundance of seed predators	1	0	0
Seed development time	1	1	0
Activity of defensive ant symbionts	1	0	0
Spatially related factors			
Complex elevation gradient	3	0	0
Vegetation cover	1	0	0
Water availability	4	0	0
Proximity to water	1	0	0
Isolation from conspecifics	7	0	0
Host plant size	3	0	0
Distribution of seed dispersers	1	0	0
Host plant indigeneity	1	0	0
Static plant attributes			
Seed size	5	1	0
Seed shape	1	1	0
Fruit surface texture	3	1	0
Hard pericarp layer	6	3	0
Toxic seed coat/pericarp	2	2	0
Toxins in seeds	3	1	0
Infructescence/capitulum size	3	0	0
Fruit seediness	3	1	0
Symbiotic protection by guard ants	3	0	0
“Host quality”	1	0	0

* These studies are drawn from Table 2.5 where their references are given.

exclusive groups; temporally related factors, spatially related factors or static plant attributes. Temporally related factors vary in their effects with time and are responsible for variations in IPSP over time. Spatially related factors vary in their effects over space and appear to underlie spatial variations in IPSP. Static plant attributes are at least in part under genetic control. Their effects tend to vary across phylogeny ie. effects differ between individual plants within species or between species. The expression of these attributes would be expected to vary within species, over space and time, however.

4.1.2 Scope of study

While a considerable amount of work has been done on IPSP, almost all of this has been focussed on individual species. Few studies have made comparisons of the effects of factors across species and almost none have looked at community-level patterns (Table 4.1). To address this lack of attention given to IPSP at the community-level this study looked for community-level patterns in the vulnerability of rainforest species to IPSP using a survey.

The survey used for this study dealt with factors that could be studied in a relatively short time, these were mainly static plant attributes. Those that have been shown in previous studies to affect IPSP are hard pericarp thickness, seed size, seed shape, seed quantity per fruit (seed number and seed mass) and fruit pericarp surface texture. Other static attributes included in this study were total pericarp thickness, diaspore size and growth form.

In addition to static plant attributes, the survey included three spatially related factors. Of these three, host indigeneity has support from previous studies as factors that may affect IPSP (Moore 1978a). Two other spatially related factors; light availability and phosphorus availability have not previously been given attention as factors that may affect IPSP. One temporally related factor – fruiting season was also included, and phylogeny, indicated by family-level taxonomic affiliation, was the final factor tested.

Hard pericarp thickness

Hard pericarp thickness can affect the vulnerability of plants to IPSP by preventing the entry of insects into seeds, either as feeding adults (Davidar 1987) or as burrowing larvae (Janzen 1977, Nwanze and Horber 1976, Podoler and Applabaum 1968). In their larval phase insect seed predators may not have sufficient energy reserves to survive the process of cutting through the pericarp (Janzen 1977). Given that hard pericarp thickness can be an effective means of protecting seeds from IPSPs, the species of a plant community that have thick hard pericarp layers within their fruit may have a smaller chance of being attacked, or may be attacked at lower intensities, than species without such pericarp layers or only thin hard pericarp layers. This study tested this hypothesis, which may be summarized thus: there is a negative correlation between the hard pericarp thickness of a species and its vulnerability to IPSP.

Seed size

Seed size was first suggested as a factor that may affect the vulnerability of plants to seed predation by Janzen (1969). He had found in a survey of IPSPs in neotropical legumes that small-seeded plant species were more likely to be attacked by insects than large seeded species. It is difficult to assess the significance of these results however, because Janzens (1969) conclusions relied heavily on untested evolutionary interpretations. He had suggested that small-seeded plant species were more likely to be attacked by insects than large seeded species because higher seed predation pressures on some species had selected for a greater number of seeds per seed crop, which necessitates a reduction in seed size (Janzen 1969). If anything there is actually more evidence to suggest that larger seeded species are subject to more, rather than less, predation pressure. For example some species of insect preferentially attack the larger seeds available on a host plant (Russell 1962, Ernst et al. 1989, Nalepa and Grissell 1993, Moegenburg 1996). This is probably because the larval survivorship (Mitchell 1975), adult size (Russell 1962, Ernst et al. 1989, Nalepa and Grissell 1993, Moegenburg 1996) and fecundity (Wilson 1988) of IPSPs is dependent on the resources available to the developing insect, which is some times determined by host seed size.

Seed size may also affect the vulnerability of plants to IPSPs because larger seeded species are able to support seed predators across a greater range of body sizes (Grieg 1993). They are thus vulnerable to a potentially greater number of insect species. With this increase in vulnerability large seeded plants could be expected to have a greater probability of being attacked and at greater intensities of seed crop predation than smaller seeded plants. These predictions do have some support. Szentesi and Jermy (1995) had found that for legumes large seeded species were more likely to be attacked than small seeded species. This current study tested the hypothesis that there was a positive correlation between the size of a plant species seeds and its vulnerability to IPSP.

Seed sphericity

That the shape of a seed could affect its vulnerability to IPSP was first suggested by Bridwell (1918, cited in Janzen 1979) - thin seeds could exclude bruchid beetles from seeds because they could not provide enough living space for them. This effect on seed predation has been supported by Szentesi and Jermy (1995) who had shown that legume species with flat seeds had a lower likelihood of being attacked than those with more spherical seeds. This study sought to test for this effect across many species with the hypothesis; there is a negative correlation between the sphericity of a plant species seeds and its vulnerability to IPSP.

Number of seeds per fruit and seed mass per fruit

The quantity of seeds per fruit can affect predispersal seed predation by insects. Herrera (1984b) and Knight (1987) had found for particular species of plant a positive relationship between the chance a fruit was attacked by IPSPs and number of seeds it contained. The number of seeds per fruit was important to these insects because they fed within the one fruit. Thus to maximise the resources available to developing larvae adults tended to oviposit on the fruits with the most seeds. To determine whether or not a there may be a similar relationship between the vulnerability of plants to IPSP and quantity of seeds within their fruit across species, rather than within species, the following hypotheses were tested:

- there is a positive correlation between the mean number of seeds that are found in the fruit of a species and its vulnerability to IPSP.
- there is a positive correlation between the mass of seed within the fruit of a species and its vulnerability to IPSP.

Fruit surface texture

There is some evidence for the effect of fruit surface texture on vulnerability to seed predation. Hare and Futuyama (1978) and Hare (1980) had found an inverse correlation between burr length in *Xanthium strumarium* and seed predation intensity. Additionally, Green and Palmbald (1975) had compared seed predation in two sympatric, congeneric legume species and found that the species *Astragalus utahensis* that had hairy pods was vulnerable to fewer species of insect than the species *Astragalus cibarius* that had smooth pods. Consequently the seed crops of *Astragalus utahensis* were attacked by IPSPs at a lower intensity than *Astragalus cibarius*.

Hairs or burrs on the surface of fruit may prevent the entry of insect seed predators by blocking their movement or perhaps by preventing any foot purchase. A sticky or glandular surface on a fruit may also prevent insects of any movement or purchase. To see if fruit pericarp texture was correlated with the vulnerability of plants to IPSP across a rainforest community the following hypothesis was tested: species with a possibly protective fruit surface pericarp texture (hairy, spiny, sticky or glandular) were less vulnerable to attack by IPSP than species that produced fruit with a smooth and dry pericarp surface.

Total pericarp thickness

Total pericarp thickness may also be related to the vulnerability of a plant to IPSP. This is because hard pericarp thickness is a component of total pericarp thickness. Because of this, any correlation between total pericarp thickness and vulnerability to IPSP is not likely to have much explanatory value. However, if species with different dispersal modes or sizes of fruit differ in their vulnerability to IPSP, this may because of differences in hard pericarp thickness, in which case, total pericarp thickness would help to provide the explanatory link. The hypothesis tested for this factor was: there is a negative correlation between the total pericarp thickness of a species and its vulnerability to IPSP.

Diaspore size

Diaspore size as a variable was included in this study speculatively, not because there was evidence that it may act as a factor affecting the vulnerability of plants to IPSP. The hypothesis tested was; diaspore size among species may be correlated (positively or negatively) with vulnerability to IPSP.

Growth form

Different plant growth forms may vary in their vulnerability to IPSP because of differences in the way they allocate resources to different functions. This is because:

1) the quantities of resources invested in different functions varies across growth form eg. a large proportion of resources are invested in structural support in trees in comparison with vines.

2) the functions of a plant drawing resources from the same source. For example, smaller, shorter-lived growth forms such as herbs and shrubs do not invest proportionately as much resources in the production of structural support as larger, longer lived plants like trees (Grime and Hunt 1975). As a result, proportionately more resources are available for growth and reproduction in smaller and faster growing species (Abrahamson 1979, Bazzaz et al. 1987, Raven 1990).

A trade-off in plants may also exist between the production of reproductive structures and their defence against herbivores and seed predators. This may mean that plants with high levels of allocation towards reproduction have low levels of allocation towards the defence of reproductive structures, such as seeds. This trade-off parallels that found between growth allocation (leaf and stem production) and defences against herbivores (Herms and Mattson 1992). Hence the smaller, shorter-lived growth forms with relatively high levels of reproductive allocation would be expected to have low levels of defences against seed predators in comparison with larger, longer-lived growth forms that have relatively low levels of reproductive allocation. If levels of allocation towards seed defences do affect seed predation levels then according to this hypothesis vines should be most vulnerable to predispersal seed predation by insects followed by shrubs and trees.

Indigeneity

Studies of herbivory and commercial crop infestation show that exotic species of plant are often less vulnerable to attack by phytophagous insects than native species (Kogan 1991, Strong et al. 1984). This can be explained by their novel characteristics, to which local potential phytophages have yet to adapt (Strong et al. 1984). These characteristics include the habitat conditions of the host species, its phenology, recognisable or camouflaging features and the presence of potential defenses.

Habitat: Even though a potential IPSP species may occur in the same community as an exotic species of plant, differences in the habitat tolerances of these species can act as ecological barriers. If the distribution of these species does not overlap in space the opportunity for the seed predators to encounter these exotic plants would not occur. For example, an exotic species of plant that grows in large rainforest canopy gaps may potentially be attacked by an insect that has adapted to a similar species of understorey plant. In the high-light conditions of the canopy gap however, the environment within the exotic fruit may heat up beyond the temperature tolerances of the insect. The insect would not then be able to exploit the exotic species.

Phenology: If a species of plant is to be attacked by an insect seed predator the occurrence of seeds and of active insects must overlap in time as well as in space (Strong et al. 1984). Thus if the seeds of an exotic plant are not available when the potential seed predator feeds then the seeds will not be attacked.

Recognisable or camouflaging features: For an insect to attack a plant it must recognise it as a potential food source. Insects may not recognise exotic species of plant as sources of food because they may differ from the original host species in terms of size, shape, colour and chemical signature (Bernays and Chapman 1994, Jermy 1993).

Defenses: Plants may possess defensive features that reduce their vulnerability to seed predators. When these plants are introduced into a new habitat some of these features may be new to potential seed predator insects. This is because these insects have adapted to coping with the features of their original host plants. An exotic plant will not be attacked by insect seed predators until they have adapted to these novel defenses. These defensive features may be morphological (eg. Janzen 1977, Scott

1982, Siemens et al. 1992), symbiotic (eg Keeler 1981) or chemical (eg. Janzen 1977a, Siemens et al. 1992).

The factors that determine how effectively a herbivore can exploit a potential host species are likely to also apply to insect seed predators. Thus IPSPs are unlikely to be as well adapted to exploiting exotic potential host species as native host species. To investigate this, the hypothesis that exotic species were less vulnerable to IPSP than native plant species was tested.

Light availability and phosphorus availability

There are a number of inclusive hypotheses on why plants adapted to high resource environments may allocate more resources towards growth and less towards anti-herbivore defences than plants adapted to low resource environments (see Herms and Mattson 1992 for review). These hypotheses are embodied in the loose term 'resource availability theory'. According to Coley et al. (1985) these patterns of allocation occur because plants in high resource environments grow more quickly than plants in low resource environments and the cost of defences, in terms of the potential growth that could have been accrued with those diverted resources is greater. Hence the cost of defences for faster growing plants in terms of lost competitive advantage is greater than for slow growing plants. Conversely the loss of competitive advantage caused by herbivore damage is less for faster growing plants than for slower growing plants because leaves are more easily replaced. Plants of high resource environments are therefore expected to have higher levels of herbivory than plants of low resource environments. There has been much support for resource availability theory, including positive associations between herbivory levels and the availability of phosphorus (Bryant et al. 1989) and light (Coley 1987) across species.

Patterns of seed predation and resource availability may parallel those found between herbivory and resource availability because allocation towards reproduction tends to match allocation towards growth (Bazzaz et al. 1987). For example Schat et al. (1989) had found a direct relationship between phosphorus availability and reproductive allocation. If the relationship resource availability and seed predation parallels the relationship that is supported between resource availability and herbivory, then:

1) plant species adapted to high resource environments should allocate more resources towards reproduction and less towards defences (against seed predators) than species adapted to low resource environments.

2) plants species adapted to high resource environments should be more vulnerable to seed predation than species adapted to resource poor environments.

To see if plant species adapted to resource rich environments were more vulnerable to IPSP than species adapted to resource poor environments this study tested the following hypotheses:

1) There is a positive correlation between phosphorus availability across species and their vulnerability to IPSP.
2) There is a positive correlation between light availability across species and their vulnerability to IPSP.

Fruiting season

The season of fruit fall was also included in the survey because there may be differences in the intensity of IPSP for different host species, according to the time of year that they fruit. These differences may be expected because different species do fruit at different times of the year and the abundance of active insects has been shown to vary seasonally in tropical rainforests (Pearson and Derr 1986, Wolda 1978, 1988). Thus some species may fruit when the abundance and activity of insect seed predators is greatest, while others may fruit when insect abundance and activity is low. Thus the hypothesis that the vulnerability of species to IPSP varies significantly according to season was tested.

Host phylogeny

Host phylogeny was included as a parameter in this seed predation survey because it may need to be taken into account when interpreting correlations between other parameters and the vulnerability of plants to IPSP. This is because closely related species, tend to be similar in terms of ecology, biochemistry or morphology for example (Harvey and Pagel 1991) and the development of different plant attributes is often correlated across species (Grime 1988, Leishman and Westoby 1992, Osunkoya 1996). Hence a correlation found between a plant attribute and vulnerability to IPSP may in fact be due to the confounding effects of another attribute via their association through common ancestry.

The taxonomic affiliation of the species sampled in the survey was used as an indicator of their phylogenetic relationships as their true ancestral history is unknown.

Although the taxonomic system of nomenclature was not in its origination developed to reflect evolutionary relationships between species (Judd et al 1999) it does do this to a degree. This is because species are grouped and named according to their morphological and biochemical similarity/dissimilarity, which are coded for by genes which may be shared through common ancestry, and increasingly by similarities/dissimilarities in their nuclear acids – the constituents of the genes themselves (Judd et al 1999). Hence, taxonomic genera for example, that belong to the same taxonomic family are more likely to be closely related in evolutionary terms than genera that belong to different families. Although this would not necessarily apply if one of these families were polyphyletic.

When variations in IPSP was correlated with a plant attribute across species, the possibility that this attribute and IPSP varied according to phylogeny was also tested.

4.1.3 Summary of hypotheses

1) There is a negative correlation between the <u>hard pericarp thickness</u> of a species and its vulnerability to IPSP.
2) There is a negative correlation between the <u>total pericarp thickness</u> of a species and its vulnerability to IPSP.
3) There is a positive correlation between <u>seed size</u> for a species and its vulnerability to IPSP.
4) There is a positive correlation between <u>seed sphericity</u> for a species and its vulnerability to IPSP.
5) There is a positive correlation between the <u>mean number of seeds per fruit</u> for a

species and its vulnerability IPSP.

6) There is a positive correlation between the <u>mass of seed per fruit</u> of a species and its vulnerability to IPSP.
7) Species with a possibly protective <u>fruit surface texture</u> (hairy, spiny, sticky or glandular) were less vulnerable to attack by IPSP than species that produced fruit with a smooth and dry pericarp surface.
8) <u>Diaspore size</u> among species may be correlated (positively or negatively) with the vulnerability of species to IPSP.
9) The <u>growth-form</u> of a species is related to its vulnerability to IPSP, so that in order of vulnerability are vines, shrubs and then trees.
10) <u>Exotic</u> species are less vulnerable to IPSP than <u>native</u> species.
11) There is a positive correlation between <u>phosphorus availability</u> across species and their vulnerability to IPSP.
12) There is a positive correlation between <u>light availability</u> across species and their vulnerability to IPSP.
13) The vulnerability of species to IPSP varies significantly according to <u>season</u>.
14) The vulnerability of species to IPSP, and correlated plant attributes, varies significantly according to <u>host phylogeny</u>.

4.2 Methods

4.2.1 Study area and sampling

This study was conducted on the Atherton Tableland in north-east Queensland. Plants were sampled for fruit opportunistically from tropical rainforest across the Tableland region over two years from 1995 to 1997 (see Chapter 3 for a description of the region and its rainforests). Originally a fixed number of sampling sites were chosen to represent both primary and secondary successional phases of rainforest over a range of soil types and soil fertility levels. This sampling strategy was later changed to opportunistic sampling to maximise the number of plant species that could be represented.

Each species sampled was represented by a single plant. Earlier attempts to represent each species with three individuals were abandoned as most species were present as highly dispersed populations and few species were represented by more than the one fruiting individual.

Fruit were harvested directly from plants, when in a near-ripe to ripe state. Dehiscent types of fruit that split open to release their seeds were collected prior to this final stage of maturity. From each sample of fruit two subsamples were taken. One subsample of 40 fruit was used to rear and document any insect seed predators already within the seeds. The other subsample of 24 fruit was used to measure the intensity of seed crop predation and to record seed/fruit morphological attributes. Accompanying each sample was the following information: date, location, plant growth form, its forest strata level, forest successional phase and soil type.

4.2.2 Rearing insect seed predators

To rear insect seed predators 40 fruit were kept on damp vermiculite in plastic bags in a shade house. The bags were 360 by 230 mm clip-lock bags. The number of bags required to contain the fruit of each species varied according to fruit size. Fruit samples for most species were easily contained within one or two bags. In the bottom of each bag was a wire ring (1mm steel wire) that spread the sides of the bag out and provide a stable flat base. A 30mm deep layer of vermiculite was poured into each bag and dampened slightly with water. On dry vermiculite some species of fleshy fruit tended to dry up so much that the seeds within became dehydrated. This water loss was prevented because it could sometimes any seed predators within the seeds (pers obs). The dampened vermiculite helped to reduce the level of desiccation in fruit.

Within each bag a screened aeration hole was provided. The screen prevented any insects from exiting the bag, and was made with a 60 by 60mm piece of 1mm cloth gauze. By using the screw on tops from 2 litre plastic milk containers, this gauze was clamped over a 20mm hole cut into the plastic bag. To do 20mm holes were cut into the milk container lids, and the threaded tops of the container necks was cut off. By placing the lid the inside a plastic bag, over the hole cut into the bag, the mesh could be sealed against the plastic, by sandwiching the gauze and the plastic bag together between the container lid and the threaded container top, which is screwed in from the outside of the bag.

The rearing bags were kept in a shade house and regularly inspected for emergent insects until each fruit sample had completely decayed. As insects emerged they were collected into killing jars, killed with ethyl acetate and pin mounted. Mounted insects were later identified by taxonomists.

4.2.3 Measuring seed predation

To measure seed predation for each plant the subsample of 24 fruit were dissected. The component seeds were counted, examined under a binocular microscope, dissected if longer than approximately two millimetres, and categorised as being either: - 1) fully developed and undamaged.

- 2) undeveloped and undamaged.

- 3) damaged; decaying only.

- 4) damaged; possessing cavities, punctures, larvae or frass (with or without decay).

To avoid misinterpreting the origin of any damage or developmental failure among seeds only the seeds of category #4 were counted as having been attacked by IPSPs. While this may underestimate seed predation, seed damage or developmental failure may also be caused by factors other than predispersal seed predation, such as the invasion of bacteria or fungi following damage to the fruit wall. This damage may be caused by pulp feeding insects for example (Sallabanks and Courtney 1992).

Two separate measures of seed predation were used for statistical analysis:

1) the presence/absence of any seed predation for a seed sample.

2) the proportion of a seed sample that was attacked by seed predators (calculated as the number of category #4 seeds divided by the total number of seeds counted).

Both measures were used so the results could be compared with those of past studies, which have variously dealt with either the presence/absence of IPSP and its intensity. Whenever any seeds were attacked by seed predators, the degree of seed damage caused by the consumption of tissue was also noted. This was measured as the estimated percentage volume of seed tissue destroyed.

4.2.4 Recording fruit/seed morphological attributes

Fruit and seed morphological attributes were recorded using 12 fruit and 12 seeds per study species; these were randomly taken from the subsample of 24 fruit used to assess seed predation levels. Measurements of fruit and seeds were taken using a vernier calliper to an accuracy of 0.01 mm.

4.2.5 Defining parameters

14 parameters, as factors that may affect seed predation, were tested for their possible relationships to seed predation (for summary see Table 4.2). 12 parameters describe fruit and seed morphology, growth form, fruiting time of year and taxonomic affiliation. The remaining two parameters relate indirectly to the plants by describing their habitat.

Fruit surface texture: This describes the texture of the outermost surface of the fruit pericarp.

Total pericarp thickness and hard pericarp thickness: The total pericarp thickness of a fruit was measured as the thickness of tissue (including the testa) from seed surface to the fruit outer surface, at its narrowest point on the fruit. As a separate variable the thickness of any hard lignified pericarp was similarly measured.

Seed and diaspore size: Seeds and diaspores were measured along their longest and shortest axes. Indices for seed and diaspore size were calculated as the product of these major and minor axes.

Diaspores are defined as the dispersal unit of a plant. As examples, a wind dispersed diaspores include the plume or wings that would be attached to the seed, or a gravity dispersed diaspore may just be the seed and surrounding testa that falls from a dehiscing pod. For flesh coated fruits, the whole fruit was considered to be the diaspore, even though some large fleshy fruits may be eaten by animals piecemeal. Depending on the fruit structure then, the pericarp may be a component of the diaspore (as for wind dispersed diaspores or for flesh coated fruit/diaspores) or a component of a fruit from which diaspores are released (as for the gravity dispersed example).

Seed sphericity: Seed shape was described in terms of how round a seed was with an index of seed sphericity. This was calculated by dividing the minor axial width by the major axial length, giving a value between 0 and 1. The closer a seed's shape was to a sphere the closer the index was to 1, the closer the seed was to a disk or needle shape the closer the value was to 0.

Seed mass per fruit: An index of the quantity of seed material per fruit was calculated by multiplying the mean seed number per fruit by mean seed dry weight (oven dried to constant mass at 70^0C).

Growth form: the categories for growth form were; trees, shrubs, vines and herbs. Trees were defined as woody plants exceeding 3m in height and shrubs as woody plants below 3m in height, including understorey 'treelets'. Vines were defined as plants that climbed with the aid of other vegetation for support and herbs as small non-woody plants.

Phosphorus availability: As a measure of the soil phosphorus availability in a plant's habitat, the extractable soil phosphorus level was used. This is an index of the level of exchangeable phosphorus level in soil and was assigned to each plant on the basis of the local soil type and soil chemical information from Laffan (1988).

Light availability: Whether a plant had high or low light availability was dependent on whether the plant was from the rainforest canopy and subcanopy, or understorey and ground layer respectively. Plants growing in canopy gaps were also recorded as having high light availability.

Host phylogeny: As an indication of a species' phylogeny its taxonomic family was used. Groups of species were compared according to their taxonomic family as this was the lowest taxonomic rank fow which reasonable numbers of representative species could be sampled. Higher ranks would have included more species per group, however, this would also have included a greater diversity of species, with greater degrees of evolutionary divergence between species and therefore a lower degree of relatedness between species.

4.2.6 Data analysis

Associations between the presence/absence of seed predation, the intensity of seed crop predation, and the 14 parameters describing plant and habitat attributes were investigated by using three types of statistical analysis: univariate analysis, phylogenetic correlations and logistic regression analysis. Where tests were concerned with the presence/absence of seed predation all plants were included, whereas only attacked plants were used for tests concerning intensity of seed crop predation. Where possible, the parameters used to describe plant attributes were transformed as necessary to minimise heteroscedasticity and non-normality (Table 4.2).

Univariate analysis

The main component of the data analysis in this study used univariate tests of association between parameters decribing plant and habitat attributes and IPSP, and between the parameters themselves to look for intercorrelations. Associations between parameters and IPSP were tested for first. Following this, tests for intercorrelations between the parameters were applied to:

- any associations between parameters that appeared in the multivariate analysis.
- all possible pair-wise combinations between parameters that were significantly associated with IPSP and all the other remaining parameters.
- any other possible intercorrelations between parameters that may have been expected according to the biology of the sampled plants and their seed predators.

Table 4.2. The parameters used in the seed predation survey.

Parameter	Type of variable	Units of measurement and categories	
Fruit/seed morphological attributes			
Fruit surface texture	categorical	smooth / hairy, spiny /sticky, resinous / glandular	-
Mean total pericarp thickness	continuous - nonparametric	mm	$x' = \log(x+1)$
Mean hard pericarp thickness	continuous - nonparametric	mm	$x' = \log(x+1)$
Mean no. seeds per fruit	continuous - nonparametric	no. seeds / no. fruit	$x' = \log(x+1)$
Mean seed mass per fruit index	continuous - nonparametric	no. seeds * mean seed dry weight(mg)	$x' = \log x$
Mean seed size index	continuous - parametric	$\sqrt{}$ (main axis(mm) * minor axis(mm))	$x' = \log x$
Mean diaspore size index	continuous - parametric	$\sqrt{}$ (main axis(mm) * minor axis(mm))	$x' = \log x$
Mean seed sphericity index	continuous - nonparametric	main axis(mm) / minor axis(mm)	$x' = \log x$
Other attributes			
Growth form	categorical	tree / vine / shrub / herb	-
Phosphorus availability	categorical	7 / 9 / 10 / 16 / 20 / 33 / 40 / 100 / 130 mg P / kg soil	-
Light availability	categorical	high (canopy, subcanopy strata level) / low (understorey, ground layer strata level)	-
Fruiting time of year	categorical	Jan, Feb / Mar, Apr / May, Jun / Jul, Aug / Sep, Oct / Nov, Dec	-
Indigeneity	categorical	native / exotic	-
Phylogeny	categorical	taxonomic family	-

* Continuous data was transformed to normalize frequency distributions where possible and minimise heteroscedasticity.

Once intercorrelations between parameters were known the experiment-wise error rate (α-level) of the initial tests between seed predation and parameters were adjusted using the Dunn-Sidak method (Sokal and Ralph 1981). This was done to take into account the possible effects any intercorrelations may have had on independence of the tests between IPSP and parameters. The possible effect of intercorrelations between phylogeny and other parameters on the independence of these tests was accounted for separately (see below) and was not used in the adjustment of experiment-wise error rates.

Phylogenetic correlations: When a plant attribute was significantly correlated with variations in IPSP, the possibility that this was confounded with some other phylogenetically related attribute was tested for. This was done by testing for significant variations in the 'significant' attribute between taxonomic families. In the event of such a correlation, the correlation between IPSP and the attribute was then to be retested, while accounting for plant family. The results gave only one correlation between IPSP and a plant attribute (hard pericarp thickness) that may have been confounded with phylogeny and this correlation was retested, accounting for phylogeny (using plant family), with Logistic Regression Analysis (see below).

In addition, correlations between the presence/absence and intensity of IPSP, and taxonomic family were tested for, in the same manner as all the other parameters.

Logistic regression analysis: Logistic regression analysis was used to clarify the interpretation of one particular phylogenetically independent comparison that was conducted. This comparison indicated that the association found between hard pericarp thickness and seed predation was not independent of plant phylogeny, indicated by family-level taxonomic affiliation. Logistic regression allowed a test of how well hard pericarp thickness and taxonomic family predicted whether or not a plant would be attacked by IPSP even though these two independent variables may have been intercorrelated to some degree.

In using logistic regression analysis variances were modelled using Generalised Linear Modelling on GLIM 4 (Crawley 1993, Francis et al. 1994) with the backward-elimination procedure and a binomial error structure. The backward elimination procedure produces an initial regression model for the data that includes all possible independent variables. As a measure of how well the model fits the data a measure of variance is produced; in a model with a binomial dependent variable a binomial error structure is used, thus χ^2 is used as the measure of variance. After the initial model successive models are then produced, each one minus a particular independent variable. By comparing how well the initial model (complete with all possible independent variables) fits the data with later models produced (each one minus a particular independent variable) it is possible to tell what single variable produces the model with the best fit and hence best predicts whether or not a plant will be attacked by IPSP. The independent variable that best predicts this is the one responsible for the greatest drop in fit when removed from the initial model (Crawley 1993, Manly 1994).

4.3 Results

211 plants were sampled, representing 211 species from 57 taxonomic families. Eight of these families included 8 or more species (Table 4.3). Most of the plants were native species (61%) - generally trees from primary rainforest (Table 4.4) on either very infertile or very fertile soils (Table 4.5). Most plants appeared to belong to species with dispersed populations; only a few plants had fruiting conspecifics found within 10m (Table 4.6).

The most common type of diaspore sampled (75%) was small (under 20mm wide) and fleshy coated (Table 4.7) which tended to have a hard pericarp layer (endocarp) surrounding the seeds within. Of these particular species 38% were single seeded diaspores while the other 62% species were multiseeded.

4.3.1 Seed predation and the seed predators

Eighty six of the 211 plants sampled (41%) were attacked by IPSPs with varying intensity. Overall, intensities of seed crop predation were low, only 12% of the plants had lost 50% or more seeds (Fig. 4.1). When seeds were attacked by insects the amount of damage done to a seed was generally extensive (Fig. 4.2).

Rearing adult insects from seed samples was partly successful; adults emerged from 40 of the 86 attacked samples. 31 species of insect were identified to family level while seven were identified tentatively to species level (see Appendix 1).

Table 4.3. The eight plant families best represented in the survey *.

Family	No. species
Rutaceae	15
Sapindaceae	14
Myrtaceae	13
Lauraceae	13
Euphorbiaceae	10
Meliaceae	8
Rubiaceae	8
Apocynaceae	8

* The other 123 plant species sampled belonged to another 41 families.

Table 4.4. The successional phases * from which species were sampled and their life forms.

Successional phase	Growth form	No. species
Primary forest	Tree	82
Primary forest	Shrub	23
Primary forest	Vine	28
Primary forest	Herb	4
Secondary regrowth	Tree	43
Secondary regrowth	Shrub	13
Secondary regrowth	Vine	11
Secondary regrowth	Herb	2

* Another five plants were sampled from parks and gardens.

Table 4.5. The numbers of species sampled per soil as indicated by their phosphorus content. [1,2]

Phosphorus level (mg P per kg soil)	No. species sampled per soil type
7	49
9	15
10	13
16	30
20	5
33	1
40	14
100	38
130	15

---

[1] Another 31 plants were sampled from mosaics of two different soil types and could not be assigned to soil of a particular phosphorus content.

[2] Figures for phosphorus content from Laffan (1980).

Table 4.6. The numbers of fruiting conspecifics found within 10m of each sampled plant.

Number of fruiting conspecifics	No. plants
0	140
1	28
2	15
3	3
4	6
5 - 10	10
> 10	9

Table 4.7. The numbers of species found with diaspore forms.

Diaspore form *	No. species
Winged/plumed	17
Coated with a fleshy layer - large	158
- small	15
Fleshy layer absent - large	15
- small	6

* Large fruit are > 20mm wide, small fruit are < 20 mm wide.

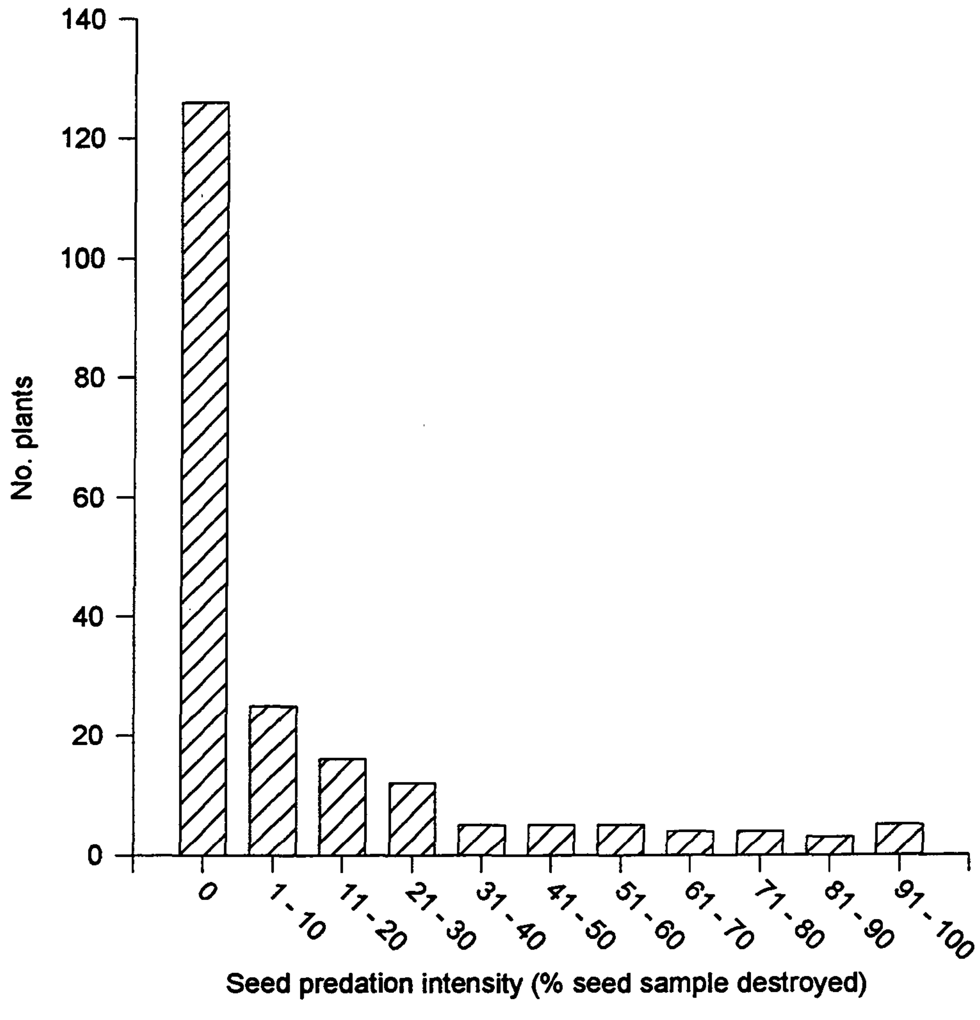

Figure 4.1. Frequency distribution of seed predation intensities for all 211 plants sampled.

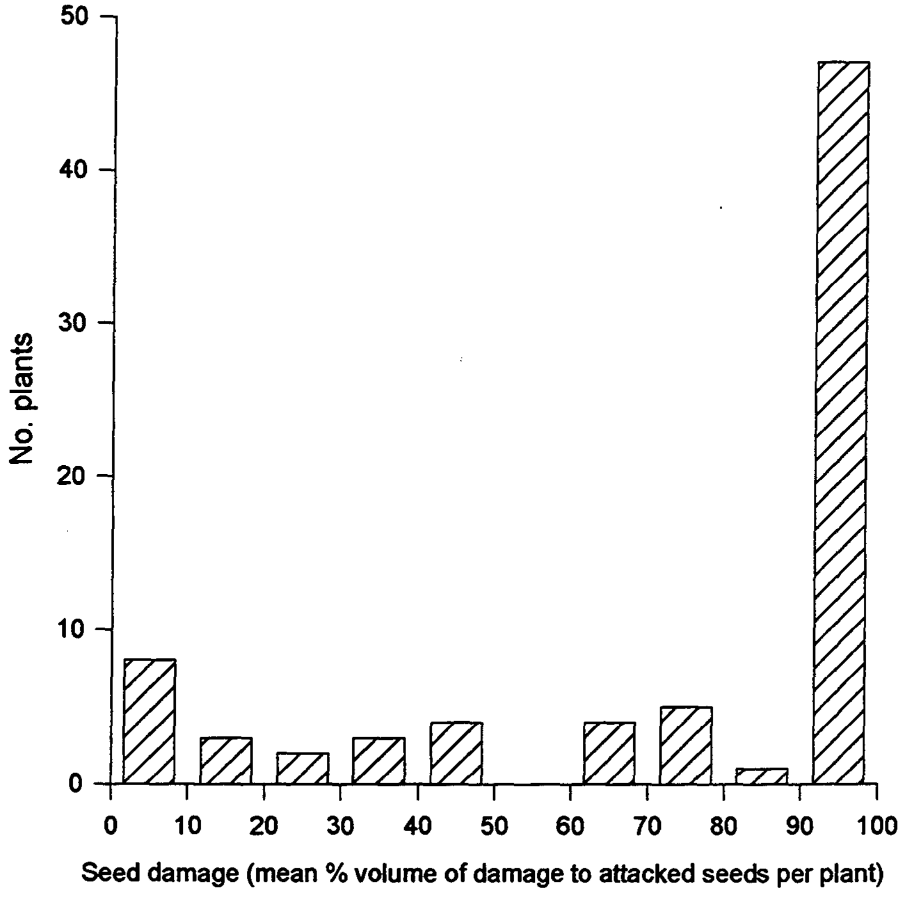

Figure 4.2. Frequency distribution for the extent to which attacked seeds were consumed.

4.3.2 Univariate analysis

Three parameters; total pericarp thickness, hard pericarp thickness and host indigeneity were found to be independently correlated with IPSP, the other 11 plant parameters were not (Table 4.8), while eight parameters were intercorrelated. The presence/absence of IPSP was significantly correlated with hard pericarp thickness and plant indigeneity, while the intensity with which a plants seed crop was attacked was correlated with taxonomic family. The intercorrelations that occurred between parameters referred primarily to fruit/seed morphological attributes, but also to site attributes (Table 4.8).

Correlations between parameters and the presence/absence of IPSP

Hard pericarp thickness

The probability of IPSP for a plant was inversely correlated with hard pericarp thickness. Hard pericarp thickness was also positively intercorrelated with total pericarp thickness (see total pericarp thickness below) and varied significantly according to taxonomic family. However these intercorrelations did not mean that the association between IPSP and hard pericarp thickness was an artefact caused by total pericarp thickness and taxonomic family acting as confounding factors.

Plants bearing fruit with a hardlayer in the pericarp (usually the endocarp) of 1.2 mm or greater had a significantly smaller chance of being attacked by IPSPs than those plants bearing fruit with either no hard layer or a hardlayer less than 1.2 mm thick (χ^2 homogeneity test (1-tailed), $\alpha = 0.025$, $\chi^2 = 7.49$, n = 211, df = 1, p = 0.006), (Fig. 4.3).

Table 4.8. Associations between parameters and the presence/absence of IPSP.

Parameter	Interrelated variables [1]			Statistical test	α (unadj')	α (adj') [2]	p-value
Fruit/seed morphological attributes							
Total pericarp thickness	**a**			Mann-Whitney U-test	0.05	0.013	**0.005**
Hard pericarp thickness	a			Chi-square homogeneity test	0.05	0.025	**0.006**
Diaspore size	a	b		T-test	0.05	0.017	0.079
Seed size	a	b		T-test	0.05	0.017	0.613
Fruit surface texture [3]				Chi-square homogeneity test	0.05	0.050	0.236
No. seeds per fruit		b		Mann-Whitney U-test	0.05	0.025	0.690
Seed mass per fruit		**b**		Mann-Whitney U-test	0.05	0.013	0.089
Seed sphericity				Mann-Whitney U-test	0.05	0.050	0.717
Other plant attributes							
Growth form			**c**	Chi-square homogeneity test	0.05	0.017	0.044
Indigeneity			c	Chi-square homogeneity test	0.05	0.025	**0.005**
Light availability			c	Chi-square homogeneity test	0.05	0.025	0.166
Phosphorus availability				Chi-square homogeneity test	0.05	0.050	0.097
Fruiting 'season'				Chi-square homogeneity test	0.05	0.050	0.056
Taxonomic family [4]				-	-	-	-

---

[1] Parameters marked by a bold letter are significantly intercorrelated with the other parameters marked by that same letter ($\alpha = 0.05$).

[2] α was adjusted for non-independence between parameters using the Dunn-Sidak method.

[3] Four originally separate categories for possibly protective types of pericarp surface were pooled into a single category.

[4] Sample sizes for the categories were too unbalanced to test with standard univariate tests. Host phylogeny was not with seed predation ($0.1 > p > 0.05$) using Logistic Regression Analysis, see text on hard pericarp thickness (an associated factor).

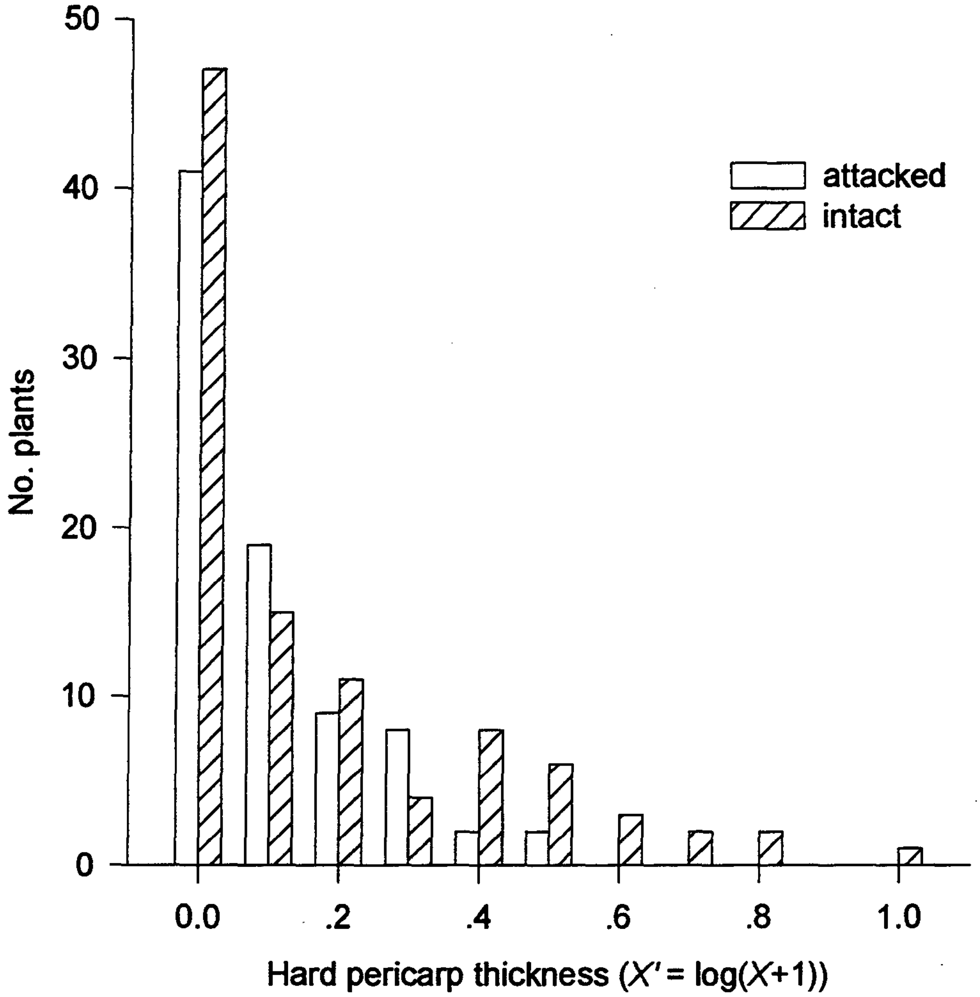

Figure 4.3. Frequency distribution for the thickness of the hard pericarp layer for attacked and intact plants. Note how the proportion of plants attacked drops when X' > 0.4 (for which the hard pericarp thickness class ranges from 1.24mm to 1.82mm).

Taxonomic family appeared to be intercorrelated with hard pericarp thickness as hard pericarp thickness differed significantly between the nine best represented plant families in the survey (Kruskal-Wallace test, $\alpha = 0.05$, $H = 30.049$, $n = 8$, $p < 0.001$) (Fig 4.4). However it is unlikely that this intercorrelation means that other intercorrelated phylogenetically related factors may be contributing to the association between IPSP and hard pericarp thickness as confounding factors. This is because:

1) taxonomic family was only weakly related to hard pericarp thickness - significant differences between families in hard pericarp thickness occurred in only 3 of 36 possible family to family comparisons (Table 4.9).

2) logistic regression analysis showed that the probability of a plant being attacked by IPSP was not related to its taxonomic family (Table 4.10).

Total pericarp thickness

The presence of IPSPs was inversely correlated with total pericarp thickness, and total pericarp thickness was positively intercorrelated with hard pericarp thickness but was not intercorrelated with taxonomic family. The significant correlation between total pericarp thickness and IPSP (Mann-Whitney test (1-tailed), $\alpha = 0.013$, $n = 211$, $p = 0.005$), (Fig. 4.5) appeared to be due to the confounding effects of hard pericarp thickness. This was because these two attributes interrelated (Pearsons correlation test (1-tailed), $\alpha = 0.05$, $r = 0.249$, $n = 211$, $p < 0.001$) and when hard pericarp thickness was accounted for, no independent association between total pericarp depth and IPSP were found (Mann-Whitney test (1-tailed), $\alpha = 0.013$, $n = 193$, $p = 0.265$). Hard pericarp thickness was accounted for by testing for an association between IPSP and total pericarp thickness, in the absence of plants

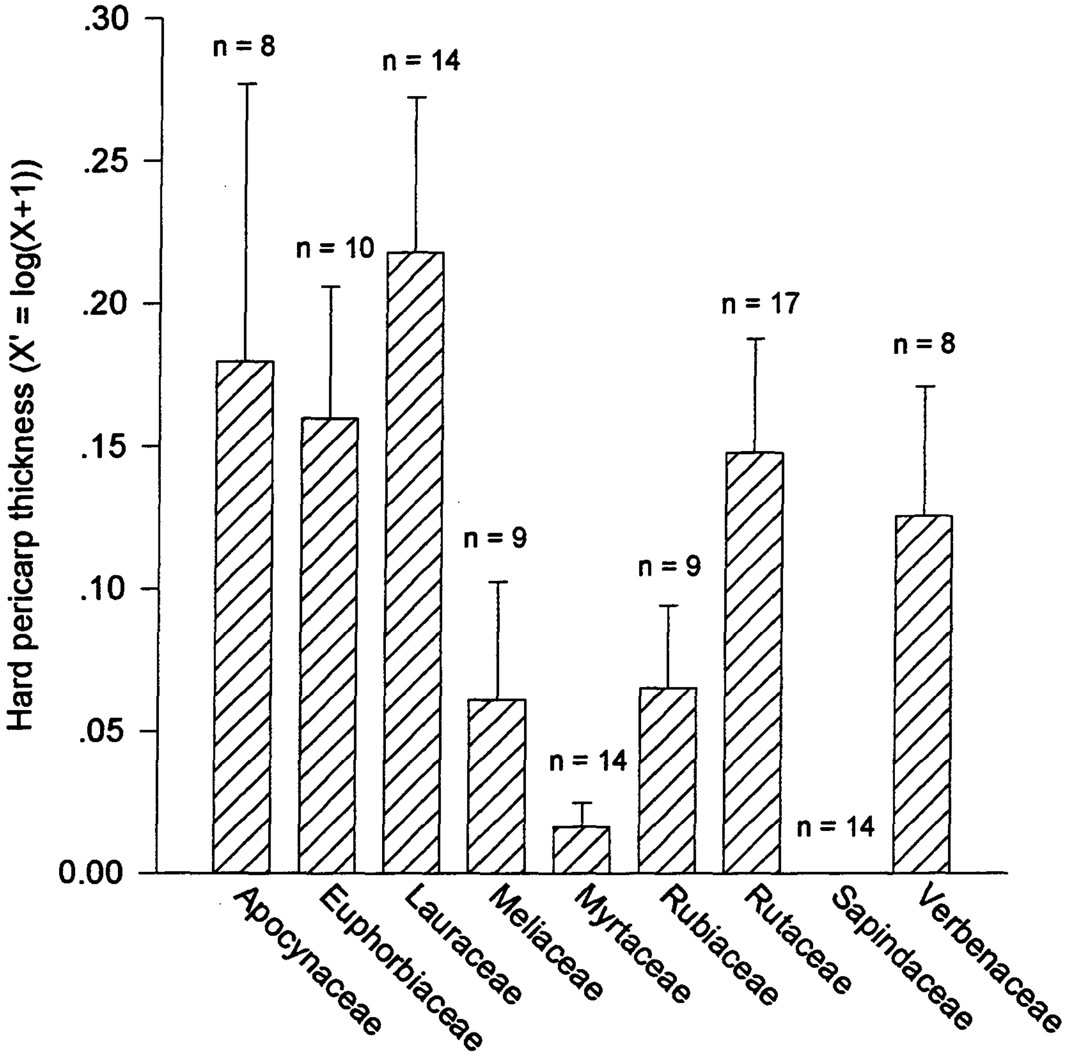

Figure 4.4. Mean hard pericarp thickness (with standard errors) for the nine best represented families (n = no. of species per family).

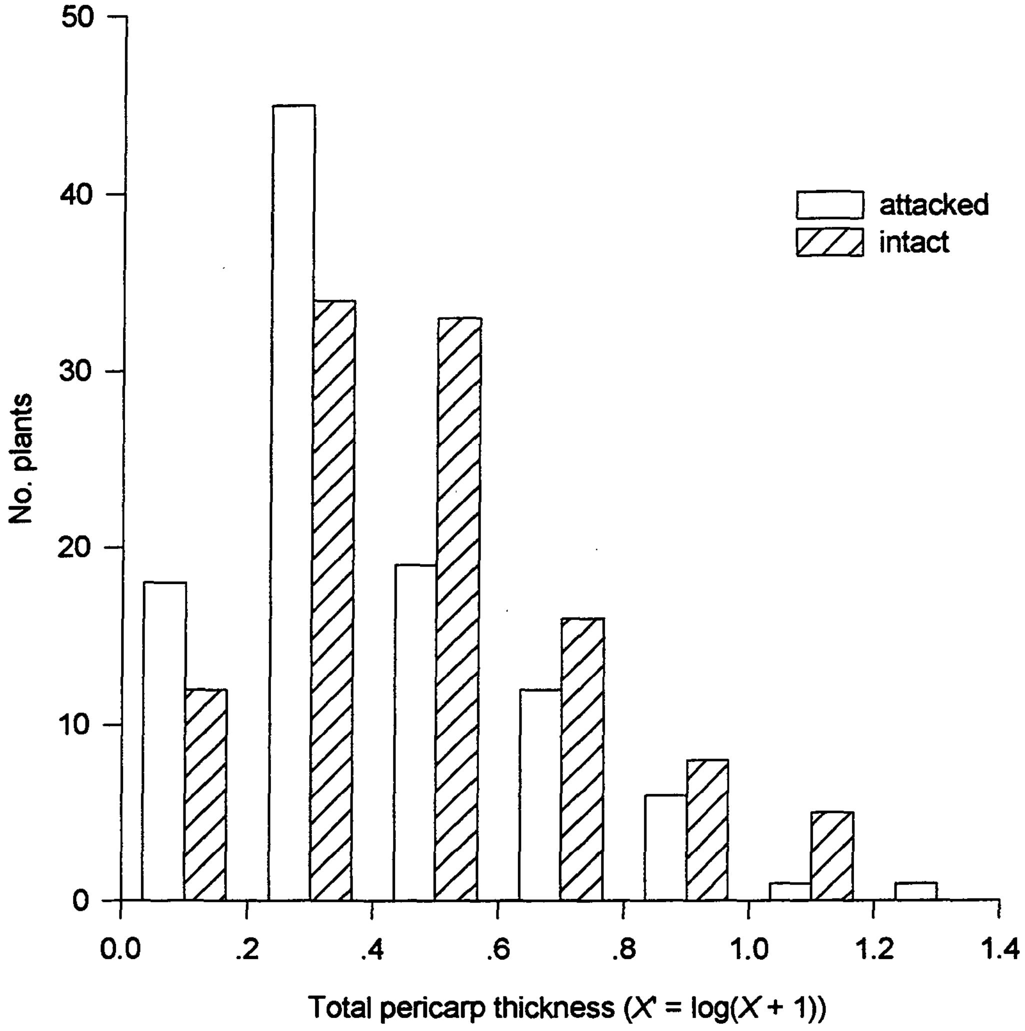

Figure 4.5. Frequency distribution for the total pericarp thickness of attacked and intact plants.

Table 4.9. Mean ranks for families based on the hard pericarp thickness of sampled species and the differences of rank between these families. The mean rank figures were calculated in a Kruskal-Wallace test, the differences in rank which were significantly ($\alpha = 0.05$) are shown in bold.

		Laura'	Euphor'	Ruta'	Verben'	Apocyn'	Rubia'	Melia'	Myrta'	Sapind'
	mean	69.3	67.8	64	61.9	55.9	50	39.8	36	26
Lauraceae	69.3	0								
Euphorbiaceae	67.8	1.5	0							
Rutaceae	64	5.3	3.8	0						
Verbenaceae	61.9	7.4	5.9	2.1	0					
Apocynaceae	55.9	13.4	11.9	8.1	6	0				
Rubiaceae	50	19.3	17.8	14	11.9	5.9	0			
Meliaceae	39.8	29.5	28	24.2	22.1	16.1	10.2	0		
Myrtaceae	36	33.3	31.8	28	25.9	19.9	14	3.8	0	
Sapindaceae	26	**43.3**	**41.8**	**38**	35.9	29.9	24	13.8	10	0

Table 4.10. Relationships between possible factors of influence and the probability a plant will be attacked by IPSPs[1].

Parameter	df	% variance explained	p-value [2]
Hard pericarp thickness	1	4.59	**$0.05 > p > 0.01$**
Plant family	8	11.77	$0.1 > p > 0.05$

---

[1] Results from Logistic Regression Analysis (GLIM) using a backward elimination proceedure, for 103 plants from the nine represented plant families, each with eight or more plants.

[2] Significant p-value in bold.

with a hard pericarp layer of 1.2 mm or more thick. Any hard pericarp layer surrounding seeds in a fruit is a component of the total pericarp layer present. Thus when a fruit has a thin pericarp only a thin hard pericarp component is possible, whereas when a fruit has a thick pericarp layer a greater range of hard pericarp thickness is possible. Hence the spread or variability of hard pericarp thickness among the species sampled increases as total pericarp thickness increases (Fig. 4.6).

Plant indigeneity

Although both native and exotic plants were attacked by IPSPs (Fig. 4.7), native plants were more likely to be attacked than exotic plants (χ^2 homogeneity test (1-tailed), $\alpha = 0.025$, $\chi^2 = 6.61$, $n = 211$, $df = 1$, $p = 0.005$). Plant indigeneity was intercorrelated with growth form (Table 4.8) as exotic plants included proportionately more shrubs and fewer trees than the native species (χ^2 homogeneity test, $\alpha = 0.05$, $\chi^2 = 22.65$, $n = 211$, $df = 1$, $p < 0.001$). However, the correlation between plant indigeneity and vulnerability to IPSP did not appear to be dependent on growth-form acting as a confounding factor. This was because growth-form itself was not significantly related to the presence/absence of IPSP among plants (χ^2 homogeneity test, $\alpha = 0.017$, $\chi^2 = 6.23$, $n = 205$, $df = 1$, $p = 0.044$).

The correlation between plant indigeneity and vulnerability to seed predation may have been, in part, affected by the over representation of the Solanaceae, which made up a significantly large proportion of the exotic species (5/29 exotic plants vs 1/181

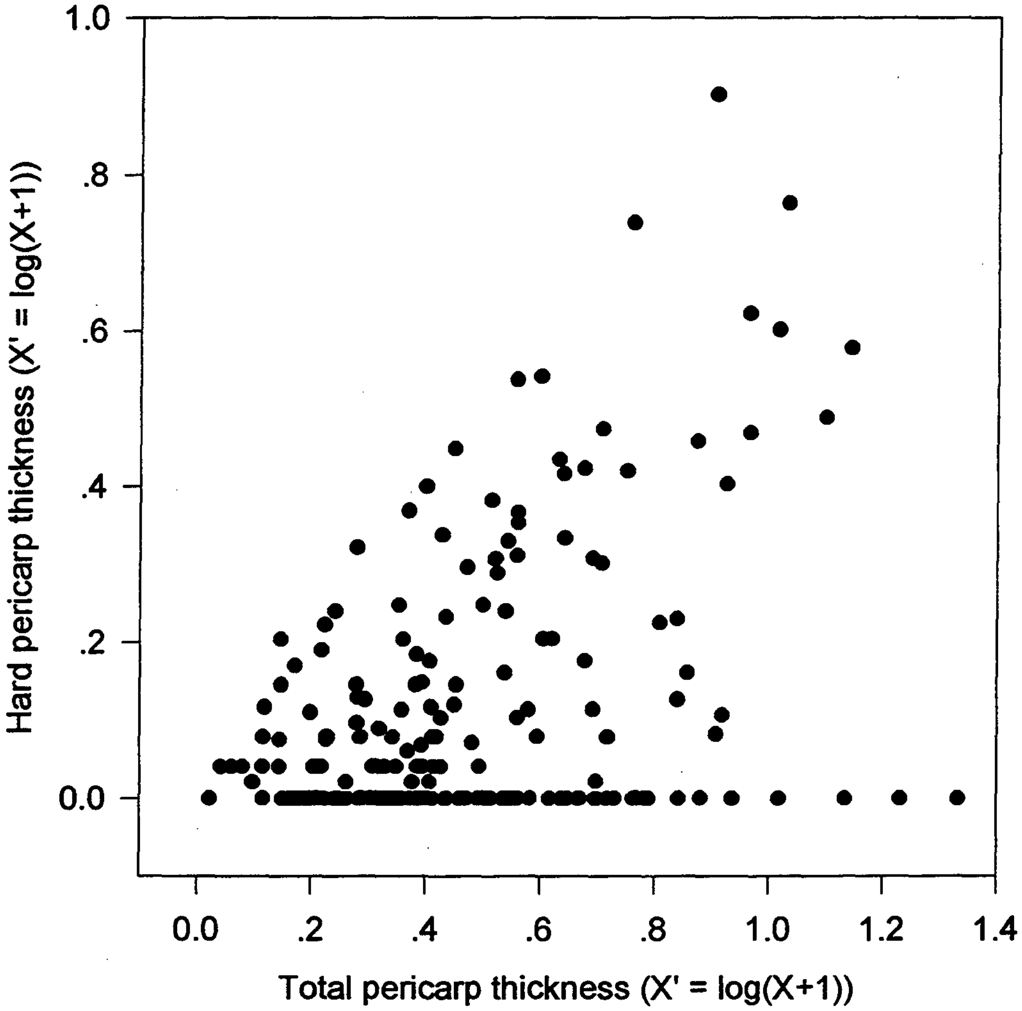

Figure 4.6. Plot showing the relationship between total pericarp thickness and hard pericarp thickness amongst 211 plants.

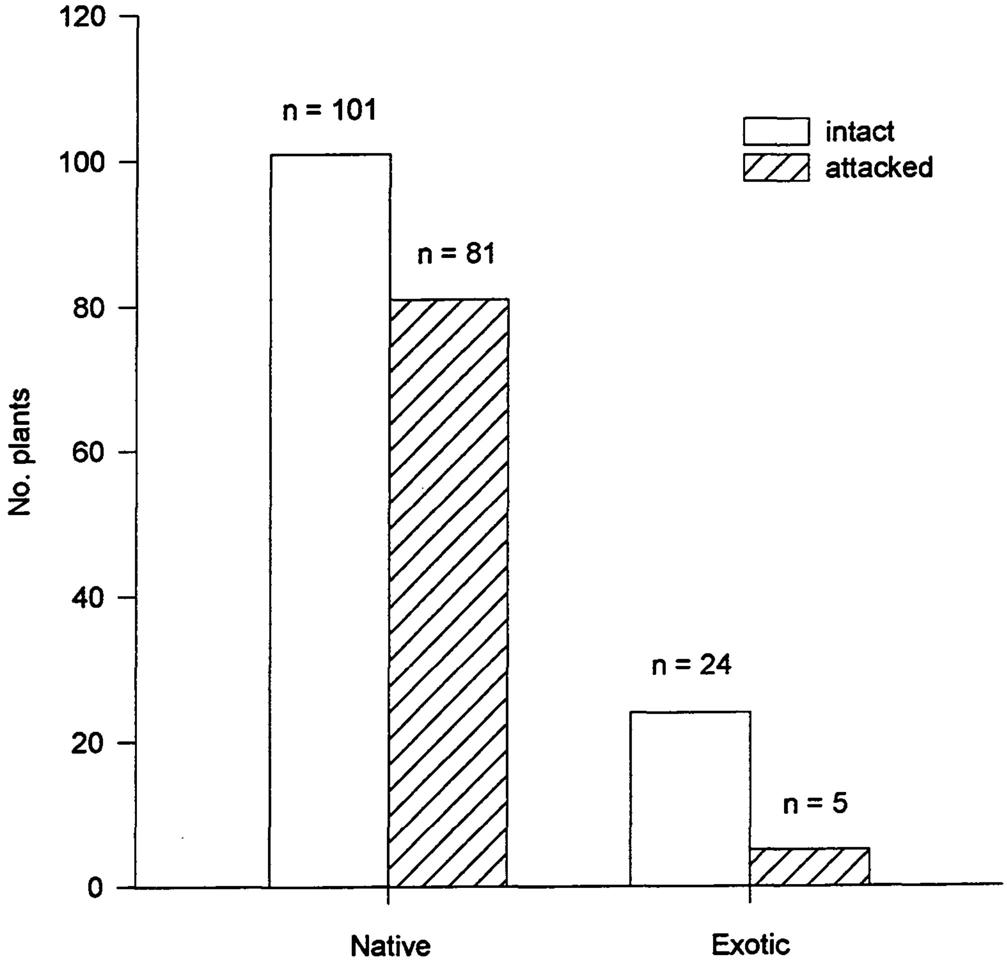

Figure 4.7. Comparison between native and exotic plants in terms of numbers of plants that were attacked by seed predators and those that were not (n = no. of plants per category).

native plants (Fishers Exact test, $\alpha = 0.05$, $p = 0.0002$)) and were, as a group, rare attacked by seed predators (1/6 species attacked). Despite this, the proportion of exotic and native plants that were attacked was still significant (χ^2 homogeneity test (1-tailed), $\alpha = 0.025$, $\chi^2 = 5.68$, $n = 205$, $df = 1$, $p = 0.008$) in the absence of the Solanaceae.

Univariate analysis: correlations between parameters and the intensity of IPSP

No correlations were found between IPSP intensity and any parameters, apart from taxonomic family (Table 4.11). Even though taxonomic family was statistically associated with IPSP intensity this was based on minimal evidence.

Plant taxonomic family

Mean IPSP intensities varied significantly between plant taxonomic families with four or more attacked species of plant (Kruskal-Wallace test, $\alpha = 0.05$, $H = 15.3$, $n = 6$, $p = 0.009$) (Fig. 4.8). This significant result was due to markedly lower intensities of seed crop predation for the Lauraceae in comparison with the Euphorbiaceae (Non-parametric multiple comparison, $\alpha = 0.05$, $q = 3.06$, $0.05 > p > 0.02$). This comparative family difference was one of 15 possible paired comparisons among the six plant families for which IPSP intensity could be measured (Table 4.12).

Table 4.11. Associations between parameters and the intensity of IPSP.

Parameter	Interrelated variables [1]			Statistical test	Test statistic	α (unadj')	α (adj') [2]	p-value
Fruit/seed morphological attributes								
Total pericarp thickness	**a**			Spearman rank correlation	r = -0.028	0.05	0.013	0.250
Hard pericarp thickness	a			Spearman rank correlation	r = 0.049	0.05	0.025	0.330
Diaspore size	a	b		Spearman rank correlation	r = - 0.173	0.05	0.017	0.136
Seed size	a	b		Spearman rank correlation	r = - 0.073	0.05	0.017	0.687
Fruit surface texture [3]				-		-	-	-
Seed number per fruit		b		Spearman rank correlation	r = - 0.094	0.05	0.025	0.250
Seed mass per fruit		**b**		Spearman rank correlation	r = - 0.239	0.05	0.013	0.028
Seed sphericity				Spearman rank correlation	r = - 0.204	0.05	0.050	0.063
Other plant attributes								
Growth form			**c**	Kruskal-Wallace test	h = 4.659	0.05	0.017	0.097
Indigeneity [3]			c	-		-	-	-
Light availability [3]			c	-		-	-	-
Phosphorus availability				Mann-Whitney U-test		0.05	0.050	0.557
Fruiting 'season'				Kruskal-Wallace test	h =1..885	0.05	0.050	0.597
Taxonomic family				Kruskal-Wallace test	h = 15.3	0.05	-	**0.009**

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[1] Parameter marked by a bold letter are significantly intercorrelated with the other parameter marked by that same letter (α = 0.05).

[2] α was adjusted for non-independence between parameters using the Dunn-Sidak method.

[3] Sample sizes for the categories were too unbalanced to test.

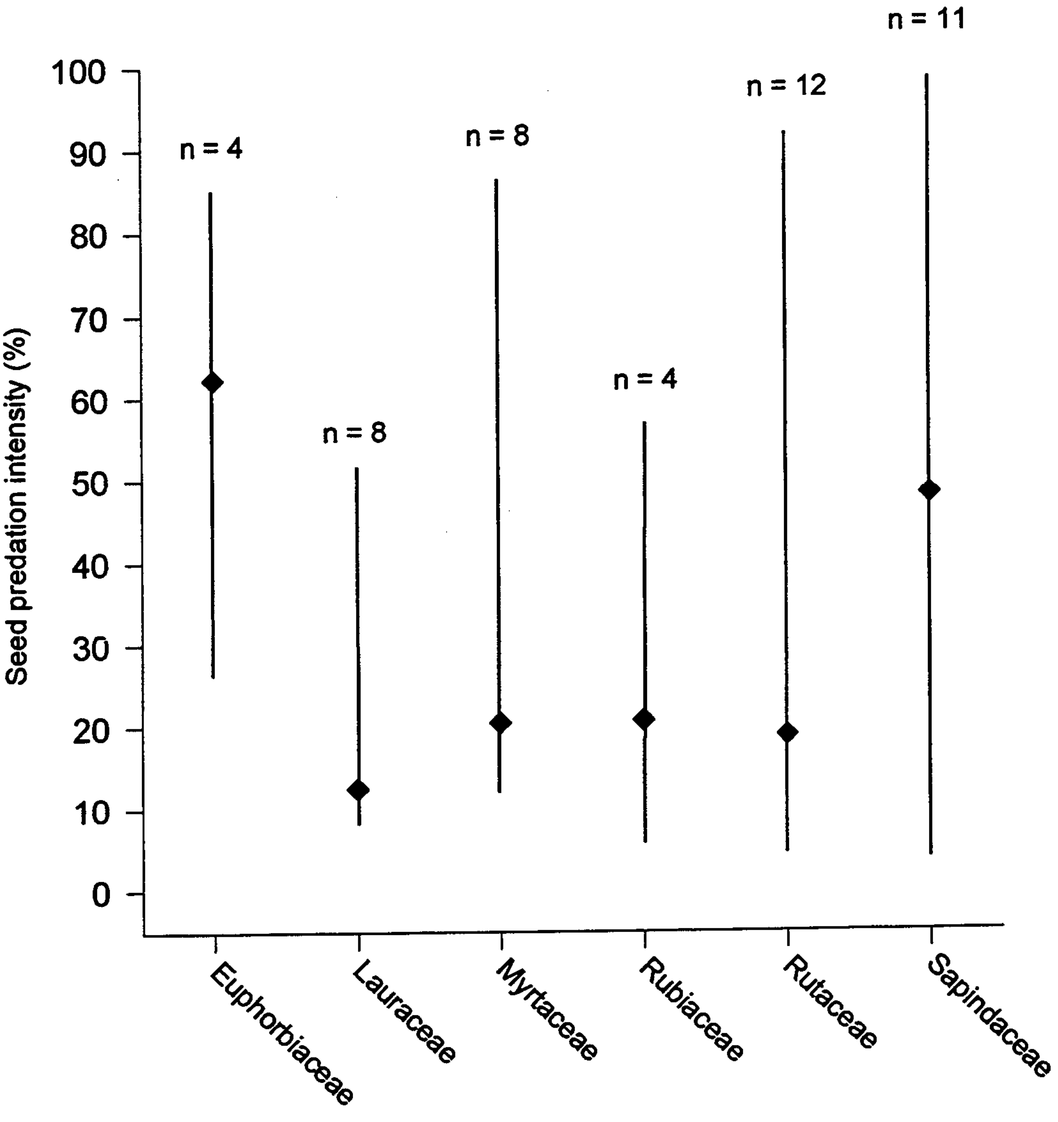

Figure 4.8. Median seed predation intensities (with ranges) for the six best represented plant families (among the attacked plants only), (n = no. of species per family).

Table 4.12. The mean rank values for the IPSP intensities of plant families and the differences of mean value between each possible pair of families. The numbers of species sampled per family are given in brackets. Only the difference between the mean rank values of the Sapndaceae and the Lauraceae (shown in bold) were significant (0.05 > p > 0.02).

			Euphor'	Sapin'	Rubia'	Myrta'	Ruta'	Laura'
			(7)	(11)	(4)	(8)	(12)	(8)
			38.3	34.1	22.3	22.1	20.3	15.3
Euphorbiaceae	(7)	38.3	0					
Sapindaceae	(11)	34.1	4.2	0				
Rubiaceae	(4)	22.3	16	11.8	0			
Myrtaceae	(8)	22.1	6.2	12	0.2	0		
Rutaceae	(12)	20.3	18	13.8	2	1.8	0	
Lauraceae	(8)	15.3	**23**	18.8	7	6.8	5	0

4.3.3 Results summary

Seeds were sampled from 211 plants, representing 211 species from 57 taxonomic families. The plants sampled included both native and exotic species from a variety of different habitats associated with mature rainforest or secondary successions. These plants displayed a diversity of fruit/seed forms, however most of the plants had small fleshy fruit containing one or more seeds surrounded by a hard endocarp layer.

Each plant was described predominantly in terms of its habitat, seed/fruit morphology and taxonomic affiliation - 14 parameters in all. Of these parameters four were correlated with differences in the vulnerability of plants to insect predispersal seed predation (Table 4.13). Three of these parameters; host indigeneity, hard pericarp thickness and taxonomic affiliation were independently correlated with IPSP. Plants that were either exotic or produced seeds enclosed within a thick hard pericarp layer were less likely to be attacked than plants that were native or that produced seeds without a thick hard pericarp layer. Some taxonomic families appeared to be more vulnerable to IPSP than others: of the six best represented families the Euphorbiaceae had generally the highest intensities of IPSP, while Lauraceaous plants had the lowest intensities. The fourth attribute; total pericarp thickness appeared to be to inversely correlated with the presence of IPSPs due to its positive intercorrelation with hard pericarp thickness.

Table 4.13. A summary of the correlations found between parameters and the vulnerability of plants to IPSP, and between the parameters themselves.

Parameter	Intercorrelations * between parameters			Correlated with IPSP?	Measure of IPSP
Fruit/seed morphological attributes					
Total pericarp thickness	**a**			yes	pres/absence
Hard pericarp thickness	a			yes	pres/absence
Diaspore size	a	b		no	-
Seed size	a	b		no	-
Fruit surface texture				no	-
Seed number per fruit		b		no	-
Seed mass per fruit		**b**		no	-
Seed sphericity				no	-
Other plant attributes				no	-
Growth form			**c**	no	-
Indigeneity			c	yes	pres/absence
Light availability			c	no	-
Phosphorus availability				no	-
Fruiting 'season'				no	-
Taxonomic family				yes	intensity

* Parameters marked by a bold letter were significantly intercorrelated with other parameters marked by that same letter.

4.4 Discussion

This discussion deals with the 14 parameters that were tested as factors possibly affecting IPSP, in two sections. The first section discusses the parameters that were found to be correlated with IPSP (hard pericarp thickness, host indigeneity and host phylogeny). The second section discusses the parameters that were not correlated with IPSP. The factors in this second section are: seed size and seed sphericity, the number of seeds per fruit and seed mass per fruit, fruit surface texture, growth form, phosphorus and light availability, and fruiting season.

4.4.1 Significant parameters

Hard pericarp thickness

The negative correlation between the chance that a plant will be attacked and the thickness of the hard, woody or stony layer in the fruit pericarp accords with the results of previous studies (Davidar 1987, Janzen 1977, Nwanze and Horber 1976, Podoler and Applabaum 1968). In additionally, the current study shows this correlation to occur at the community level, across many species.

Seed samples taken from species that possessed fruit with thick, hard pericarp layers ('protected' species) may have had a lower probability of being attacked by IPSP than samples from species without such layers ('unprotected' species) because a greater proportion of 'protected' species than 'unprotected' species do not have any IPSPs at all. Support for this explanation comes from the fact that some rainforest plant species do appear to be generally free of IPSPs (Table 4.14). However, some apparently 'protected' species were attacked by IPSPs (*Dichapetalum papuanum*, *Carronia protensa*) suggesting that regardless of their level of protection it is possible that most species are susceptible to some kind of seed predator.

Table 4.14. Species that appear to be generally immune to IPSP. *

Species	No. plants attacked
Alphitonia petriei	0/12
Callicarpa longifolia	0/12
Cordyline cannifolia	0/22
Dendrocnide moroides	0/11
Pittosporum rubiginosum subsp. wingii	0/9
Polyscias elegans	0/14
Solanum mauritianum **	0/28
Solanum torvum **	0/11

* The data in this table comes from samples taken in addition to those taken for the seed predation survey.
** Introduced species

A more likely explanation for the lower probability of attack for 'protected' species than unprotected species is that 'protected' species tended to have lower intensities of seed predation than 'unprotected' species. Lower intensities of IPSP may have occurred for a number of reasons but without an in depth study sampling across many individual plants within species as well across species it is not possible to tell why fruit with thick, hard pericarp layers were less likely to be attacked than 'unprotected' fruit.

Not all the plants that had thick hard pericarp layers were immune to attack however, for example the fruit of *Delonix regia* (Caesalpiniaceae) and *Sarcomelicope simplicifolia* (Rutaceae) were penetrated while green and soft, before any lignification had occurred. This is a common mode of attack for IPSPs (Auld 1983, De Steven

1981, Ernst et al. 1989, Ironside 1974, Manzur and Courtney 1984). Apart from simply allowing an insect to mine through the pericarp tissue, attacking the seeds of unripe fruit may minimise the energy expenditure for an invading insect. This may also allow time for the development and emergence of the insect before encountering the hazards of seed dispersal (Lamprey et al. 1974, Herrera 1989b, Miller 1994) or the post seed dispersal environment (Janzen 1971b, Johnson 1981).

Some species of plant producing fruit with thick hard pericarp layers were also attacked after fruit lignification had occurred. In the fruit of *Dichapetalum papuanum* (Dichapetalaceae) and *Carronia protensa* (Menispermaceae) the lignified endocarp was consumed by lepidopteran larvae, along with the soft fleshy exocarp and the seeds within the fruit.

Plant indigeneity

Samples of seeds from exotic species were less likely to be attacked than samples from native species. This may have been because in comparison with native species, a greater proportion of exotic species did not have any IPSPs. Exotic species of plant may have a lower chance of being attacked by potential IPSPs than native species because they have certain characteristics or combinations of characteristics that are novel. These characteristics include (as detailed in the introduction) the habitat conditions of the species, its phenology, recognisable or camouflaging features and the presence of potential defenses.

While most of the seed samples taken from exotic species escaped seed predation 5 of 24 were attacked. The seed predators of those particular species are most likely to have been generalists with the capacity to recognise a diversity of plants as food sources and deal with a variety of plant defences (Strong et al. 1984). *Isotenes sp. miserana* (Lepidoptera: Tortricidae) reared from the exotic *Senna occidentalis* (Caesalpiniaceae) is an example. This species has a broad host range of at least 12 plant taxonomic families (Common 1990) including, from this survey, the native species *Alectryon semicinereus* (Sapindaceae), *Siphonodon membranaceus* (Celastraceae) and *Acmenosperma claviflorum* (Myrtaceae). Another insect species *Cryptophlebia ombrodelta* (Lepidoptera: Tortricidae) reared from the exotic *Delonix regia* (Caesalpiniaceae) also has a broad host range including at least four different plant families (Common 1990).

Plant taxonomic affiliation

The seed crops of Euphorbiaceous species were attacked by IPSPs with greater intensities than those of Lauraceous species. This may have occurred because the Euphorbiaceous species were each attacked by a greater number of insect species. Of the 10 Euphorbiaceous species that were sampled, adult insects were collected from five and three of these species yielded three or more species of insect each (Appendix 1). Although the numbers of insect species that attacked Euphorbiaceous species cannot be compared to the numbers of species that attacked the Lauraceous species (just the one Lauraceous species yielded one species of insect), the Euphorbiaceae do appear to be attacked by a particularly high number of insect species, in comparison with all other species sampled in the seed predation survey (Appendix 1).

Differences in the vulnerability of Euphorbiaceous and Lauraceous species to IPSPs may ultimately be due to differences in their chemistry. Secondary chemistry may also explain the variation in the proportions of seeds attacked in samples from the other plant families. The secondary chemistry of plants has been shown to affect herbivory by insects with causative mechanisms (see Bernays and Chapman 1994, Crawley 1983, Rosenthal and Janzen 1979 for references), may affect seed predation by insects (Janzen 1977, Siemens et al. 1992) and does covary with phylogeny (D'Arcy 1986, Isman et al. 1996, Murray et al 1982). Secondary compounds may affect the vulnerability of seeds to predation by insects by making either the seeds or the surrounding pericarp toxic.

4.4.2 Insignificant parameters

Seed size

No correlation was found between seed size and IPSP (Tables 4.8 and 4.11). One possible reason why seed size might have been important is because seed size can limit the resources available to an IPSP. Thus some insects will preferentially attack the larger seeds on a host plant (Ernst et al. 1989, Mitchell 1975, Moegenburg 1996, Nalepa and Grissell 1993, Russell 1962, Wilson 1988). However, most of the insects in this current study appeared to be able to move between the seeds of a plant, either within a single fruit or between fruit. Thus IPSPs would not have had the need to select for seed size, either within species or across species, to maximise resources.

Larger seeded species may also have been more vulnerable to attack because they could accommodate a greater size range of insects and hence range of insect species, as seen in the study by Szentesi and Jermy (1995). This current study differs from that of Szentesi and Jermy though for two reasons. Firstly, this current study had sampled a greater range of insect types (see Table 4.15) and secondly, had sampled species across a much greater seed size range. The insects in Szentesi and Jermy (1995) study were bruchid beetles that either 1) fed and grew wholly within a single seed or 2) moved from one seed to another, but remained within the one pod. Although seed size was not significantly associated with the vulnerability of plant species to attack by the second type of insect seed size did appear to have been associated with the vulnerability of plant species to attack by the first type of insect strongly enough for this to show up in the overall pattern. This current study on the other hand had sampled four types of insect (Table 4.15). In addition to the two types of insect just previously described were insects that moved from fruit to fruit, either eating seeds or drawing sap from them. In this current study the proportion of insect species, for which seed size may have been important, was much smaller. So any association between seed size and the probability of attack by insects that feed within the one seed would have been less likely to contribute to an overall pattern.

Table 4.15. The number of plant species found to be attacked according to any one mode of seed predation[1] and the orders represented by the insects for each mode.

Feeding mode of seed predator	No. plant species	Insect orders
Feeds within 1 seed only	31	Coleoptera, Lepidoptera, Hymenoptera, Diptera
Feeds within > 1 seed (within 1 fruit)	12	Coleoptera, Lepidoptera
Feeds on seeds within many fruit	4	Lepidoptera
Draws sap from seeds from > 1 fruit	6	Hemiptera

[1] Modes of predation for insects were inferred from field observations, fruit dissections and typical characteristics of some of the taxa. Only the insects for which a feeding mode could be identified were included in this table.

Furthermore, the seeds sampled in this current study tended to be much larger than those sampled in Szentesi and Jermy's study (1995). The mean dry weight for seed species in this study was 360.85 mg (n = 211, S.D. = 1442.02) whereas for the seed species of Szentesi and Jermy (1995) it was 60.65mg (n = 14, S.D. = 113.23) (derived from mean dry weights given for plant tribes covering 110 species in total). Because of this, seed size would have been less likely to limit the resources available to insects feeding within the one seed and would be less important to host selection among the insects that attacked the plants sampled in this current study than among those that attacked the plants in Szentesi and Jermy's (1995) study.

Seed sphericity

The vulnerability of plants to IPSP was not related to how round, flat or needle shaped their seeds were. This could be because of the diversity of seed/fruit morphologies and IPSP feeding modes apparent in this study, and because of the large size of many of the seeds sampled.

That the shape of a seed could affect its vulnerability to IPSP was first suggested by Bridwell (1918, cited in Janzen 1979) and supported by Szentesi and Jermy (1995) who had shown that legume species with flat seeds had a lower likelihood of being attacked than those with more spherical seeds.

Seed shape was a factor affecting seed predation in the study of Szentesi and Jermy (1995) because 9/13 species of seed predator bruchid beetles involved developed within the one seed. Seed width therefore constrained the space available for these seed predators and the narrowest seeds were too narrow to inhabit. Amongst the seed predators in this current study, those that fed within the one seed were a minority. Any preference they may have had for round seeds over flat or needle-shaped seeds would be less important to community-level patterns of seed predation. This current study also differs from that of Szentesi and Jermy (1995) because the seeds sampled tended to be larger so even the minimum width of the flat or needle-shaped seeds in this study were less likely to be a constraint for space and hinder seed predation.

A third reason why seed shape was not important to the seed predators of this study was because the least spherical of the seed species sampled tended to be multiseeded (14/16 species) with little resistant tissue surrounding the seeds. This allowed seed predators of five of these species (*Flindersia brayleyana, F. pimenteliana, Toona ciliata, Parsonsia latifolia, Pandorea pandorana*) to eat their way through a matrix of seed, testa and any septum walls within the fruit.

Seed number per fruit and seed mass per fruit

The number of seeds per fruit and the mass of seed per fruit were not correlated with the presence/absence or the intensity of IPSP at the community level. The number of seeds per fruit and the seed mass per fruit can affect the vulnerability of fruit on a plant to IPSP, when the seed predators develop entirely within the one fruit (Herrera 1984b, Knight 1987). But at a community level, that involves a diversity of plant species and a diversity of IPSP species with a range of different feeding modes and requirements, this effect is unlikely to be important. This was because only a minority of the IPSPs attacking plants in this survey fed on more than the one seed within a single fruit (Table 4.15).

The quantity of seeds per fruit may be important to some of the seed predator species that were sampled in for this current study, but for many other species it would not be. From this current study only 12/53 species of host plant, for which insect feeding modes could be identified, were attacked by insects that fed on multiple seeds within the one fruit (Table 4.15).

Fruit surface texture

Seed samples from fruit that had a smooth surface did not have a greater chance of being attacked by IPSPs than seed samples from fruit with spiny, hairy, sticky or glandular surfaces, nor were they attacked at greater intensities. Thus species producing fruit with what may have been a potentially protective surface did not appear to be any less vulnerable IPSP than other species.

These results differ from those of Hare and Futuyama (1978) and Hare (1980) who had found an inverse correlation between burr length on fruit and seed predation intensity, and from Green and Palmbald (1975) who had found that hairs on fruit can lower intensities of IPSP. The lower power of the statistical tests used in this study may explain why no association was found between seed predation and fruit surface texture. In this respect there are two major differences between this study and previous studies. Firstly, the previous studies that had shown how the texture of the fruit surface can affect vulnerability to IPSP had compared congeneric species (Green and Palmbald 1975) or populations and variants within species (Hare 1980, Hare and

Futuyama 1987). The statistical tests of these previous studies may therefore have been subject to fewer interfering factors than this current study. Secondly, in the previous studies the sampling had been more balanced, whereas in this study the number of species representing each type of fruit pericarp surface were very unbalanced. Of the 211 species sampled 37 had a surface texture that was not merely rough or smooth. Of these 37 species 28 had surface spines or hairs.

Plant growth form

The probability that a seed sample was attacked by IPSPs did not vary significantly according to the sample plants growth form. This indicates that growth forms did not differ greatly in their vulnerability to IPSPs, in contrast to what might be expected according to resource allocation responses in plants. Vines were expected to be more vulnerable to seed predation than shrubs, and shrubs more so than trees.

Plant growth form may not have been important to the vulnerability of plants to IPSP because:

1) The allocation of resources towards the defence of reproductive structures does not differ greatly according to growth form. Within a plant there are a number of different functions drawing resources from the same source. The resources allocated to these functions would be expected to vary from species to species according to growing conditions, plant growth strategies (Abrahamson 1979, Bazzaz et al. 1987, Grime and Hunt 1975, Raven 1990) and the contribution of each function to plant fitness (Venable 1996). Given the possible complexity of inter-relationships between allocation towards plant functions and growing conditions for plants, the relationship

between allocation towards reproduction and allocation towards the defence of reproductive structures may be more complex than suggested and may not simply parallel the relationship between allocation towards plant growth and allocation towards anti-herbivory defences. Even this latter relationship appears to be more complex than previously thought (Grubb 1992).

2) The statistical methods used in this seed predation survey were not sensitive enough to detect any differences in predispersal seed predation by insects between growth forms. As one plant was sampled per species, the high variance in seed predation intensities between plants meant that there was also a high variance between species. Comparing seed predation for sets of species would have been more useful if variances were lowered by representing each samples species with replicate individuals.

Light and phosphorus availability

No associations were found between the probability or intensity of IPSP for seed samples and the availability of light or phosphorus for the parent plant. Seed samples from plants growing in conditions of high light or soil phosphorus availability were expected to have a greater chance of seed predation and/or at higher intensities than those from plants growing in conditions of low light and phosphorus availability.

These expectations were based on two premises:

1) that plants adapted to high resource environments allocate more resources towards growth and less towards defences (against herbivores) than plants adapted to

low resource environments.

2) that patterns of allocation towards reproduction and defences against seed predators parallel those towards growth and anti-herbivore defence.

The lack of any correlation between IPSP and the availability of light or phosphorus suggests that at least one of the original premises was wrong. Given the support that exists for the first premise, that resource availability is important to the allocation of plant resources towards anti-herbivores defences, these results suggest that the second premise was wrong. That is, that the allocation of resources in a plant to reproduction and the defence of reproductive structures does not parallel allocation towards leaf and stem production and their defences against herbivores. Given the complex manner in which resource availability is related to anti-herbivore defences in plants and the possible interactions between different plant functions that compete resources, drawing parallels between resource availability and allocation towards anti-herbivore defences, and resource availability and anti-seed predator defences is perhaps an simplification.

Another reason why the vulnerability of seed samples to IPSP was not associated with plant resource availability may have been because the correlation was obscured by the high variation in seed predation intensities among plants. Previous studies that have shown how aspects of a plants defences are related to its resource availability had taken replicate samples either within a single species (eg. Nichols-Orians 1991, Onuf et al. 1977) or within a broad range of species (Bryant et al. 1989, Coley 1982, Coley 1983). This current study however had taken one sample per plant species.

Comparing seed predation in between sets of species would have a greater statistical power if replicate plants were sampled for each species.

Fruiting season

The absence of any correlation between the probability or intensity of attack for seed samples and their season of availability suggests that the vulnerability of plants to IPSP does not change significantly across the year. These results are perhaps to be expected given that most of the IPSP sampled in this study appear to be specialists (Table 4.16).

Table 4.16. The host range of the predispersal insect seed predators sampled in the seed predation survey.

Number of insect species *	Number of host species
36	1
8	2
1	1
1	1

* This includes unidentified species that were given tentative morphospecies labels for this study.

If an IPSP is a specialist feeder with a single species of host plant, its life history will be co-ordinated with the phenology of the host species. Adult insects will tend to emerge from pupae or diapause at the time most suitable for egg laying - when the flowers or fruit of their host species are available (eg. De Steven 1981b, Ironside 1974, Jordano et al. 1990, Sauer and Feir 1973). Any species of plant should therefore be vulnerable to IPSP regardless of the time of year it flowers and fruits.

4.5 Summary and conclusions

In the tropical rainforests of North Queensland a diversity of fruit/seed forms were found among the plants and a diversity of life-history strategies were found among the IPSPs. Because of this diversity community-level patterns of association between fruit/seed morphology and IPSPs were unlikely to occur. This was why the vulnerability of plants to IPSP did not vary according to seed size and shape, seed mass per fruit, seed number per fruit and fruit surface texture.

Hard pericarp thickness was the one aspect of fruit/seed morphology that was correlated with the vulnerability of plants to IPSP. Plants that produced fruit with seeds surrounded by a hard barrier of 1.2mm thick or more were less likely to be attacked by IPSP than plants producing fruit with a thin hard layer or no hard layer. Not all plants with a thick hard pericarp were immune to seed predation however. Some insect species were able to eat their way through this hard layer while other species penetrated the barrier before it matured and lignified.

The indigeneity and taxonomic family a plant was also correlated with its vulnerability to predispersal seed predation by insects. Host indigeneity is not however a truly independent factor in itself. Rather, exotic plants were less likely to be attacked than native plants because they probably possessed novel combinations of plant and habitat characteristics. Taxonomic family is not a truly independent factor either because it is also dependent on other plant characteristics. The differences of seed predation intensity found for Euphorbiaceous and Lauraceous plants may be caused by other untested factors such as seed/fruit chemistry.

There were no community-level correlations between the vulnerability of plants to IPSP and growth form, light and phosphorus availability, fruiting season. The importance of these factors cannot be strongly rejected however as the statistical tests used in this survey were weakened by sampling limitations and the high variance for seed predation intensities across plants. Other studies indicate that light availability, phosphorus availability and growth form may indeed affect the vulnerability of plants to IPSP. To determine the significance of these particular factors more focussed studies are needed. The value of this seed predation survey was also limited by the intercorrelations that occurred between factors. More focussed studies should eliminate this. For example, plant indigeneity should be given further attention accounting for differences in the habitat conditions and growth form of plants.

CHAPTER 5: HOST PLANT RESOURCE AVAILABILITY

Abstract

Species of plant characteristic of resource poor habitats were hypothesised to have lower levels of insect predispersal seed predation (IPSP) than species of resource rich environments because they produce seeds with a greater degree of protection. This hypothesis was tested by studying the fruit structure and insect predispersal seed predation of tropical rainforest plant species in relation to the availability of light and soil nutrients.

Species fruiting in well lit habitats were more likely to be attacked by IPSP than species fruiting in poorly lit habitats. A similar trend was seen for high vs low nutrient habitats but this was not significant. Although the chance a species was attacked by seed predators was inversely related to the presence of structural barriers around seeds (eg. hard pericarp layers, spines or resin), these barriers were not themselves associated with light availability. Thus the evidence that the vulnerability of plants was related to resource availability (ie. light) was very limited and this association was not mediated by the presence/absence of possibly defensive fruit characteristics. The association between the vulnerability of plants to IPSP and light availability may be due to confounding differences in growth form or unknown variation in chemistry associated with specific growing conditions or insect activity associated with microclimate.

5.1 Introduction

The intensity of seed predation sustained by a plant species is often high (Crawley 1992) and can be capable of limiting subsequent seedling recruitment by reducing seed availability (Inouye et al. 1980, Louda 1982a, b, Louda and Potvin 1995, and Reader 1993). Levels of seed predation can, however, vary widely between species (eg. Auld 1983 and 1991, Crawley 1992, Davidar 1987, Greig 1993, Kelly et al. 1992). The population dynamics of some plant species are therefore more likely to be affected by seed predation than others. Such differential effects can be important to the species composition of plant communities (Davidson 1993).

To account for interspecific differences in the susceptibility of species to IPSP, studies have been made of fruit and seed morphology (Davidar 1987, Janzen 1977 and Szentesi and Jermy 1995) and chemistry (Janzen 1977 et al., Janzen et al. 1986 and Siemens et al. 1992). Although these studies were concerned with the task of identifying plant characteristics that inhibit seed predation they did not approach the broader issue as to why some plant species might possess these characteristics while others do not. One study has raised the possibility of understanding these differences within the framework of resource availability theory. Louda et al. (1987) had found that IPSP in plants was positively associated with water availability because putative anti-seed predator defences within these plants were negatively associated with water availability. These results agree with those that might be expected according to resource availability theory.

Resource availability theory encompasses hypotheses that try to explain why faster growing plants, characteristic of resource rich environments, tend to have greater levels of herbivory than slower growing plants characteristic of resource poor environments. These hypotheses seek to explain these patterns by relating the availability of resources to the trade-off between the allocation of photosynthate towards plant growth and plant defence. Currently there are four separate, non-exclusive hypotheses; the Growth Differentiation Hypothesis, Carbon Nutrient Balance Hypothesis, Environmental Constraint Hypothesis and the Growth Rate Hypothesis. Although there are differences in the mechanisms and predictions of these hypotheses, in general they all predict that plants of resource rich environments will have higher growth rates and lower levels of defence than plants of resource poor environments (Herms and Mattson 1992).

The patterns of resource allocation within plants that support resource availability theory may be either the product of resource source/sink interactions at the physiological level (Bryant et al. 1983, Loomis 1953 in Herms and Mattson 1992), an adaptation to optimise resource use that has evolved through natural selection (Rhoades 1979) or an integration of both these mechanisms (Herms and Mattson 1992). The selection of these patterns of allocation is expected to have occurred because they maximise a plant's chances of establishment and/or reproductive output. If resource availability theory extends to the defence of seeds against predators, patterns of allocation towards these defences must also be optimised, to maximise the plant's reproductive output.

The expected relationships between resource availability across different species, patterns of resource allocation and seed predation are given in a hypothetical model, summarised in Table 5.1. In this model the relationship between resource availability and resource allocation towards reproduction follows that between resource availability and resource allocation towards growth (Herms and Mattson 1992). Thus species that are adapted to environments rich in resources allocate a greater proportion of resources to reproduction than species adapted to environments poor in resources (Bazzaz et al. 1987). If there is a trade-off between the allocation of resources to reproduction and the allocation of resources to the defence of reproductive structures, paralleling the trade-off between the allocation towards growth and towards anti-herbivore defences (Coley 1985, Herms and Mattson 1992), then species that grow in resource rich environments may invest proportionately fewer resources in anti-seed predator defences than species that grow in resource poor environments. Higher levels of IPSP may therefore be expected among species of resource rich environments than species of resource poor environments.

Table 5.1. The relationships between plant resource availability, resource allocation and vulnerability to seed predation that might be expected according to resource availability theory.

Factor	Response	
Resource availability	High	Low
↓		
Proportion of resources allocated to reproduction	Higher	Lower
↓		
Proportion of resources allocated to the defence of reproductive structures	Lower	Higher
↓		
Vulnerability to IPSP	Higher	Lower

Louda et al. (1987) had dealt with variation in seed predation intensity within a single species of plant. This current study tests the extension of resource availability theory to seed predation across species.

The effect of light availability on the investment of resources towards potential defences against seed predators was tested because of its marked effects on plant growth. Soil nutrient availability was also included in this experiment as it has a demonstrated effect on the allocation of resources towards defences against herbivory (Bryant et al. 1989) and may also affect the degree to which species invest in defences against seed predation. Rainforest productivity is positively correlated with soil nutrient availability, as indicated by a higher incidence of deciduous species and higher rates of leaf turn-over (Webb 1968). At the community level at least, rainforests may also have a higher level of reproductive output on more fertile soils (Gentry and Emmons 1987). If this is in part due to species with a characteristically high reproductive output, these species may also have characteristically low levels of investment in seed defence and therefore higher levels of seed predation.

The possibility that differences in the vulnerability of plants to IPSP were related to resource availability had been tested previously in Chapter 4. In that previous study no correlations had been found between light availability and soil fertility, and the vulnerability of plants to IPSP. These results did not therefore support the hypothesis that resource availability can affect the vulnerability of plants to IPSP. This may, however, have been due to Type 2 error. This is because the species studied were represented by a single individual each and any patterns that may have been found in the data were obscured by high variation. This current study was conducted to further test the hypothesis that there is a relationship between the vulnerability of plants to IPSP and plant resource availability with a stronger statistical design and less risk of Type 2 error.

5.1.1 Aim of study

The aim of this study was to test the general hypothesis that resource availability affects the degree to which plant species invest in defences against seed predators and that this in turn affects their vulnerability to IPSP. The following specific hypotheses were tested in a tropical rainforest community:

1) Plant species of the well illuminated, high energy environment of the rainforest canopy are more vulnerable to seed predation than species of the poorly lit, low energy environment of the rainforest understorey and ground layer.

2) Rainforest plant species characteristic of highly fertile soil are more vulnerable to seed predation than species characteristic of low fertility soils.

3) Plant species with possibly defensive structures around their seeds are less vulnerable to seed predators than species without.

4) Plant species of the rainforest understorey and ground layer are more likely to have 'defended' seeds than species of the rainforest canopy.

5) Rainforest plant species characteristic of low fertility soils are more likely to have 'defended' seeds than species characteristic of highly fertile soils.

5.2 Methods

5.2.1 Study Area

This study was conducted on the Atherton Tablelands plateau of north Queensland (see Chapter 3 for a description of the study region and its rainforests), from January to March 1996 during the wet season. Eight locations were used for sampling; four on low fertility soil and four on high fertility soil. Owing to the distribution of rainforest both forest fragments and continuous forest was used, and the distances between these locations were variable (Table 5.2). The soil type of low fertility was the Galmarra association derived from strongly weathered Mid Palaeozoic Barron River metamorphics. The highly fertile type of soil was the Barron association derived from young, weakly weathered Pliocene to Mid Pleistocene basaltic lava and scoria (Henderson and Stephenson 1980, Laffan, 1988).

Each location was divided effectively into two sample 'sites'; the well lit rainforest canopy, including forest edges and the poorly lit rainforest understorey and ground layer. Henceforth these two types of sites are referred to as 'high light' and 'low light' sites. Thus were 16 sites in total, four in low light conditions and four in high light conditions on soil of low fertility, and four in low light conditions and four in high light conditions on high fertility soil.

Table 5.2 Maximum and minimum distances between sampling locations.

	Distances between locations (km)	
	Minimum	Maximum
Between low fertility locations	1.0	3.8
Between high fertility locations	2.8	23.8
Between high and low fertility locations	2.5	21.0

High light sites were sampled for species that reproduce under conditions of high light availability and conversely low light sites were sampled for species that reproduce under conditions of low light availability. To minimise variation in the number of plants sampled per location the sampling time for each location was standardised to a total of two days sampling effort. The proportions of plants sampled between high light sites and low light sites at any one location is a reflection of not only the abundance of fruiting plants in a site but also of the relative ease with which fruiting plants were found.

5.2.2 Assessing intensities of seed predation

From each fruiting plant 25 ripe to near-ripe fruit were sampled, although some species yielded fewer fruit per individual. This method of sampling risks under-estimating seed predation levels by overlooking the effects of seed predator induced fruit and seed abortion (Andersen 1988), however it is still considered suitable for comparative studies (Andersen 1989). The alternative use of insect exclusion experiments to quantify seed loss caused by seed predator induced abortion during fruit development was impractical because of the large number of plants to be sampled and the difficulties of gaining access to the canopies of many of these plants.

To measure intensities of IPSP the seeds of each fruit were dissected. During dissection the seeds from each sampled plant were apportioned to four categories: 1) intact developed seeds; 2) intact undeveloped seeds; 3) rotting seeds; and 4) seeds with larvae, frass or cavities. Factors other than seed predation may also cause the retarded development or abortion of seeds and seed decay. To avoid overestimating intensities of seed predation only the seeds of category #4 were counted as having been attacked by seed predators. The predispersal seed predation intensity of a plant was calculated as the total number of category #4 seeds divided by the total number of seeds counted in that sample.

5.2.3 Assessing defences against seed predators

The assessment of defences against seed predators was limited to the structural characteristics of the fruit. Because these structural characteristics cannot simply be assumed to have evolved specifically as defences against seed predators they are henceforth referred to as 'possible' defences. The fruit characteristics noted were: the type of pericarp surface (spiny, trichomatous, glandular or resinous); the presence of latex or resins within the pericarp; and the presence of a stony or woody layer 1.2 mm or more thick within the pericarp. This particular thickness was chosen as the cut-off as this was the thickness that appeared to be necessary to exclude insect seed predators from seeds in Chapter 4.

5.2.4 Statistical Analysis

Each sampled plant was assigned to two of four possible categories depending on the site in which it was found. A sample was therefore from either a high light site or low light site and a fertile site or an infertile site.

To compare seed predation intensities of plant species at high and low light sites (Hypothesis 1), and high and low fertility sites (Hypothesis 2), the mean intensities of seed predation for the species of each site were calculated (henceforth the 'mean species/site' seed predation intensity. This figure provides a single, community-level measure of seed predation intensity for each site. This figure was calculated as follows:

1) For any one site, mean seed predation intensities for each species were determined. However, at any one site, species were often represented by a single individual, so for these particular species, intensities of seed predation were not actually mean figures, but still treated as such in the calculations.

2) For any one site, the mean species seed predation intensities were then averaged to produce a mean species/site seed predation intensity.

By using mean species/site seed predation intensities instead of simply the mean seed predation intensity of all the plants at a particular site, the possibility that a site will have a low or high mean intensity because it is dominated by a particular species of plant is avoided.

5.3 Results

From all 16 sites a total of 219 seed samples were collected representing 77 plant species. The number of plants and species sampled per site, and the number of plants sampled per species was quite variable (Table 5.3).

Of the 77 species sampled, 46 species were found at fertile soil sites and 36 from infertile soil sites with 7 species in common, and 53 were found at high light sites and 27 from low light sites with 2 species in common (Table 5.4). For statistical tests the species common to either high and low light sites or high and low fertility sites were later labeled as either high or low light species, or high or low fertility species depending on where the majority of their representative individuals were found.

Table 5.3 The numbers of fruiting plants and species sampled at the different types of site (with standard deviations, n = 8 sites each for both high and low soil fertility sites, n = 8 sites each for both high light and low light sites).

	Soil fertility		Light availability	
	High	Low	High	Low
$\bar{x}$ plants per site	17.13 + 8.94	10 + 4.28	16.5 + 8.7	10.63 + 5.63
$\bar{x}$ species per site	9.63 + 4.31	6.13 + 2.42	9.63 + 4.37	6.13 + 2.3
$\bar{x}$ plants per species*	3.21 + 3.0 (n = 43)	2.35 + 2.21 (n = 34)	2.75 + 2.46 (n = 51)	3.0 + 3.16 (n = 26)

* Of the 77 species sampled 31 were represented by single plants only.

Table 5.4 Species common to sites of both high and low light availability, and/or sites of high and low soil fertility. The enumerated columns show how many plants were found at each type of site, for each species.

	High light availability		Low light availability	
	High soil fertility	Low soil fertility	High soil fertility	Low soil fertility
Alocasia brisbanensis (Araceae)	1	0	2	0
Alpinia caerulia (Zingiberaceae)	0	4	6	3
Cordyline cannifolia (Agavaceae)	0	0	9	5
Dichapetalum papuanum (Dichapetalaceae)	0	0	6	5
Emmenosperma alphitoniodes (Rhamnaceae)	2	1	0	0
Guettardella tenuiflora (Rubiaceae)	0	1	0	2
Rapanea subsessilis (Myrsinaceae)	0	0	1	2
Viticipremna queenslandica (Verbenaceae)	4	1	0	0
Zanthoxylum veneficum (Rutaceae)	7	2	0	0

Most of the species sampled were trees, but also included shrubs, vines and herbs (Table 5.5). The representation of different growth forms differed little between sites of high and low fertility but did differ considerably between sites of high light and low light availability. The ratio of tree species to species of small size (ie. shrubs and herbs) was significantly greater at high light sites than low light sites (χ^2 test, with Habers correction, 1-tailed test, $n = 66$, $\alpha = 0.05$, $df = 1$, $chi^2 = 19.26$, $p < 0.0005$).

Table 5.5. The number of species found in fruit per growth form at each type of site.

Growth form	High light	Low light	High fertility	Low fertility
Tree	39	10	27	22
Shrub	2	9	6	5
Vine	9	2	7	4
Herb	1	5	3	3

The mean intensities of seed predation among the 77 plant species varied greatly but tended to be low, while 42 species did not show any damage by seed predators. As a consequence the frequency distribution of mean predation levels for species is highly skewed to the left (Fig. 5.1).

5.3.1 Seed predation and resource availability

One statistical test had found a significant association between the vulnerability of plants to IPSP and plant resource availability while another three tests did not. As hypothesised, the proportions of species at high light sites that were attacked by seed predators tended to be greater than that of low light sites (Fig. 5.2). This difference was significant (Wilcoxon Rank Sign test, 1-tailed, $n = 8 + 8$, $\alpha = 0.05$, $p = 0.029$).

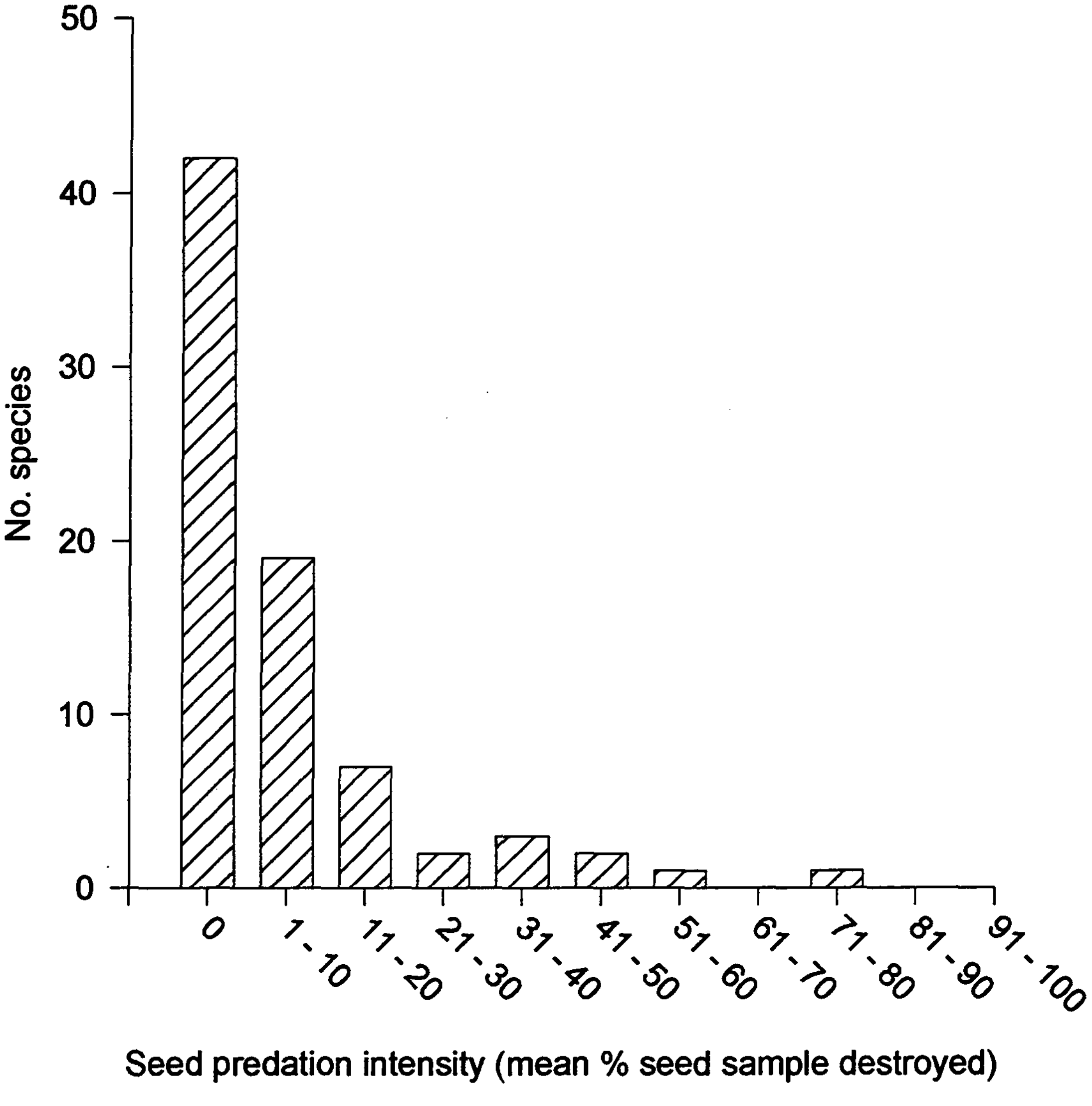

Figure 5.1. Frequency distribution of seed predation intensities for all 77 sampled species.

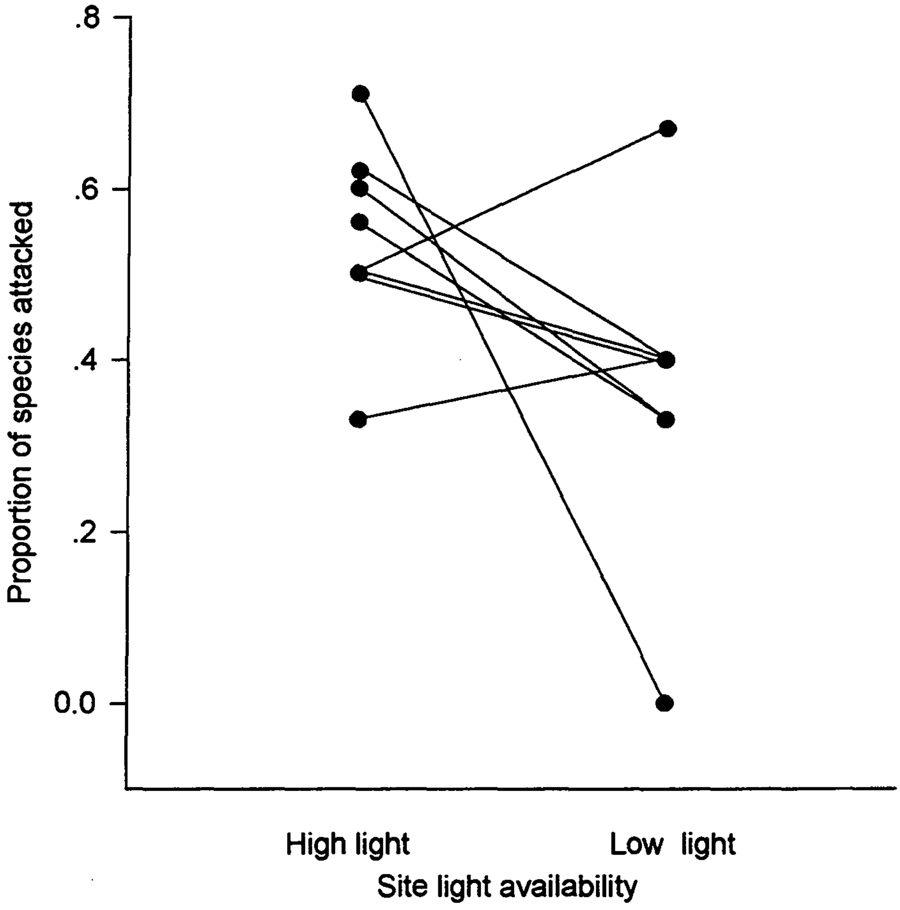

Figure 5.2. A paired comparison of the proportions of species attacked at high light and low light sites.

As hypothesised the proportions of species attacked at sites on soil of high fertility were also higher on average than the proportions of species attacked at sites on soil of low fertility (Fig. 5.3). However, this difference was not significant (Mann-Whitney U-test, 1-tailed, $n = 8 + 8$, $\alpha = 0.05$, $p > 0.1$).

From amongst the plants that were attacked by seed predators, the median species/site seed predation intensities of high resource sites were not significantly greater than those of low resource sites. In only three of seven possible comparisons did high light sites have greater median species/site seed predation intensities than low light sites (Fig. 5.4). Thus, against expectations, the median species/site seed predation intensities of high light sites were not significantly greater than those of low light sites (Wilcoxon Rank Sign test, 1-tailed, $n = 7 + 7$, $\alpha = 0.05$, $p = 0.17$). Nor were the median species/site seed predation intensities of sites on high fertility soils significantly greater than those on low fertility soils (Mann-Whitney U-test, 1-tailed, $n = 8 + 8$, $\alpha = 0.05$, $0.1 > p > 0.05$ (Fig. 5.5).

5.3.2 Seed predation and possible defences against seed predators

Of the 77 plant species sampled, 21 had possible structural defences (Table 5.6). The most common potentially defensive characteristic was a thick hard pericarp layer within the fruit (usually the endocarp). In nine species this layer was over 1.2mm thick - the minimum thickness which appeared to be effective as a barrier against insect predispersal seed predators amongst the species sampled for Chapter 4. Another 39 species also had woody or stony pericarp layers, but these were not as thick. The

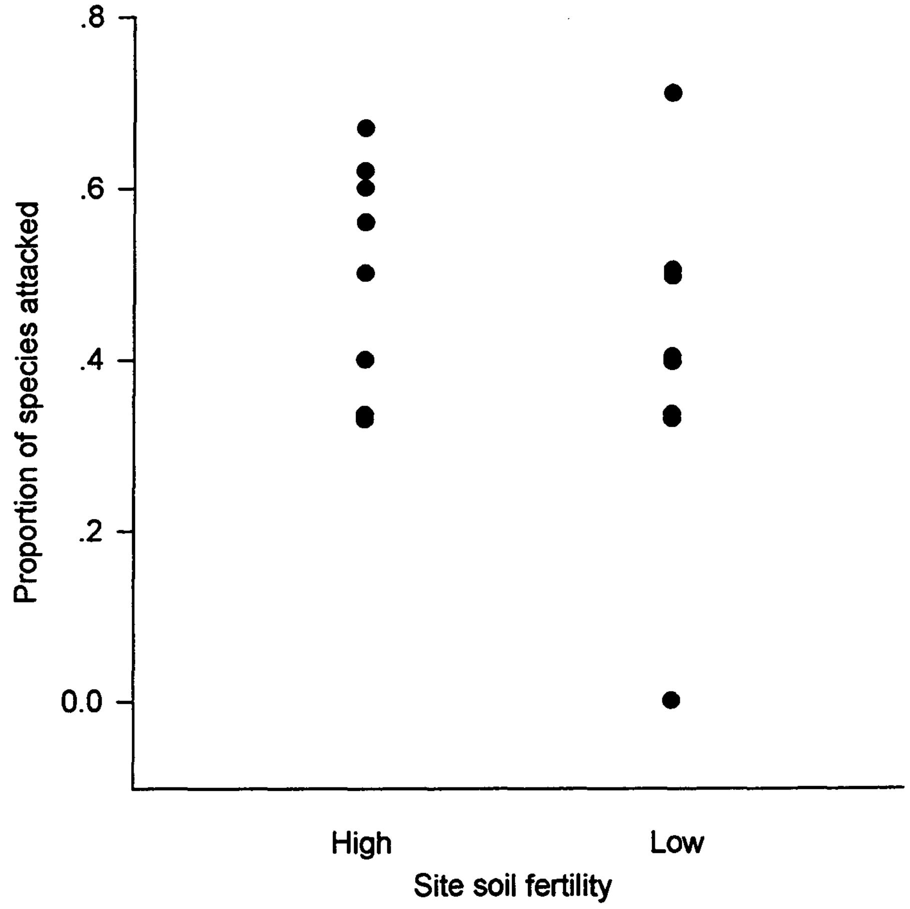

Figure 5.3. A comparison of the proportions of species attacked at sites on high and low soil fertility.

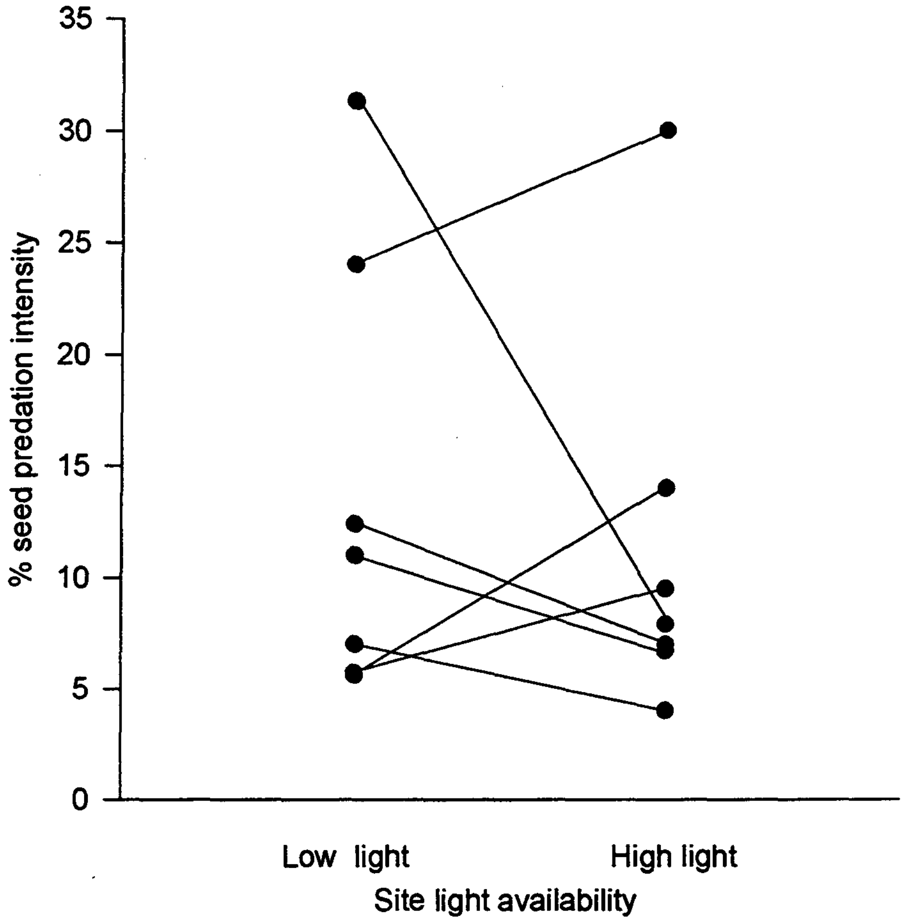

Figure 5.4. A paired comparison of median species/site seed predation intensities for high light and low light sites. Note: seven rather than eight comparisons were possible as no species were attacked by seed predators at one of the sites, thus the pair to which this site belonged was not used.

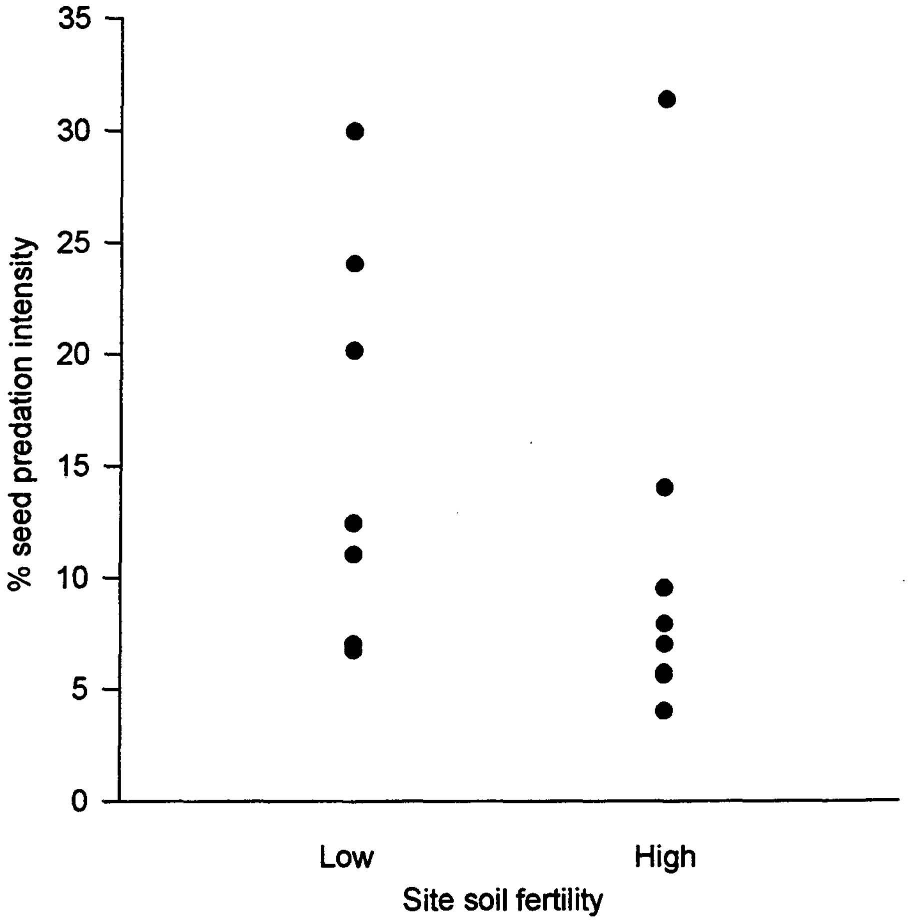

Figure 5.5. A comparison of median species/site seed predation intensities for sites on soil of high fertility and low fertility. Note: seven rather than eight comparisons were possible as no species were attacked by seed predators at one of the sites, thus the pair to which this site belonged was not used.

Table 5.6. The numbers of species with and without possible defensive fruit characteristics*. The species have been divided up into those characteristic of high and low light environments, and also into those characteristic of soil with high and low fertility.

	No defences	Hairs, spines or trichomes	Hard pericarp > 1.2mm	Latex or resin	Surface glands	Calcium oxalate
High light	34	5	6	1	2	1
Low light	21	4	1	1	0	0
High fertility soil	32	5	3	0	2	0
Low fertility soil	23	4	4	2	0	1

* Although a total of 77 species were sampled the totals of high and low light, and high and low soil fertility equal 78. This is because one species (*Pittosporum wingii*) had two types of possible defences - a hairy pericarp that also produced resin.

other fruit characteristics that may function as a defence against seed predation by insects were hairy, trichomatous or glandular fruit surfaces and the production of latex or resin when the pericarp was damaged. Additionally the flesh of one species of fruit (*Cissus penninervis* (F. Muell) Planch: Vitaceae) had what were possible possibly calcium oxalate crystals, indicated by their irritant effects on the skin after fruit dissection.

The probability a plant species will be attacked by insect predispersal seed predators was found to be negatively associated with the presence of one or more of these possible defences (χ^2 test, with Habers correction, 1-tailed test, n = 77, $\alpha = 0.05$, df = 1, $\chi^2 = 5.1$, $0.013 > p > 0.005$), (see Table 5.7 for proportions).

Table 5.7. The numbers of defended and undefended species attacked by seed predators.

	With possible defences	Without possible defences
No.s attacked species	5	30
No.s intact species	16	26

However, the presence or absence of possible defences was not associated with any differences in seed predation intensity. Attacked species with defences were expected to have lower intensities of seed predation than unprotected species, but this was not so (Mann-Whitney U-test, 1-tailed, $n = 8 + 24$, $\alpha = 0.05$, $p > 0.1$).

5.3.3 Anti-seed predator defences and resource availability

No association was found to occur between the presence of possible defences against seed predators among plant species and either the availability of light (χ^2 test, with Habers correction, 1- tailed test, $n = 77$, $\alpha = 0.05$, $df = 1$, $\chi^2 = 0.288$, $0.375 > p > 0.25$) or soil fertility (χ^2 test, with Habers correction, 1- tailed test, $n = 77$, $\alpha = 0.05$, $df = 1$, $\chi^2 = 0.066$, $0.45 > p > 0.375$), (see Table 5.8 for the category sizes).

Table 5.8. The numbers of attacked and intact species found at each type of site.

Site type	No.s species with possible defences	No.s species without defences
High light	15	35
Low light	6	21
High fertility	11	32
Low fertility	10	24

5.4 Discussion

The minimum evidence required to support the hypothesis that resource availability affects the vulnerability of different plant species to IPSP via effects on defence allocation must be based on three points. These are:

1) A positive correlation between the resource availability of different plant species and their vulnerability to seed predation.

2) A negative correlation between the degree to which different plant species invest in possible defences against seed predators and their vulnerability to seed predation.

3) A negative correlation between the resource availability of different plant species and the degree to which they invest in possible defences.

Point 1; that there was a positive relationship between resource availability and IPSP intensities was not supported as far as soil nutrient availability was concerned. There appeared to be a trend of increasing seed predation with increasing soil fertility but this was not statistically significant. The lack of a relationship agrees with the results of Chapter 4 suggesting that either; 1) soil fertility affects the vulnerability of plants to IPSP in a manner more complex than expected, possibly involving interactions with other factors for example, or 2) the vulnerability of plants to IPSP is not affected by soil fertility at all. There was, however, a positive relationship between light availability and predispersal seed predation levels. This result is in contrast to that of Chapter 4, where this relationship was tested previously, and the results of a study of rainforest vines by Grieg (1993).

The difference between the results of this current study that supports a positive relationship between light availability and the vulnerability of plants to IPSP and the results of the previous study in Chapter 4 may be due to differences in the experimental design. For the current study the sampling of plants was 1) replicated within species, to a degree, although 31of 77 species were represented by one plant only, 2) replicated within sites (see Table 5.3), and 3) replicate sites were used for each set of conditions (high light vs low light). Both this study and the previous study of Chapter 4 were looking for essentially species-level differences in vulnerability to IPSP. With the replication used, variations in the vulnerability of plants to IPSP would not have had as great a confounding effect on differences in the vulnerability of species to IPSP or as great a confounding effect on site to site differences in the vulnerability of plants to IPSP as would have occurred in the previous study. Thus the design of this current study would have been more effective at reducing the degree by which plant-to-plant variations in vulnerability to IPSP might obscure any species-level patterns than the previous study in Chapter 4. This suggests that the previous study had falsely rejected the hypothesis that high-light and low-light species differ in their vulnerability to IPSP due to a lack of statistical power and the proposed relationship does have real support.

Grieg (1993) had found that *Piper* species fruiting in late successional rainforest settings had higher intensities of IPSP than those that fruited in early successional settings where light availability was greater. However these results and the results of the current study are not mutually exclusive for three reasons. Firstly, the trend shown by Greig (1993) is not statistically significant because of the small number of *Piper* species studied. Secondly, because the 'early successional/high-light' *Piper* species produced more seeds than the 'late successional/low-light' species this trend may as be, Grieg (1993) suggests, the result of predator satiation and may not related to the presence or absence of anti-seed predator defences. Thirdly, when comparing seed predation intensities between limited numbers of closely related taxa the effect of seed predator satiation on seed predation intensities may be apparent, but this effect may be overshadowed by other factors when a larger variety of more disparate taxa are compared.

Point 2; that there was a negative correlation between the presence of possible structural defences in a plant species and the presence of seed damage was supported by the results. These results accord with those of Davidar (1987), Janzen (1977), Nwanze and Horber (1976) and Scott (1982) showing that hard tissue layers can hinder seed predator insects. Not all of the species that produced seeds within defensive fruit escaped seed predation. One out of seven species possessing a thick, hard endocarp surrounding the seed were attacked. Such cases are not uncommon in tropical rainforests, some species of seed predator are capable of cutting through the hardened endocarps of mature fruit (Delobel et al. 1995), while others may attack developing fruit prior to endocarp hardening (Auld 1983, De Steven 1981, Ernst et al. 1989).

Point 3; that there is negative correlation between resource availability for different species and their degree of investment towards structural defences against predispersal seed predation was not supported. Thus even though light availability and possibly defensive fruit characteristics were both related to seed predation intensities, light availability and the presence of possible defenses were themselves not associated (Fig. 5.6).

Because the general hypothesis, that resource availability affects the degree to which plant species invest in possible defences against seed predators and consequently their intensities of IPSP, was not given the minimum support by the results it must be rejected. Either this study was unable to detect the proposed relationships or the positive results found require an alternative interpretation.

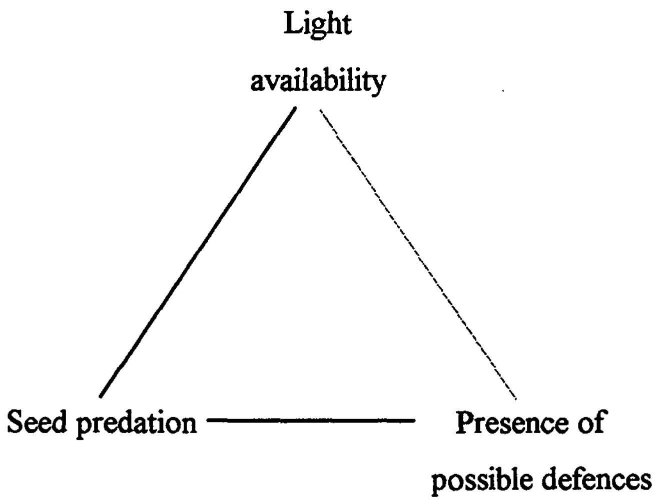

Figure 5.6. A summary of the correlations found between light availability, seed predation at the species/site level and the presence of possible defences in species. Bold lines indicate significant correlations between variables, the broken line indicates an expected, but unsupported, correlation.

5.4.1 Limitations of the data

This study may not have detected the proposed relationships because species were inadequately represented in the samples, the measurement of seed predation intensities was inaccurate or the assessment of anti-seed predator defences was inaccurate.

The sampling of species

The number of plants sampled per species was variable (Table 5.3) and at any one site many species were represented by a single individual. Species would have been better represented had more time been available for sampling fruiting plants. Considering that many plants have low population densities the necessary increase in effort to get replicate samples for all species would be very large.

Assessing seed predation

Measurements of seed predation intensities for plants would be more accurate if seed abortion caused by seed predators was also taken into account. As this would require monitoring the fruit as they develop on the parent plant this would present logistical problems when applied to replicate individuals for a large number of canopy species.

Assessing possible defences in species

Assessing the degree to which plants invest resources towards anti-seed predator defences may have been more accurate if chemical defences were also included. This however requires assumptions to be made on the functions of different classes of chemical compounds and a means of equating investments made in structural defences with chemical defences. The quantity of carbon allocated towards defences per seed may be the most appropriate measure for future studies.

5.4.2 Alternative interpretations of the results

Because the general hypothesis that resource availability affects the degree to which plant species invest in possible defences against seed predators and consequently their intensities of predispersal seed predation by insects was not given the minimum support it was rejected. There may be other reasons for the positive results found.

Seed defences and seed predation

The fruit characteristics that had been interpreted as possible anti-seed predator defences may well hinder insect seed predators, however this effect may only be an incidental to some other function. For example the presence of a thick hard pericarp layer surrounding the seed may for some plant species impose innate germination quiescence (Murdoch and Ellis 1992) by excluding air and water. Thick hard pericarp layers may also protect seeds from damage during dispersal or infection by pathogens. If species have evolved these layers for these alternative functions their presence may therefore not necessarily be related to resource availability in the manner expected according to the general hypothesis.

Light availability and seed predation

Higher intensities of IPSP may have been associated with higher levels of light availability not through the effects of resource availability on plant defences, but because of the effects of other confounding factors. Differences in the chemistry of plants from high and low light environments, that are not directly related to plant defences may have occurred, such as differences in water potential in response to insolation levels (eg. Louda and Rodman 1996). Changes in 1) microclimate (air temperature, movement and humidity) and 2) plant growth form (growth habit, size and seed crop size) were also associated with changes in light availability.

Microclimate may possibly affect seed predation via effects on plant growth and chemistry (Nobel 1999), or on insect activity (Bernays and Chapman 1994, Louda and Rodman 1996, Willmer et al 1996). Isolating the possible effects of microclimate from light availability in a community-level study such as this is not feasible as the microclimate for species that fruit in high-light conditions will always tend to be different to the microclimate associated with species that fruit in low-light conditions. The combined effects of light availability and microclimate on seed predation levels could be tested within species by the measuring seed predation levels of plants that belong to species capable of producing fruit in both high-light and low-light conditions. However, if microclimate was found to actually affect seed predation levels within species the significance of this could not be translated to any community-level differences in seed predation levels. This is because community-level differences are based on differences between species not within species.

Plant growth form was confounded with light availability because plants growing in high-light conditions tended to be larger than those growing in low-light conditions (Table 5.5). Plant size may influence seed predation intensities by effecting seed crop size. Small plants will tend to have a smaller total reproductive output than large plants (Bazzaz et al. 1987, Raven 1990). For a plant with a small reproductive output each seed will represent a greater proportion of the total chance that the parent plant will produce successful offspring than that represented by a seed from a plant with a large reproductive output. In terms of the fraction of the total probability a plant will produce successful offspring, individual seeds produced by small plants may be considered to be of greater 'value' than seeds produced by large plants. There may therefore be a greater selection pressure to protect the seeds of small low-light plants than large high-light plants. In this case low-light plants may have a lower vulnerability to seed predation than high-light plants (Table 5.9). The outcome of this, in terms of the vulnerability of species to IPSP is the same as that expected according to resource availability (Table 5.1).

Table 5.9. Possible relationships linking resource availability, plant size and vulnerability to seed predation.

Factor	Response	
Resource availability	High	Low
↓		
Capacity for growth	Higher	Lower
↓		
Reproductive output	Higher	Lower
↓		
Proportion of resources allocated to defences for reproductive structures	Lower	Higher
↓		
Vulnerability to seed predation	Higher	Lower

However, according to current views of plant allocation, the confounding association between light availability and plant growth form may lead to a negative relationship between light availability and IPSP, rather than the positive relationship found in this study. Larger plant growth forms, such as the canopy trees which dominated the high-light species of the rainforest, tend to invest a smaller proportion of their resources towards growth and reproduction than smaller growth forms like herbs and shrubs (Abrahamson 1979, Bazzaz et al. 1987, Raven 1990) that were found growing in low-light conditions. If a trade-off, such as the one thought to occur between leaf production and their defence against herbivores (Herms and Mattson 1992) exists between allocation towards reproduction and the defences of reproductive structures then the proportion of resources allocated towards the defence of reproductive structures in herbs and shrubs would be lower than that of large canopy trees. Low-light herbs and shrubs in the rainforest would thus be expected to be more vulnerable to IPSP than well lit canopy trees (Table 5.10). To

Table 5.10. Possible relationships linking resource availability, allocation to structural support and reproduction, and the defence of reproductive structures.

Factor	Response	
Resource availability	Low	High
↓		
Plant size	Small	Large
↓		
Allocation to reproduction	Higher	Lower
↓		
Allocation to the defence of reproductive structures	Lower	Higher
↓		
Vulnerability to seed predation	Higher	Lower

clarify why light availability was associated with differences in the vulnerability of plants to seed predation thus requires testing for associations between light availability and seed predation within separate plant growth forms and testing for associations between growth form and seed predation within particular light regimes. The current data does not allow this.

In summary this study did not support the general hypothesis that resource availability affects the degree to which plant species invest in possible defences against seed predators and consequently their levels of predispersal seed predation by insects. Although a positive relationship between light availability and seed predation intensities was found, lending partial support to the general hypothesis, alternative interpretations can be made of this association. These interpretations relate to differences of allocation towards defences in response to plant size and growth form, rather than growing conditions per se.

CHAPTER 6: HOST PLANT INDIGENEITY

Abstract

According to Chapter 4 native plants were more likely to be attacked by predispersal seed predators than exotic plants. However this association was confounded with taxonomic affiliation and plant growth-form. Retesting this association while accounting for these two confounding factors and an additional two; light availability and hard pericarp thickness further supports the observation that native plants are more vulnerable to seed predation than exotic plants. Previous studies of interactions between piants and phytophagous insects (Connor 1991, Kogan 1991) would suggest that the exotic species of plant that were attacked by seed predators should more closely related to local native species than those that were not. This current study did not support this. The residency time (Strong et al. 1984) and geographic range (Strong et al. 1977 and 1984) of the exotic species may have been more important to their vulnerability to seed predation.

6.1 Introduction

Studies of herbivory and commercial crop infestation show that exotic species of plant are often less vulnerable to attack by phytophagous insects than native species (Kogan 1991, Strong et al. 1984). This can be explained by their novel characteristics, to which local potential phytophages have yet to adapt (Strong et al. 1984). The study in this chapter tested for the effect of indigeneity on the predispersal seed predation of tropical rainforest plants by insects.

The results of Chapter 4 suggested that exotic species of plant were less likely to be attacked by seed predators than native species. However, host indigeneity appeared to be confounded by plant growth-form and phylogeny, indicated by family-level taxonomic affiliation. These may act as independent factors affecting the vulnerability of these plants to seed predation. This current study tested for the effects of plant indigeneity on predispersal seed predation whilst controlling for these other two factors and two additional factors; light availability and hard pericarp thickness.

On the Atherton Tablelands exotic plants tend to be early successional species of small stature ie. herbs and shrubs (Jenkins 1993, Chapter 4.). As a result, the effects of indigeneity on seed predation levels may be confounded by factors associated with plant growth-form. This is because plant growth-forms differ in their allocation of resources towards reproduction and defence. Larger, longer-lived growth forms such as trees invest proportionately less towards reproduction than smaller, shorter-lived growth forms such as herbs (Abrahamson 1979, Bazzaz et al. 1987, Hancock and Pritts 1987). If there is a trade-off between investment in reproductive structures and their defence then seeds of larger, longer-lived growth-forms may be better defended against seed predators. This trade-off parallels the trade-off between investment in leaves and stems, and their defence against herbivores (Herms and Mattson 1992). Smaller, shorter-lived growth-forms would therefore expected to be more vulnerable to attack than larger, longer-lived growth-forms (Louda 1989, 1995).

Phylogeny may be a confounding factor as certain plant taxonomic families are particularly common among the exotics of the Atherton Tablelands; ie the Asteraceae, Caesalpiniaceae, Fabaceae, Poaceae and Solanaceae (Hopkins et al. 1996a and b, Jenkins 1993, pers obs). Phylogeny may be important as a confounding factor because some taxonomic families appear to be characteristically well protected by defences. For example, the Solanaceae are well known for their alkaloidal secondary defence compounds (D'Arcy 1986).

Light availability may also be important as a factor confounded with plant indigeneity. This is because exotic plants tend to establish in disturbed habitats (Batianoff and Franks 1998, Bicon et al. 1989, Humphries and Stanton 1992) where shading by other plants is reduced and light availability is high. The high light condition may be important for exotic plants because it may indirectly affect the allocation of resources to defensive secondary compounds in seeds and hence their vulnerability to seed predation. If this is so, these effects would probably parallel the effect resource availability can have on plant growth and the allocation of resources to anti-herbivore defenses (Herms and Mattson 1992). A possible relationship between light availability and the vulnerability of plants to seed predation is supported by the positive correlation found between light availability and intensities of predispersal seed predation by insects among the native rainforest plants studied in Chapter 5.

Hard pericarp thickness will also be controlled for in this study because it has previously been shown to reduce the vulnerability of plants to seed predation (Janzen 1977, Nwanze and Horber 1976, Podoler and Applabaum 1968, Chapter 4) and may mask any effects plant indigeneity may have on seed predation levels. The fruit of some plant species had seeds that were enclosed within a hard stony or woody layer of lignified tissue. This tissue layer was a component of the pericarp (usually the inner layer or endocarp). Plants that produced fruit with a thick hard pericarp layer were found to have a lower chance of being attacked by seed predators than those that produced fruit with a thin hard pericarp layer or only a soft, fleshy pericarp layer (see Chapter 4).

In addition to testing for an association between plant indigeneity and seed predation levels, this study looks at one aspect of the mechanism that may underlie this association: phylogenetic relatedness between exotic and native species. Exotic species of plant are more likely to be attacked by seed predators if they are phylogenetically related to local native species. This is because the seed predators are more likely to be pre-adapted to the exotics with a greater chance of recognising the plants as a potential resource and overcoming possible defences. This explanation has been shown to apply to herbivory (Moran 1980) and seed predation in legume crops (Kogan 1991). This study expands the application of this explanation to predispersal seed predation in a natural and diverse ecosystem, such as the tropical rainforest.

This study aimed to test the following specific hypotheses:

1) Exotic species of plant are less likely to be attacked by predispersal insect seed predators than native plant species.

2) Exotic plant species have lower mean intensities of insect predispersal seed predation than native plant species.

3) There is a positive correlation between the probability that exotic plant species are attacked by seed predators and their taxonomic affiliation to local native rainforest species.

4) There is a positive correlation between the intensity with which exotic plant species are attacked by insect predispersal seed predators and their taxonomic affiliation to local native rainforest species.

6.2 Methods

6.2.1 Study area, species selection and field sampling

Plants were sampled from across the Atherton Tableland area over 6 months during the 1996 wet season (see Chapter 3 for a description of the region and its rainforests). The Atherton Tablelands area was divided into 38 sites, each associated with a particular public access/State Forest road, or section of road defined by catchment area. These sites were then successively searched for fruiting plants. Sampling was limited to plants growing in highlight conditions at rainforest edges along roadsides and forest fragments, and from adjacent areas of disturbance and forest regrowth. Sampling plants only from highlight conditions removed the possibility of confounding light availability with plant indigeneity. If plants were sampled at random across a range of light conditions the proportion of fruiting exotic plants growing in highlight conditions would probably have been much greater than the proportion of native plants fruiting under highlight conditions (Chapter 4). Sampling aimed at having each species represented by 6 replicate plants; 2 plants from each of three sites. However, not all of the species sampled were abundant and widespread enough for this. As a compromise a minimum representation of 3 plants in total, from 2 sites was accepted.

To compare the vulnerability of exotic and native species to predispersal seed predation by insects (hypotheses 1 and 2) a stratified random sampling design was used. With this design equal numbers of exotic and native species were used. To eliminate the possibility of any confounding differences in plant growth-form between these two groups equal numbers of herb, shrub, vine and tree species were used. This sampling design thus included eight different categories of plant species: native herbs, shrubs, vines and trees, and exotic herbs, shrubs, vines and trees. Each category comprised five species. The choice of species was determined by the availability of fruiting plants. Wherever possible, species were chosen because they had no hard pericarp layer or only the thinnest of such layers. This was to reduce any possibly interfering effects of hard pericarp thickness on the vulnerability of plants to seed predation.

The possibility that the vulnerability of plants to seed predation was associated with factors that were confounded with phylogeny was reduced by selecting the species for each category from as many different taxonomic families as possible, hence minimising the dominance of any particular family. Possibly confounding associations with phylogeny were also minimised in another manner. Where species did belong to the same taxonomic family, only the average intensity was used (see Table 6.1).

To compare exotic species that were attacked by seed predators with exotic species that weren't, in terms of their taxonomic similarity to the native flora (for Hypotheses 3 and 4) a total of 30 exotic species were used (including attacked and intact species). Again mean intensities of seed predation were calculated for families represented by two or more species (see Table 6.2).

6.2.2 Assessing seed predation

To assess seed predation in each plant 25 ripe to near-ripe fruit were taken. This quantity of fruit was enough to get a measure of the proportion of the plant's seed crop that was attacked by seed predators and could readily be found on shrubs and herbs which tend to have a smaller fruit crop than trees and vines.

Dehiscent types of fruit were collected prior to splitting. Each fruit was dissected and the component seeds were counted, and examined under a binocular microscope. Seeds were then categorised as being either:

- 1) fully developed and undamaged.
- 2) undeveloped and undamaged.
- 3) damaged; decaying only.
- 4) damaged; possessing cavities, punctures, larvae or frass (with or without decay)

To avoid misinterpreting the origin of any damage or developmental failure among seeds only the seeds of category #4 were counted as having been attacked by predispersal insect seed predators. This does mean that intensities of seed attack for

Table 6.1. The derivation for the final data set of seed predation intensities for the 40 plant species. For the final data set all taxonomic families were given equal representation by averaging seed predation intensities of species, within families, producing final mean figures. To calculate the proportions of exotic and native species that were attacked by seed predators only the final mean figures were used.

	Species	Family	Intensity of seed predation (% seed sample attacked)	
			Original mean	Final mean
Exotic species				
Herbs	*Ageratum conyzoides*	Asteraceae	0	0
	Indigofera suffruticosa	Fabaceae	1.5	1.5
	Lycopersicon esculentum	Solanaceae	0	0
	Tristemma mauritianum var mauritianum	Melastomataceae	0	0
	Rivina humilis	Phytolaccaceae	0	0
Shrubs	*Senna X floribunda*	Caesalpiniaceae	1.3	1.3
	Sida rhombifolia	Malvaceae	2	2
	Solanum torvum	Solanaceae	0	0
	Coffea arabica	Rubiaceae	0	0
	Duranta erecta	Verbenaceae	0	0
Trees	*Citrus sinensis*	Rutaceae	0	0
	Ligustrum sinense	Oleaceae	0	0
	Delonix regia	Caesalpiniaceae	14.3	14.3
	Cinnamomum camphora	Lauraceae	0	0
	Spathodea campanulata	Bignoniaceae	0	0
Vines	*Protasparagus plumosus*	Liliaceae	0	0
	Desmodium uncinatum	Fabaceae	17.4	17.4
	Solanum seaforthianum	Solanaceae	0	0
	Turbina corymbosa	Convolvulaceae	0	0
	Lantana camara	Verbenaceae	2	2
Native species				
Herbs	*Alocasia macrorrhiza var brisbanensis*	Araceae	0	0
	Alpinia arctiflora	Zingiberaceae	3.9	
	Alpinia caerulia	Zingiberaceae	6.2	
	Alpinia racemigera	Zingiberaceae	23.9	11.3
	Helichrysum rupicola	Asteraceae	8.5	8.5
Shrubs	*Callicarpa pedunculata*	Verbenaceae	0	
	Dendrocnide moroides	Urticaceae	0	0
	Mackinlaya macrosciadea	Araliaceae	0	0
	Pavetta australiensis	Rubiaceae	14.1	14.1
	Callicarpa longifolia	Verbenaceae	0	0
Trees	*Daphnandra repandula*	Monimiaceae	2.5	2.5
	Glochidion harveyanum	Euphorbiaceae	73.1	73.1
	Mischocarpus	Sapindaceae	5.6	5.6
	Neolitsea dealbata	Lauraceae	0.7	0.7
	Zanthoxylum veneficum	Rutaceae	4	4
Vines	*Calamus caryotoides*	Arecaceae	1.3	1.3
	Cissus hypoglauca	Vitaceae	0	0
	Ripogonum album	Smilacaceae	4.9	4.9
	Melodorum leichardtii	Annonaceae	1.3	1.3
	Rubus moluccanus	Rosaceae	0	0

Table 6.2. The intensities of seed predation for exotic species and their indices of taxonomic affiliation to the local native rainforest flora. Mean intensities of seed predation are given for taxonomic families represented by two or more species.

Species	Family	Seed predation intensity	$\bar{x}$ seed predation intensity per family	Number of confamilial species
Ageratum conyzoides	Asteraceae	0	0	15
Turbina corymbosa	Convolvulaceae	0	0	26
Macrotyloma axillare	Fabaceae	0	0	54
Cinnamomum camphora	Lauraceae	0	0	93
Protasparagus plumosus	Liliaceae	0	0	14
Urena lobata	Malvaceae	0	0	20
Tristemma mauritianum var mauritianum	Melastomataceae	0	0	6
Chukrasia tabularis	Meliaceae	0	0	32
Psidium guajava	Myrtaceae	0	0	42
Ligustrum lucidum	Oleaceae	0		15
Ligustrum sinense	Oleaceae	0	0	15
Phytolacca octandra	Phytolaccaceae	0		0
Rivina humilis	Phytolacaceae	0	0	0
Coffea arabica	Rubiaceae	0	0	89
Citrus sinensis	Rutaceae	0	0	64
Lycopersicon esculentum	Solanaceae	0		20
Solanum mauritianum	Solanaceae	0		20
Solanum seaforthianum	Solanaceae	0		20
Solanum torvum	Solanaceae	0	0	20
Duranta erecta	Verbenaceae	0	0	37
Delonix regia	Caesalpiniaceae	14.3		24
Senna occidentalis	Caesalpiniaceae	12.8		24
Senna X floribunda	Caesalpiniaceae	1.3	9.5	24
Crotolaria pallida	Fabaceae	8.2		54
Desmodium uncinatum	Fabaceae	17.4		54
Indigofera suffruticosa	Fabaceae	1.5	9.0	54
Sida rhombifolia	Malvaceae	2	2	20
Mimosa pudica	Mimosaceae	0.4	0.4	40
Nicandra physalodes	Solanaceae	1.4	1.4	20
Lantana camara	Verbenaceae	2	2	37

some samples may be underestimated because some seed predator damage may not be recorded. The level of seed predation for each plant was measured as :

- 1) the presence or absence of any seed predation in a sample.

- 2) the percentage proportion of seeds attacked by predators.

6.2.3 Assessing the phylogenetic similarity of exotic species to the local native rainforest species

As an indicator of the phylogenetic relationships between species their taxonomic classification was used (Hendersen 1997). The phylogenetic similarity of exotic species to local native rainforest species was measured with an index. This index was the number of native species belonging to the taxonomic family of each exotic species (see Table 6.2). Using the family level taxonomic rank was a compromise, seen as a better option than using either the genera or order ranks. Because the number of species in any one genera will tend to be fewer than the number of species in any one family, there will tend to be less variation in the degree to which an exotic species is phylogenetically related to congeneric species than confamilial species. However, the genera level rank was too restrictive to use in this study as not all the exotic genera that were sampled had native congeneric representatives in the local rainforest flora. Conversely, the chance that a particular exotic species will share an order level rank with local rainforest species will be much greater. However, the order level rank, encompassing a greater diversity of species, wiill tend to include a greater degree of variation in phylogenetic relatedness to local flora.

The number of native species that shared a family level taxon with the exotic species sample in this study was taken from Cooper and Coopers (1994) "Provisional Species List" of angiosperms and gymnosperms occurring in Queenslands rainforests, monsoon forests and vine thickets north of Townsville. This index thus measured the number of confamilial species from across a larger area than merely the Atherton Tablelands.

6.2.4 Rearing insect seed predators

In addition to the fruit harvested to assess seed predation intensity, another 40 fruit were harvested from each plant to rear adult insect seed predators from larvae already within the seeds. The methods used to rear these insects are described in Chapter 4 (Section 4.2.2).

Fruit were harvested directly from plants, when in a near-ripe to ripe state. Dehiscent types of fruit that split open to release their seeds were collected prior to this final stage of maturity. From each sample of fruit two subsamples were taken. One subsample of 40 fruit was used to rear any insect seed predators already within the seeds. The other subsample of 24 fruit was used to measure the percentage intensity of seed crop predation and to record seed/fruit morphological attributes. Accompanying each sample was the following information: date, location, plant growth form, its forest strata level, forest successional phase and soil type.

6.3 Results

In total 63 species of plant were sampled. The numbers of species representing each plant growth-form category varied among both the exotics and natives (Table 6.3). Each species was found across a mean of 2.48 sites (SD = 0.56, n = 63) and represented by a mean of 4.37 fruiting plants (SD = 1.15, n = 63).

Table 6.3. Numbers of species found per plant growth-form.

Growth-form	Native	Exotic
Tree	12	9
Shrub	8	7
Vine	6	5
Herb	5	11
Total	31	32

Of the 63 sampled species 27 were attacked by predispersal insect seed predators. Adult insects were reared from 11 of these species and six were identifiable to species level. Four of these were reared from exotic species of plant (Appendix 2).

6.3.1 Selection of species for comparing natives versus exotics

The two categories most poorly represented from among the original 63 species sampled (native herbs and exotic vines) each contained 5 species. Hence to maintain equal numbers of species per growth-form in this study the size of the other six categories were also limited to 5 species each. Thus for all eight categories a total of 40 species were selected (Table 6.1). Although any bias towards particular plant families was minimised among these selected species, three families were relatively well represented. The Zingiberaceae were represented by three species (all native herbs), the Solanaceae were represented by three species and the Verbenaceae (2 exotic and 2 native species). In selecting species for each category, priority was given to those species with no hard pericarp layer, then to species with only the thinnest hard pericarp layers. In this manner hard pericarp thickness of the selected species was well controlled - most of the species that were selected had no hard pericarp layer (Table 6.4). Only one species had a hard pericarp layer over 1.2 millimetres thick, which was the minimum thickness that appeared to be effective at reducing the chances of seed predation (see Chapter 4).

6.3.2 Seed predation in the selected species

The overall proportion of selected species attacked by predispersal insect seed predators was 48 %. Hypothesis # 1; that exotic plant species are less likely to be attacked by predispersal insect seed predators than native species was supported by this study. Taking into account any possible taxonomically related bias caused by the better represented plant families (see Table 6.1), native species were attacked in asignificantly greater proportion than the exotic species (11/17 vs 6/20) (Chi^2 test (1-tailed) with Habers correction for continuity, $\alpha = 0.05$, $n = 37$, $\chi^2 = 3.94$, $df = 1$, $0.025 > p > 0.013$). Hypothesis # 2; that exotic species have lower mean intensities of seed predation than native species remains untested. This is because the number of measurements of seed predation intensity (11 for native species vs 4 for exotic species), were too few to apply a statistical test of adequate power. Within this data set no clear trends were apparent (Fig. 6.1).

Table 6.4. The raw data set for the 40 plant species selected for study, showing their thickness of hard pericarp and mean intensities of predispersal seed predation by insects.

	Species	Family	Hard pericarp thickness (mm)	Intensity of seed predation (% seed sample attacked)		
				$\bar{x}$	S.D.	n
Exotic species						
Herbs	*Ageratum conyzoides*	Asteraceae	0	0	0	5
	Indigofera suffruticosa	Fabaceae	0	1.5	0.02	4
	Lycopersicon esculentum	Solanaceae	0	0	0	3
	Tristemma mauritianum var mauritianum	Melastomataceae	0.05	0	0	4
	Rivina humilis	Phytolaccaceae	0.1	0	0	6
Shrub	*Senna X floribunda*	Caesalpiniaceae	0	1.3	0.02	6
	Sida rhombifolia	Malvaceae	0	2	0.02	4
	Solanum torvum	Solanaceae	0	0	0	6
	Coffea arabica	Rubiaceae	0.23	0	0	3
	Duranta erecta	Verbenaceae	0.5	0	0	6
Trees	*Citrus sinensis*	Rutaceae	0	0	0	4
	Ligustrum sinense	Oleaceae	0	0	0	6
	Delonix regia	Caesalpiniaceae	0.37	14.3	0.13	4
	Cinnamomum camphora	Lauraceae	0.4	0	0	6
	Spathodea campanulata	Bignoniaceae	1.51	0	0	3
Vines	*Protasparagus plumosus*	Liliaceae	0	0	0	3
	Desmodium uncinatum	Fabaceae	0	17.4	0.14	4
	Solanum seaforthianum	Solanaceae	0	0	0	6
	Turbina corymbosa	Convolvulaceae	0.2	0	0	3
	Lantana camara	Verbenaceae	0.45	2	0.04	6
Native species						
Herbs	*Alocasia macrorrhiza var brisbanensis*	Araceae	0	0	0	3
	Alpinia arctiflora	Zingiberaceae	0	3.9	0.04	4
	Alpinia caerulia	Zingiberaceae	0	6.2	0.09	6
	Alpinia racemigera	Zingiberaceae	0	23.9	0.33	5
	Helichrysum rupicola	Asteraceae	0	8.5	0.07	6
Shrub	*Callicarpa pedunculata*	Verbenaceae	0	0	0	5
	Dendrocnide moroides	Urticaceae	0	0	0	4
	Mackinlaya macrosciadea	Araliaceae	0	0	0	4
	Pavetta australiensis	Rubiaceae	0	14.1	0.2	2
	Callicarpa longifolia	Verbenaceae	0.05	0	0	5
Trees	*Daphnandra repandula*	Monimiaceae	0	2.5	0.02	4
	Glochidion harveyanum	Euphorbiaceae	0	73.1	0.22	4
	Mischocarpus	Sapindaceae	0	5.6	0.1	5
	Neolitsea dealbata	Lauraceae	0.17	0.7	0.02	6
	Zanthoxylum veneficum	Rutaceae	0.6	4	0.04	3
Vines	*Calamus caryotoides*	Arecaceae	0	1.3	0.02	3
	Cissus hypoglauca	Vitaceae	0	0	0	3
	Ripogonum album	Smilacaceae	0	4.9	0.04	4
	Melodorum leichardtii	Annonaceae	0.1	1.3	0.03	5
	Rubus moluccanus	Rosaceae	0.1	0	0	3

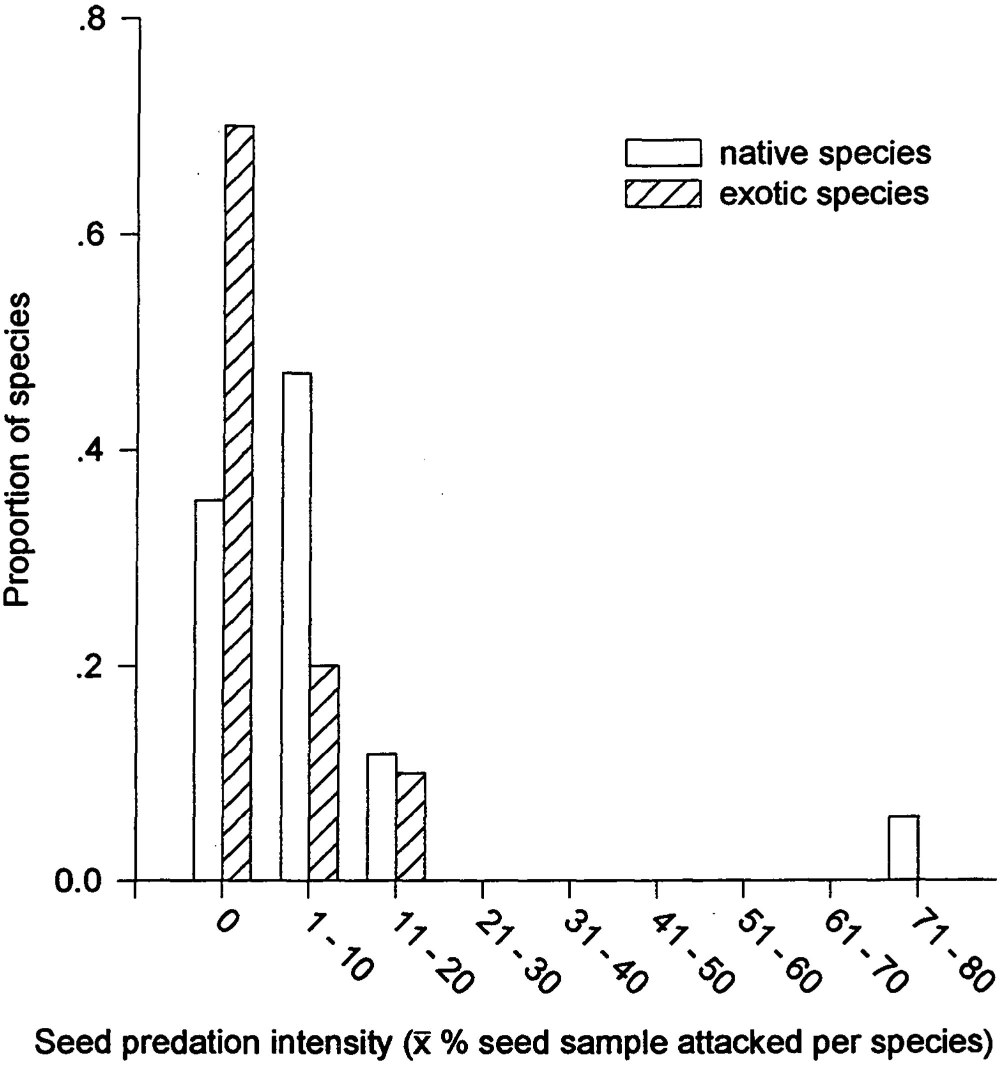

Figure 6.1. Frequency distribution for the final set of seed predation intensities for exotic and native species. For exotics n = 20, for natives n = 17.

6.3.3 Phylogenetic similarity of exotic species to local native rainforest species

Hypothesis # 3; that exotic species attacked by seed predators have a greater degree of phylogenetic similarity to the local native rainforest species than those that are not attacked was not supported. In a frequency histogram no indication was given of any difference between attacked and intact exotic species in terms of their phylogenetic similarity to local native species (Fig. 6.2). This lack of difference was confirmed statistically (Mann-Whitney test (1-tailed), $\alpha = 0.05$, $n_1 = 6$, $n_2 = 15$, $p = 0.513$). Hypothesis # 4; that there is a positive correlation between seed predation intensity in exotic species and their phylogenetic similarity to the local native rainforest species, could not be adequately tested as there were too few attacked exotic species (6 species) to apply statistical tests with reasonable power. Within the small data set that does exist there was no suggestion of a relationship between seed predation intensity and phylogenetic similarity among exotic plant species (Fig. 6.3).

6.4 Discussion and conclusions

In this study exotic species of plant were found to have a lower chance of being attacked by predispersal insect seed predators than native species of plant. This may have been because:

1) in comparison with the native species, a smaller proportion of exotic species were host to any species of seed predator at all, or

2) in comparison with the native species a smaller proportion of the individuals of each exotic plant species were attacked. This would mean that exotic species had a lower chance of being represented by one or more attacked plants than native species and therefore being recorded as attacked by seed predators. No differences were

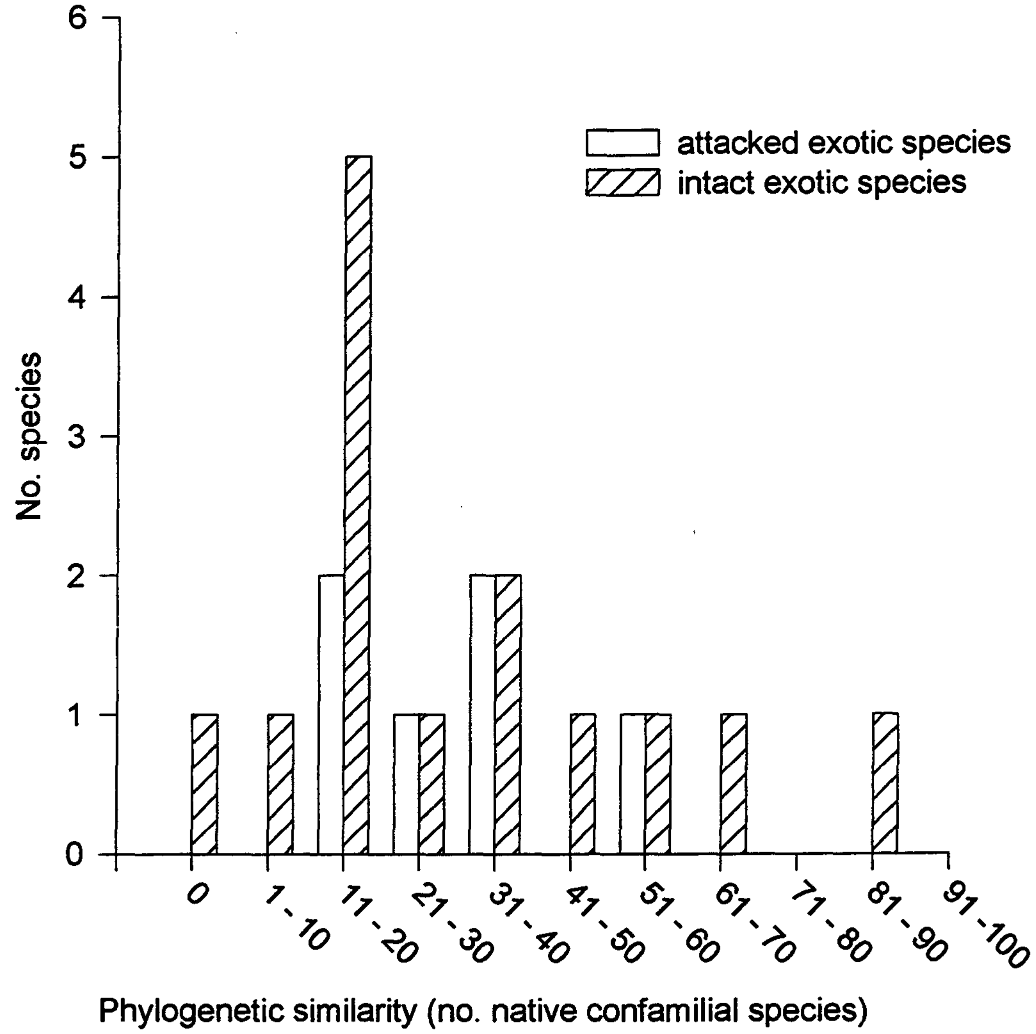

Figure 6.2. Frequency distribution of the numbers of local confamilial species for attacked and intact exotic species (including average intensities for the better represented families, see Table 6.1).

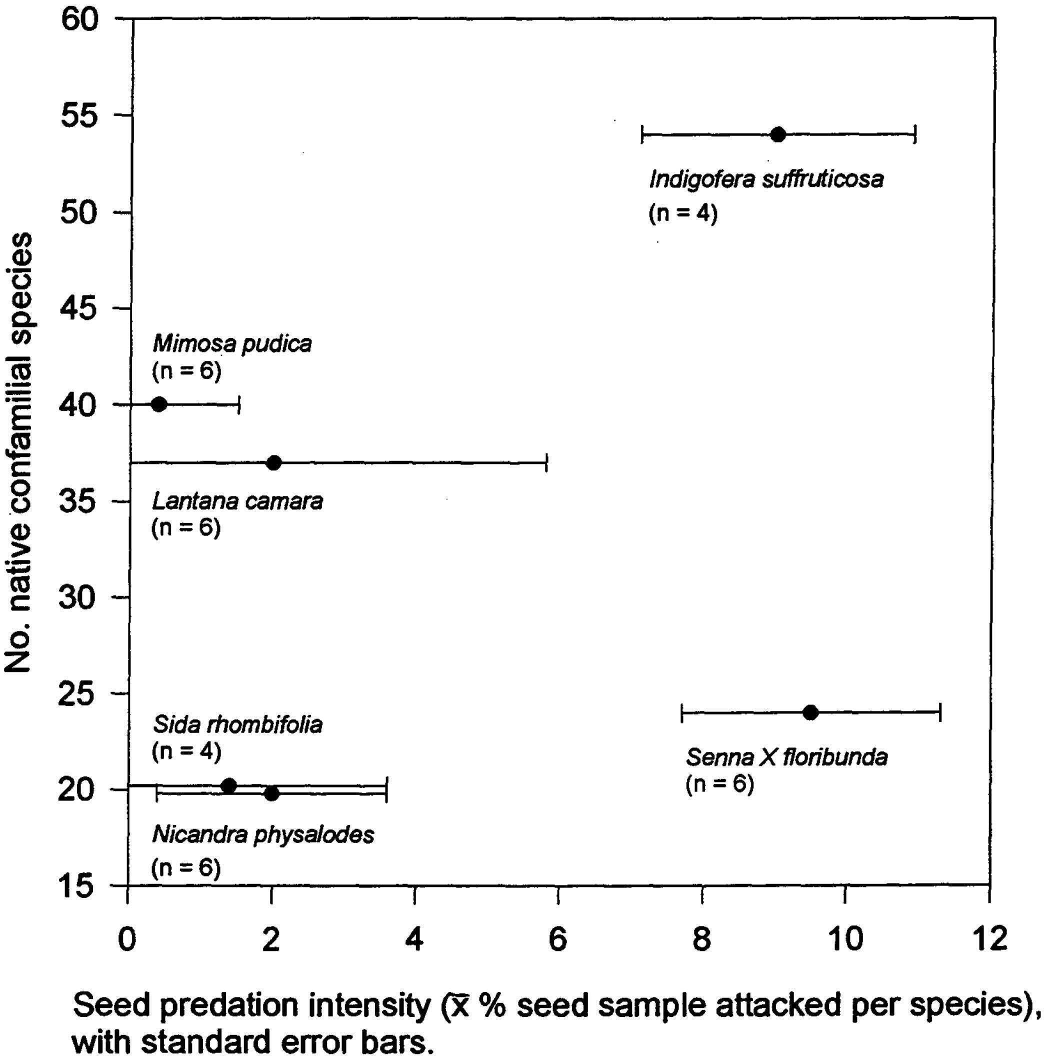

Figure 6.3. Seed predation intensities for attacked exotic species and their phylogenetic similarity to the local native rainforest flora, indicated by the number of native species belonging to each of their taxonomic families.

apparent between exotic species and native species in the proportions of individuals within species that were attacked (Fig. 6.4). This suggests that there was simply a greater proportion of exotic plants than native plants that are not host to any seed predators.

As relatively recent arrivals to an ecosystem exotic plant species may have characteristics that are new to potential seed predators. Exotic species will be attacked once there has been sufficient time for potential seed predator species to encounter them, and evolve means of finding and exploiting them. Until then, exotic plant species may have a lower chance of being attacked by any insect predispersal seed predators than native species.

The colonisation of exotic plant species by phytophagous insects begins when insects evolved to exploit native species make mistakes in host plant identification and oviposit on species that are not normally their host (Bernays and Funk 1999, Fox and Lalonde 1993). If the eggs of an insect seed predator, for example, hatch and some larvae are able to grow and develop on a new host plant the seed predator species may begin to evolve a different host range.

For an exotic species of plant to be mistakenly attacked by a species of insect seed predator both species must occur in the same habitat. This principle has greater support from herbivory studies (Fraser and Lawton 1994, Strong et al. 1984) and may explain, for example, why specialist insect herbivores of *Solidago virgaurea*, a native of Switzerland, have yet to colonise the closely related exotic *S. altissima*. These

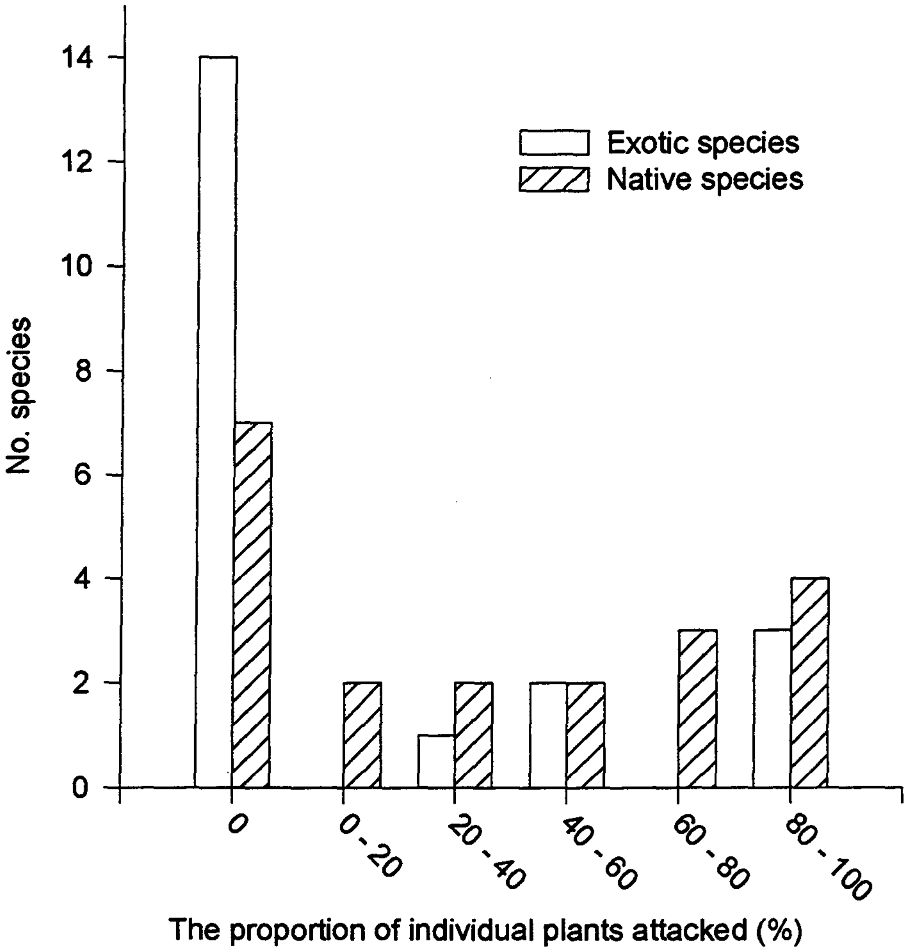

Figure 6.4. Frequency distributions of the proportions of individual plants belonging to exotic and native species that were attacked. Note: a maximum of six individual plants were sampled per species (see text 6.2.1).

plant species do not appear to grow in the same habitat, thus insect herbivores of one species will not encounter the other species as a new potential host (Jobin et al. 1996). The vulnerability of an exotic species of plant to colonisation by an insect phytophage species is also dependent on their relative distributions in time as well as in space. Thus the phenology of a plant species and the natural history of any potential insect phytophages can also be important (Kogan 1991, Strong et al. 1984). Again examples come from studies of herbivory. Slansky (1976) for example suggests that although the butterfly *Pieris virginiensis* is able to feed on a number of plant genera within its natural habitat it is restricted to *Dentaria sp.* partly because of its phenology.

The chemical and morphological characteristics of exotic plant species may further lower the probability that they will be attacked by insect seed predator species. The chemistry of exotic plants is important for two main reasons. Firstly, if an exotic plant possesses secondary compounds that are novel to potential seed predator species it may not be recognised as a potential host plant (Bernays and Chapman 1994, Connor 1991, Jermy 1993). Secondly, exotic plants may have novel secondary compounds which have inhibitory or toxic properties (Dowell et al. 1990, Janzen 1977, Olckers and Hulley 1989, Pajni 1987, Wiseman et al. 1996). To be able to exploit a new species of plant potential seed predator insects would have to evolve the ability to cope with these compounds. The presence of these compounds can therefore restrict the number of insect species that may be able to exploit a species of plant (eg Lindroth 1991). Such insects tend to be generalists that already have a broad host range (Jobin et al. 1996, Wilson and Flanagan 1993). Morphological characteristics that can reduce the access insect seed predators have to seeds, such as thick woody endocarps or trichomes can further reduce the number of potential seed predator species that may be capable of attacking an exotic species of plant (Janzen 1977, Johnson and Siemens 1991).

Because there are many possible factors that may contribute to the relatively low vulnerability of exotic species to predispersal seed predation by insects, it is not possible to say why particular exotic species in this study were not affected. The reasons for this will probably differ from species to species. To determine why an exotic species of plant was not attacked by seed predators can only be determined by studying the plant, the insects most likely to attack them and their native host plants. However, there is one general reason that may explain why some exotic species of plant were attacked whereas others were not: those exotic species of plant most likely to be colonised by phytophagous insects may be those that are associated with closely related native species (Connor 1991, Kogan 1991).

The reason why exotic species that are closely related to local native plants are most likely to be attacked by predispersal insect seed predators is because phytophagous insects are generally adapted to feeding on a limited range of similar species (eg. Dilawari et al. 1998, Huber and Vasssieres 1990) under a limited range of environmental conditions (Bernays and Chapman 1994). If they expand or switch their host range this is often towards species that are related to the original host and that have a similar phenology (Kogan 1991), secondary chemistry (Dowell et al. 1990, Fay 1996, Strong et al. 1984) and possibly similar habitat requirements. This current study did not however find a relationship between the vulnerability of exotic species to predispersal seed predation by insects and their phylogenetic similarity to native species. There are a number of possible reasons for this including methodological shortfalls.

There are three reasons why the methods used in this study were not ideal:

1) Taxonomic relationships between plants do not always follow their phylogenetic relationships (eg Chase et al. 1993, Judd and Kron 1993, Judd and Manchester 1997). To use taxonomic relationships between species as a means of indicating phylogenetic relationships is to make inferences on past processes (the evolutionary history of organisms) based on information derived mainly from the present. As there are no sources of information from another time, no truly independent tests of these inferences are possible. The closest thing to an independent test of an inferred evolutionary relationship, based on extant species, is the fossil record. However, the significance of fossils are based on interpretations of their age, which is dependent on geological interpretations, and interpretations of their similarity to extant forms.

Furthermore these inferences on the evolutionary history of the organisms are inferences on their genetic similarities/differences based primarily on morphological attributes. Inferences on their genetic similarity (and hence relatedness) based on morphology can be confused because similar structures shared by species (homologies) may sometimes have different developmental origins and hence a different genetic basis. This is known as convergence or parallelism. Conversely, structures homologous across species may not be identified as such if they differ greatly and intermediate forms are not found. Reversals, where a derived character state changes with time back to an earlier state, form will also add to misinterpretations (Judd et al 1999). Biochemical characteristics are less susceptible to such misinterpretations, while genetic sequencing, by providing a much greater range of (molecular) characters, is even less so, although these problems still occur (Judd et al 1999).

2) The method used to determine the index of taxonomic affiliation may not have been the best. The rainforest species listed in Cooper and Cooper (1994) come from an area that extends well beyond the Atherton Tablelands bioclimatic region and therefore would not have given an accurate index of the number of native species that might have been associated with closely related exotic species. Because of this, the total number of native confamilial species possibly associated with each exotic species would have been overestimated. Also, the relative numbers of confamilial species possibly associated with each exotic species may have been inaccurate. This is because the relative degree to which different plant families are represnted on the Atherton Tablelands, in terms of species, may differ from their representation on the species list of Cooper and Cooper (1994). An alternative method of assessing how many local native rainforest species belong to the same family as a particular exotic species is to use herbarium records. For an exotic species, only the native confamilial species that have been found within a certain distance, as represented among herbarium specimens, could be counted for the index.

3) Phylogenetic relationships may not reflect the ecological similarity of species. There are a number of reason why this is so. This, for example, may be because phylogenetic relationships between species, being inferred by taxonomic relationships, are not necessarily based on the same set of traits that characterise a plants ecological interactions. Two species that are very similar in terms of their morphological characteristics, including fruit structure, might be expected to be equally susceptible to attack by IPSPs. However, the two species may establish under different conditions, one growing in disturbed high light environments while the other under stable shady conditions. As a consequence of this, the high light species may produce many more fruit and seeds per stem than the shade dwelling species and be under lower selective pressure to synthesise defensive secondary compounds than the less fecund shade dwelling species. This may mean that the more fecund species is more vulnerable to attack by IPSP than the less fecund shade dwelling species.

Another reason why phylogenetic relatedness and taxonomic similarity may not parallel ecological similarity is because taxa do not evolve and diversify at the same rates. Hence some taxonomic families contain a great diversity of species while other taxonomic families contain very few species. If taxonomic nomenclature is used as a guide to how closely related species are, the species of a family that is diverse in a region (eg. the Proteaceae of Queenslands's wet tropics) will be considered to be as closely related as the species of a species poor family (eg the Lecythidaceae). But any random pairing of species from the Proteaceae is more likely to include species with different morphological and ecological characteristics than a random pair selected from the less diverse family. Hence the native confamilial species listed for one exotic species may be closely related while the native confamilial species listed for another exotic species may include distantly related species.

Other factors, apart from how ecologically similar exotic and native species are, can also affect the vulnerability of exotic species to predispersal insect seed predation, such as the geographical range of the species (Strong et al. 1977 and 1984) and the length of period for which they have been introduced (Strong et al. 1984). As the geographical range of an exotic plant species increases, so does the total number of phytophagous insects it supports (Leather 1985, 1991, Strong et al. 1977, 1984). This is probably because the broader the distribution of an exotic plant the more opportunity there has been for potential phytophagous insects to encounter it - initiating the process of host expansion. It follows that exotic species with an extensive distribution may have a greater chance of being attacked by insect predispersal seed predators than species with a limited distribution.

The period of time over which an exotic species has occupied an area may also affect its vulnerability to insect predispersal seed predation because this also affects the opportunity potential insect phytophages have had to encounter and colonise it. With time there may also be a greater chance that genetic variations in populations of potential insect phytophages have occurred, allowing for example, changes in host recognition or oviposition preferences (see Jermy 1993, Via 1990). The geographic range of exotic species may however be a better predictor of vulnerability to insect predispersal seed predation than its residency time. This is because insect species can expand their host range relatively quickly (eg. Fay 1996, Hsiao 1986) and so the recruitment of new insect phytophages by an exotic species can asymptote within just one to two hundred years (Strong et al. 1984). If an exotic species has occupied a region for around a hundred years, the number of insect phytophage species it has accumulated may well have already stabilised. Hence, the vulnerability of that exotic species to insect predispersal seed predation is unlikely to change any further over time.

CHAPTER 7: GENERAL DISCUSSION AND CONCLUSIONS

Abstract

Because seed predation reduces the availability of viable seeds, potentially reducing seedling recruitment, seed predation may suppress population growth in host species. IPSPs are most likely to suppress population growth for plant species that; 1) are native rather than exotic, 2) produce fruit lacking a thick hard pericarp layer, 3) belong to the Euphorbiaceae and Sapindaceae. Light dwelling species may also be more susceptible to IPSP than shade dwelling species. However, tropical rainforests are very complex ecosystems. The availability of seeds and the effect this has on the adult abundance of species will be affected by other factors. Hence the degree to which adult densities could respond to seed predator release will vary from species to species. The effect of IPSP on the species composition of a rainforest community must therefore be interpreted within the context of other possible factors. To provide examples of how other factors may modify the effect of IPSP on seed availability and adult densities for different species, the additional effects of two factors will be discussed in detail: postdispersal seed predation and seed longevity. This discussion concludes with an overview of further research that would help clarify some of the issues developed in this thesis.

7.1 The vulnerability of plants to IPSP

The results of the experimental chapters allows groups of species to be ranked in their relative vulnerability to IPSP. Attributes associated with the vulnerability of plants to IPSP are shown in Table 7.1. The results show:

1) Native plant species were clearly more vulnerable to IPSP than exotic species.

2) Species with a thick hard pericarp layer were clearly less vulnerable to IPSP than species without such a layer.

3) The vulnerability of species to IPSP varied from family to family, although these family differences were not so clear - the Euphorbiaceae and possibly the Sapindaceae appeared to be particularly vulnerable to IPSP whereas the Lauraceae was particularly invulnerable.

4) Species fruiting in high light conditions appeared to be more vulnerable to IPSP than shade-dwelling species, but this difference was not strongly supported.

Table 7.1 Attributes associated with the vulnerability of plants to IPSP, ranked according to the strength of association indicated by p-values.

Species attribute	P value for association (Seed predation survey)[1]	Additional studies	Rank importance as a differentiating factor
Indigeneity	$p = 0.005$	$0.025 > p > 0.013$[2]	1
Hard pericarp thickness	$p = 0.006$		2
Taxonomic family	$p = 0.009$		3
Light availability	$p = 0.166$	$p = 0.029$[3]	4

[1] P values from tests of association Chapter 4.

[2] P value for test of association in Chapter 6.

[3] P value for test of association in Chapter 5.

Although the current data cannot be used to rank individual species according to their vulnerability to IPSP, some species did stand out as being particularly vulnerable or immune to attack. The few species that had IPSP intensities of over 30% were considered vulnerable. These were native species that fruited in high light conditions and had soft and/or thin seed coats (Table 7.2). The species that appeared to be quite immune to attack by IPSPs included both exotics and natives - most of which had either a protective pericarp layer of some kind, or were shade dwelling (Table 7.3).

Table 7.2 Species that appeared to be particularly vulnerable to IPSP and the attributes they possess that were related this vulnerability. *

Species	Family	Species attributes			
		Native	Pericarp soft and thin	Pericarp hairy or resinous	High - light dwelling
Glochidion harveyanum	Euphorbiaceae	●	●		●
Mallotus mollissimus	Euphorbiaceae	●	●	●	●
Toona ciliata	Meliaceae	●	●		●
Dendrocnide photinophylla	Urticaceae	●	●		●
Acmena resa	Myrtaceae	●	●		●

* For each species five or more individual plants had been sampled over the course of the study. Species represented by less than five individuals were excluded from this table because such a limited sample size was considered insufficient to provide evidence of consistent vulnerability to attack.

7.2 Possible effects of IPSP on species abundance

Because seed predation reduces the availability of viable seeds, potentially reducing seedling recruitment, seed predation may suppress population growth in host species. However, this effect will only be apparent if comparisons are made between plant populations that are attacked by seed predators and plant populations from which

Table 7.3 Species that appeared to be particularly immune to IPSP and the attributes they possess that were related to this lack of vulnerability. *

Species	Family	Species attributes			
		Exotic	Pericarp hard and thick	Pericarp hairy or resinous	Shade dwelling
Alphitonia petriei	Rhamnaceae		•		
Melia azedarach	Meliaceae		•		
Schizomeria whitei	Cunoniaceae		•		
Dendrocnide moroides	Urticaceae			•	
Pittosporum rubiginosum	Pittosporaceae			•	
Cordyline cannifolia	Agavaceae				•
Hodgkinsonia frutescens	Rubiaceae				•
Mackinlaya macrosciadia	Araliaceae				•
Rapanea subsessilis	Myrsinaceae				•
Callicarpa longifolia	Verbenaceae				
Polyscias elegans	Araliaceae				
Cascabela thevetia	Apocynaceae	•	•		
Coffea arabica	Rubiaceae	•			•
Rivina humilis	Phytolaccaceae	•			•
Cinnamomum camphora	Lauraceae	•			
Citrus sinensis	Rutaceae	•			
Duranta erecta	Verbenaceae	•			
Ligustrum lucidum	Oleaceae	•			
Ligustrum sinensis	Oleaceae	•			
Macrotyloma axillare	Fabaceae	•			
Solanum mauritianum	Solanaceae	•			
Solanum seaforthianum	Solanaceae	•			
Solanum torvum	Solanaceae	•			
Tristemma mauritianum	Melastomataceae	•			
Turbina corymbosa	Convolvulaceae	•			

* For each species five or more individual plants had been sampled over the course of the study. Species represented by less than five individuals were excluded from this table because such a limited sample size was considered insufficient to provide evidence of consistent vulnerability to attack.

seed predators have been excluded (eg. Brown and Heske 1990, Davidson et al. 1984, Inouye et al. 1980, Louda 1982a, Putz et al. 1990). The effect of seed predation on plant populations and the composition of a rainforest is thus best described in terms of the changes that may occur if seed predation pressure is lifted.

Seed availability for species that were immune to IPSP (Table 7.3) would not be expected to change as a direct result of an absence of IPSPs. However, the seed availability for species that are vulnerable to IPSP may change in the absence of seed predation. Thus:

1) Native species may be expected to increase in abundance to a greater degree than exotic species.

2) Species without a hard thick pericarp may be expected to increase in abundance to a greater degree than species with a hard thick pericarp.

3) Euphorbiaceous and possibly Sapindaceous species may be expected to increase in abundance to a greater degree than Lauraceous species.

4) Light dwelling species may possibly increase in abundance to a greater degree than shade dwelling species.

The species most likely to increase in abundance are those most vulnerable to IPSP (Table 7.2). These particular species are already fairly common in some rainforest types and with a release of seed predation pressure they could become dominant species. However, other factors in addition to IPSP can also affect seed availability and the abundance of adults, and these factors may be subject to interspecific variation (Fig. 7.1). Consequently the degree to which adult densities may respond to seed

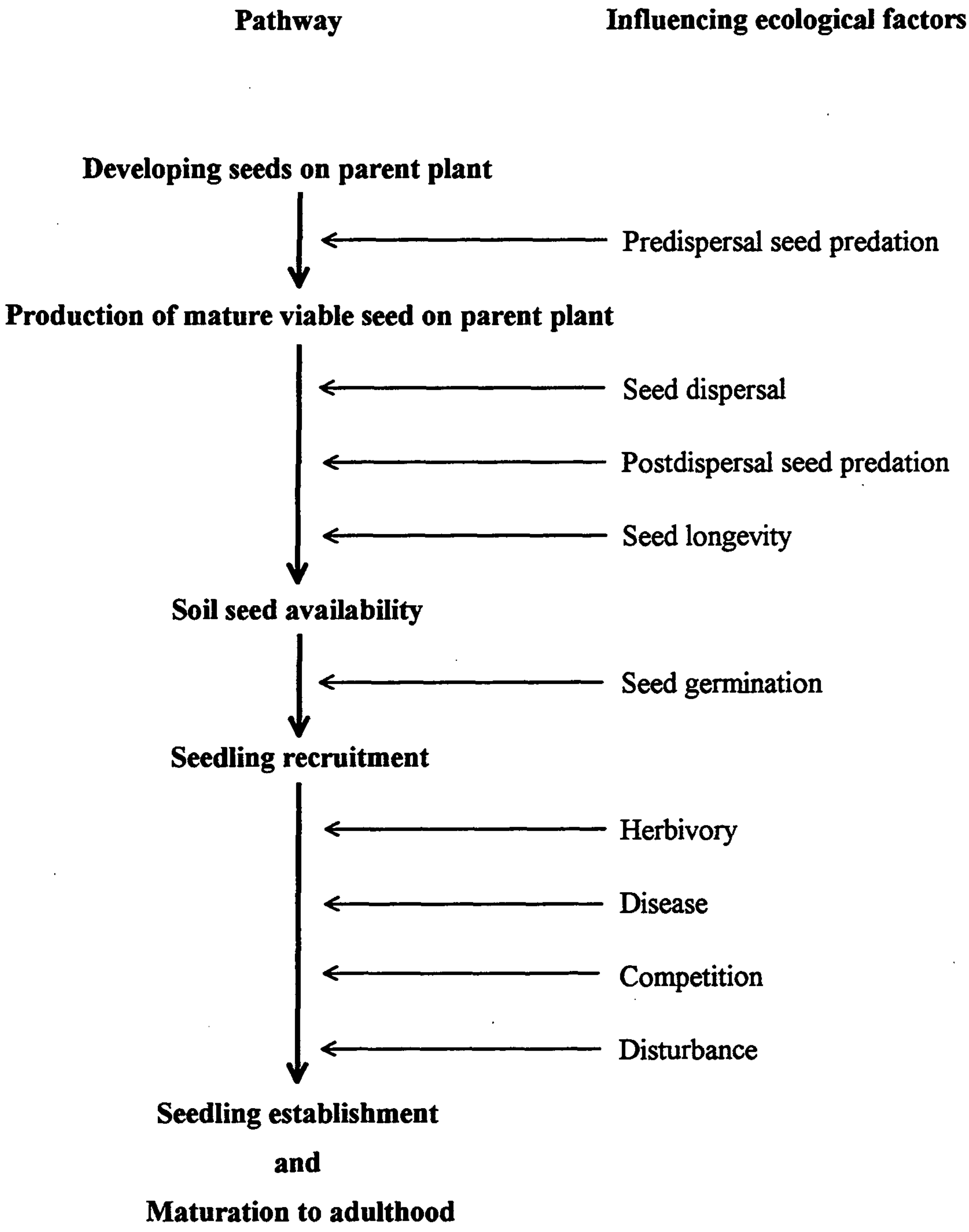

Figure 7.1 The pathway that seeds take from their development on the parent plant to their maturity as adults and the factors that may alter their abundance along this path.

predator release will vary from species to species. The effect of IPSP on the species composition of a rainforest community must therefore be interpreted within the context of these other factors. As an example of how additional factors may interact with and modify the effect of IPSP on seed availability and adult densities for different species, two factors will be discussed in detail: postdispersal seed predation and seed longevity.

7.3 Factors that may modify the effects of IPSP on species abundance

7.3.1 Postdispersal seed predation

Postdispersal seed predation may exacerbate the effects of IPSP on seed availability by increasing seed loss. In the absence of IPSP, postdispersal seed predation can still limit the numbers of seeds that reach the forest floor and survive to germinate. Potential increases in seed availability that could occur in the absence of IPSP may be suppressed by postdispersal seed predation. Therefore, postdispersal seed predation can mask the effects of IPSP on species abundances and forest composition. In the rainforests of the North Queensland dispersed seeds are eaten by rodents, pigs, Musky rat-kangaroos and insects (Dennis 1997, Lott et al. 1995, Osunkoya 1994). Thus the influence of IPSPs on the relative availability of seeds of different species may be mitigated by another set of seed predators. At the most general level however, postdispersal seed predators (particularly rodents) would appear to actually reinforce any patterns of seed loss across species that are caused by IPSPs. This is because one of the factors that appears to reduce the vulnerability of seeds to IPSP; hard pericarp thickness, appears also to affect the vulnerability of seeds to postdispersal seed predation (Blate et al 1998, Osunkoya 1994).

Direct support for the effect of hard pericarp thickness on the vulnerability of seeds to postdispersal seed predation comes from Osunkoya (1994). This study compared postdispersal seed predation rates for 12 tree species on the Atherton Tablelands and found that their different rates of seed predation could partly be explained by diaspore size, albeit in a rather complex manner. However, the hard pericarp thickness - a factor not considered in the study, can also explain some of the differences in seed predation rate. Reanalysing the data from Osunkoya (1994) shows that across the 12 species studied there was a negative nonparametric correlation between hard pericarp thickness and mean postdispersal seed predation rate (Fig. 7.2). This association has also been found for the seeds of another tropical rainforest community (Blate et al. 1998). Of the five species identified in this study as being particularly vulnerable to IPSP (Table 7.2, Table 7.4) the relatively large seeded species *Acmena resa* is most likely to be consumed by vertebrate postdispersal seed predators as well. The other species may not be so vulnerable because their seeds are very small (Table 7.4) and could easily settle into leaf litter and soil where they are less likely to be found by vertebrates.

7.3.2 Seed longevity

Seed longevity may modify the effects of IPSP on seed availability because species that produce long-lived seeds can accumulate a high density of seeds in the soil (Fenner 1985, Garwood 1989). The presence of a soil seed bank provides a buffer against fluctuations in the input of new seeds. In contrast, plants with short-lived seeds tend to be poorly represented in the soil seed bank. Hence, if plants at a site were protected from IPSPs, allowing seed production to increase, seed availability

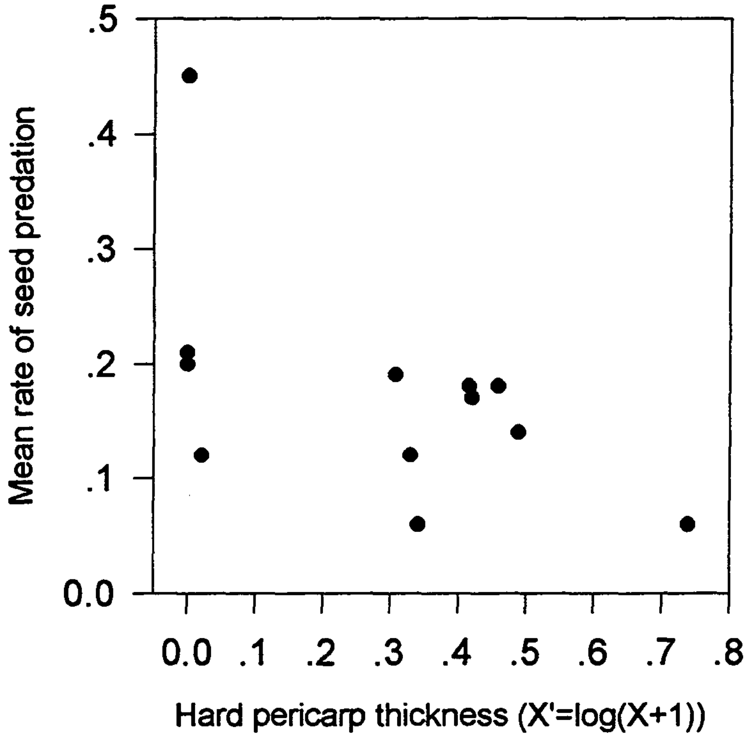

Figure 7.2. Plot showing the relationship between the hard pericarp thickness of 12 rainforest tree species and their mean rate of postdispersal seed predation measured in the study of Osunkoya (1994). This relationship is statistically significant (Spearman rank correlation, a = 0.05, $r_s = -0.627$, p = 0.029).

Table 7.4 Seed sizes* for the species most vulnerable to insect predispersal seed predation.

		Dry weight (mg)	Maximum dimension (mm)	Minimum dimension (mm)
Glochidion harveyanum	Euphorbiaceae	8.6	5	2.4
Mallotus mollissimus	Euphorbiaceae	7.3	3	2.2
Toona ciliata	Meliaceae	2	4.7	0.4
Dendrocnide photinophylla	Urticaceae	0.5	1.5	0.6
Acmena resa	Myrtaceae	195	9.7	7.7

* Seed sizes given are mean figures calculated from 12 seeds from one plant per species.

would be expected to increase by a greater proportion for species that produce short-lived seeds than for species with long-lived seeds (Fig. 7.3). This suggests that IPSP may not suppress seed availability for species with long-lived seeds to as great a degree as that for species with short-lived seeds.

Seed longevity has only been studied for a small subset of the species included in this current study (Hopkins and Graham 1987), so it is not possible to say directly which species are most likely to increase in availability in response to a drop in IPSP pressure and which species are not. There is, however, a close association between the presence of a hard pericarp layer around seeds and their ability to retain viabilityfor long periods of time (Hopkins and Graham 1987). Hence the availability of soft coated seed species could be expected to be more responsive to a decrease in IPSP than hard coated seeds (Fig. 7.4). Drawing from this association and the association between hard pericarp thickness and vulnerability to IPSP, some predictions may be made at the community level and at the species level.

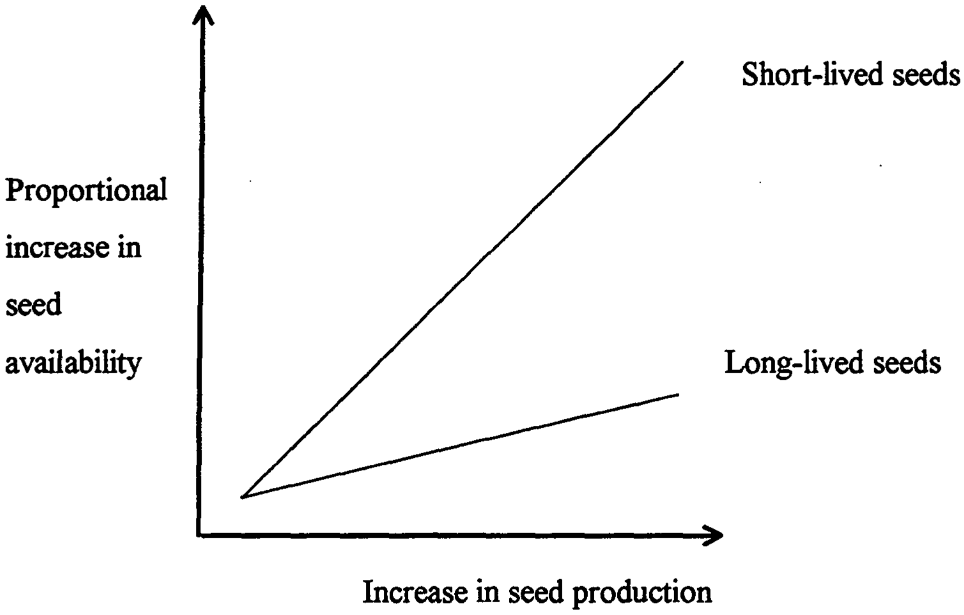

Figure 7.3. The degree to which seed availability at a site will respond to increases in seed production may be greater for short-lived seed species than for long-lived seed species, as densities of long-lived seeds in the soil tend to be buffered.

At the community level, the potential for high seed availability and possibly high adult densities is most likely to be suppressed in species that have soft pericarp layers. This is because these species are both the most vulnerable to IPSP and the least likely to form buffering seed banks. Among the species that produce seeds with a thin hard pericarp layer there is less chance that potential adult abundances are suppressed by IPSP.

Although species with thin hard pericarps are still vulnerable to IPSP, their seeds are likely to be long-lived and form seed banks. The species least likely to be suppressed in terms of high adult abundances are those with thick hard pericarps as they are least likely to be attacked by IPSPs, while most likely to form seed banks

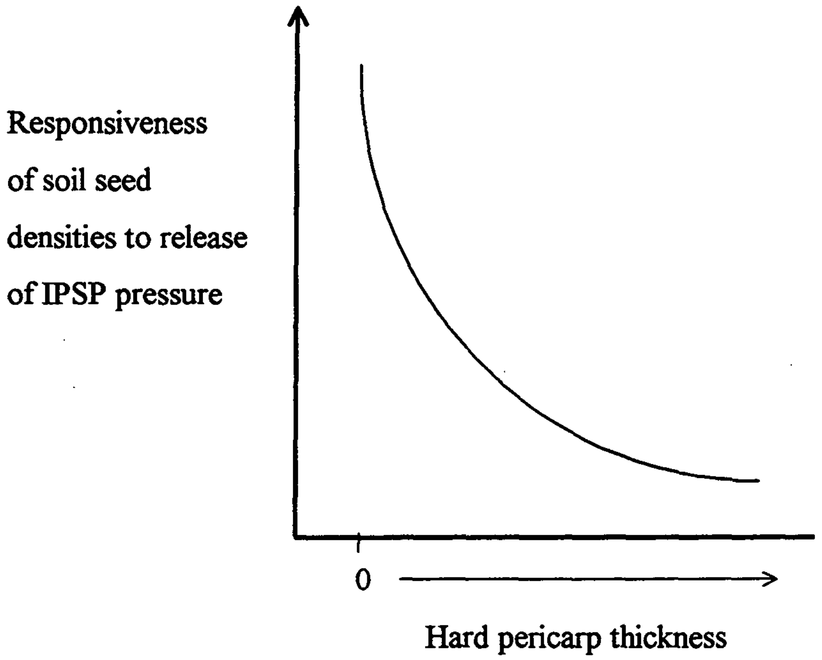

Figure 7.4 Soft coated seeds (no hard pericarp)are more likely to respond to a decrease in IPSP with an increase in seed availability than hard coated seeds as their availability is less likely to be buffered by seed banks.

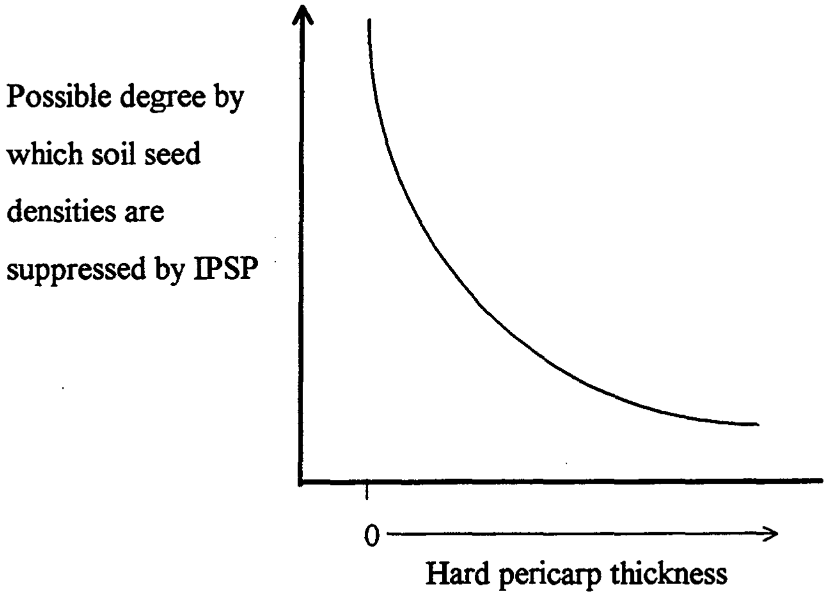

Figure 7.5 The combined effects of hard pericarp thickness on seed longevity and vulnerability to IPSP may mean that the availability of seeds with soft coatings are most likely to be suppressed by IPSP whereas the availability of seeds of species with thick hard seed coats are least likely to be suppressed by IPSP.

In this current study, *Acmena resa* and *Toona ciliata* are probably suppressed by IPSP to the greatest degree in terms of seed availability and seedling abundance. Not only are these species relatively vulnerable to IPSP, but they appear unlikely to form a seed bank as they do not have a hard pericarp layer.

7.4 Conclusions

1) IPSP is more likely to cause reductions in seed availability and suppress population growth for rainforest species that;

a) are native rather than of exotic origin.

b) have soft, thin fruit pericarps rather than hard, thick fruit pericarps.

c) belong to the Euphorbiaceae, and possibly the Sapindaceae.

d) do not produce long-lived seeds that form persistent soil seed banks.

Light dwelling species may also be more susceptible to IPSP than shade dwelling species.

However, it is unlikely that any species in the rainforest will show a dramatic increase in recruitment and adult population densities in the absence of IPSP. Single factors, such as seed predation may have dramatic effects on species composition and community dynamics in simple plant communities, such as deserts (Brown and Heske 1990, Davidson 1993, Davidson et al. 1984 and 1985, Inouye et al. 1980). In contrast, more complex communities a greater number of factors may affect plant population densities. The complexity of tropical rainforest ecosystems means that the effects of a single factor are likely to be confounded by other processes acting upon seed or plant survival.

For example, even if the availability of *Toona ciliata* seeds were to increase in the absence of IPSP, its population density may still be limited by the effects of herbivores. This is because *T. ciliata* is host to a shoot boring moth (*Hypsipyla robusta* - Red Cedar Tip Moth), which coincidentally is the same species that attacks the seeds. At high host densities this moth can cause extensive damage to growing plants, making plantations of this species impractical (Campbell 1998, Mo et al. 1997). It is therefore possible that under natural conditions population densities of *T. ciliata* may not increase as a result of increases in seed availability.

Furthermore, where there are greater numbers of species, there is more potential interspecific variation in response to any one factor. Hence as species richness increases, the combinations of species responses to factors such as seed predation, herbivory and competition might be expected to increase. Although seed predation may play a part in limiting the population density of potentially dominant plant species, as suggested by Janzen (1970), it is most likely to apply to particular species under a limited set of circumstances.

7.5 Further research

7.5.1 The vulnerability of rainforest plant species to IPSP

This current study has identified associations between levels of IPSP in rainforest plants and four different factors: hard pericarp thickness, host indigeneity, phylogeny and light availability. The evidence supporting two of these associations (phylogeny and light availability) is however very limited. Further research is required to confirm, qualify or reject the generality of these associations.

Host plant phylogeny

There are many well represented plant taxonomic families in Queenslands rainforests that could be compared for their vulnerability to IPSP. Attendant chemical assays could investigate whether family-level differences are due to secondary defence compounds.

Light availability

Confirming the association between light availability and a plants vulnerability to IPSP would contribute to developing theories on plant resource allocation and the effects of resource availability on plant defenses. This information would also show if the vulnerability of species to IPSP varies according to their successional status: eg. low-growing shade-dwelling species vs tall-growing, canopy-dwelling species. To confirm the association between host plant light availability and IPSP levels, plant stature and growth form would also have to be studied as possibly confounding factors.

Another logical step in research into IPSP would be to explore the mechanisms which underlie the significant associations that arose from this study. For example:

1) Are plant species with hard thick pericarps less vulnerable to IPSP than those without hard thick pericarps because they are simply attacked by a smaller number of

insect species?

2) Are exotic species less vulnerable to IPSP than native species because they are also attacked by a smaller number of insect species?

7.5.2 The effects of insect predispersal seed predation on the population dynamics of rainforest plants

This study has identified some species as being either vulnerable or relatively immune to IPSP. These species may be used to further the study of what effects IPSP may have on seed availability and recruitment.

Following the effect of seed availability through to adult plant population densities for most rainforest plants is clearly impractical because they are perennial with long generation periods. This is why the only studies that have so far linked the seed phase of a plant's life cycle to the adult phase have dealt with annuals and short-lived perennials (Baker and Normano 1975, Brown and Heske 1990, Borchert and Jain 1978, Davidson et al. 1984 and 1985, Greig-Smith and Sagar 1981, Inouye et al. 1980, Klinkhamer et al. 1988, Louda 1982a, 1982b, Putz et al. 1990, Risch and Carroll 1986). As an alternative to following a single cohort through a long period of time, different cohorts could be studied simultaneously, so the phase transitions from undispersed seeds to dispersed seeds or from seeds in soil to seedlings, for example, can be studied simultaneously. This information can be used to develop transitional matrices which can be used for modelling the population dynamics of species. This information can also be used to determine at what stage in the life-cycle of a plant are factors most likely to affect population sizes (eg. Pinero et al. 1984, Solbrig et al.

1990, Valverde and Silvertown 1998). Sensitivity analysis that compares plant species of different functional types could be used to determine:

1) how important IPSP is to plant population growth across species, in relation to other factors, and

2) what types of species are most sensitive to IPSP in terms of population growth.

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Appendix 1.

A list of the adult insect predispersal seed predators reared from the plants sampled for Chapter 4.

Host Species	Family	Seed Predator Species[1]	Family	Subfamily	Order
Acacia aulacocarpa	Mimosaceae	*Xerometra* (Meyrick, 1925) *sp. nr. crocina* (Meyrick 1904)	Gelechiidae	Dichomeridinae	Lepidoptera
Acacia cincinnata	Mimosaceae	*Xerometra* (Meyrick, 1925) *sp. nr. crocina* (Meyrick 1904)	Gelechiidae	Dichomeridinae	Lepidoptera
Acacia cincinnata	Mimosaceae	*Brachyacma palpigera* (Walsingham, 1891)	Gelechiidae	Dichomeridinae	Lepidoptera
Acacia cincinnata	Mimosaceae	"morpho sp. 117"	?	?	Hymenoptera
Acmena smithii	Myrtaceae	"morpho sp. 22"	Curculionidae	Anthribidae	Coleoptera
Acmenosperma claviflorum	Myrtaceae	"morpho sp. 9"	Curculionidae	?	Coleoptera
Acmenosperma claviflorum	Myrtaceae	*Isotenes* (Meyrick, 1938) *sp. miserana* (Walker, 1863)?	Tortricidae	Tortricinae	Lepidoptera
Acmenosperma claviflorum	Myrtaceae	*Conogethes haemactalis* (Snellen, 1890)	Pyralidae	Pyraustinae	Lepidoptera
Acronychia parviflora	Rutaceae	"morpho sp. 101"	?	?	Hymenoptera
Acronychia vestita	Rutaceae	*Ardozyga* (Lower, 1902) *'emeles'* (Turner)	Gelechiidae	Chelariinae	Lepidoptera
Alectryon semicinereus	Sapindaceae	*Isotenes* (Meyrick, 1938) *sp. miserana* (Walker, 1863)?	Tortricidae	Tortricinae	Lepidoptera
Brachychiton acerifolius	Sterculiaceae	"morpho sp. 11"	Curculionidae	?	Coleoptera
Brachychiton acerifolius	Sterculiaceae	*Pyroderces* (Herrich-Schaffer, 1853) *sp.*	Cosmopterigidae	Cosmopteriginae	Lepidoptera
Calamus moti	Arecaceae	"morpho sp. 112"	?	?	Hymenoptera
Casearia dallachii	Flacourtiaceae	? (Tribe: Eucosmini)	Tortricidae	Olethreutinae	Lepidoptera
Castanospora alphandii	Sapindaceae	"morpho sp. 13"	Curculionidae	?	Coleoptera
Castanospora alphandii	Sapindaceae	?	?	?	Hymenoptera
Crotalaria pallida[2]	Fabaceae	"morpho sp. 38"	?	?	Lepidoptera
Cryptocarya putida	Lauraceae	"morpho sp. 21"	Curculionidae	Anthribidae	Coleoptera
Daphnandra repandula	Monimiaceae	"morpho sp. 8"	Curculionidae	?	Coleoptera
Daphnandra repandula	Monimiaceae	"morpho sp. 83"	?	?	Lepidoptera

Appendix 1. Continued…

Host Species	Family	Seed Predator Species [1]	Family	Subfamily	Order
Delonix regia [2]	Caesalpiniaceae	*Cryptophlebia ombrodelta* (Lower, 1898)	Tortricidae	Olethreutinae	Lepidoptera
Delonix regia [2]	Caesalpiniaceae	"morpho sp. 91"	?	?	Hymenoptera
Diospyros cupulosa	Ebenaceae	"morpho sp. 10"	Curculionidae	?	Coleoptera
Eugenia reinwardtiana	Myrtaceae	*Baris sp.* 1	Curculionidae	Baridinae	Coleoptera
Flindersia brayleyana	Rutaceae	"morpho sp. 2"	Curculionidae	Cryptorhynchinae	Coleoptera
Flindersia brayleyana	Rutaceae	"morpho sp. 22"	Curculionidae	Anthribidae	Coleoptera
Glochidion harveyanum	Euphorbiaceae	"morpho sp. 1"	Curculionidae	?	Coleoptera
Glochidion harveyanum	Euphorbiaceae	*Conogethes haemactalis* (Snellen, 1890)	Pyralidae	Pyraustinae	Lepidoptera
Glochidion harveyanum	Euphorbiaceae	"morpho sp. 81"	Gracillariidae	?	Lepidoptera
Glochidion harveyanum	Euphorbiaceae	"morpho sp. 86"	Tortricidae	Olethreutinae	Lepidoptera
Glochidion hylandii	Euphorbiaceae	*Conogethes haemactalis* (Snellen, 1890)	Pyralidae	Pyraustinae	Lepidoptera
Glochidion hylandii	Euphorbiaceae	*Coscinoptycha improbana* (Meyrick, 1881)	Carposcinidae	?	Lepidoptera
Glochidion hylandii	Euphorbiaceae	"morpho sp. 81"	Gracillariidae	?	Lepidoptera
Guettardella tenuiflora	Rubiaceae	"morpho sp. 106"	?	?	Hymenoptera
Harpullia pendula	Sapindaceae	*Opogona* (Zeller, 1853) *sp.*	Tineidae	Hieroxestinae	Lepidoptera
Mallotus mollissimus	Euphorbiaceae	"morpho sp. 138"	?	?	Hymenoptera
Mallotus paniculatus	Euphorbiaceae	*Conogethes* (Meyrick, 1884) *sp.*	Pyralidae	Pyraustinae	Lepidoptera
Mallotus paniculatus	Euphorbiaceae	"morpho sp. 85"	Gracillariidae	?	Lepidoptera
Mallotus paniculatus	Euphorbiaceae	"morpho sp. 95"	?	?	Hymenoptera
Mallotus repandus	Euphorbiaceae	"morpho sp. 138"	?	?	Hymenoptera
Melicope elleryana	Rutaceae	"morpho sp. 1"	Curculionidae	?	Coleoptera
Mischocarpus lachnocarpus	Sapindaceae	"morpho sp. 74"	Cosmopterigidae	Cosmopteriginae	Lepidoptera
Mischocarpus stipitatus	Sapindaceae	"morpho sp. 95"	?	?	Hymenoptera
Parsonsia latifolia	Apocynaceae	*Baris sp.* 2	Curculionidae	Baridinae	Coleoptera

Appendix 1. Continued…

Host Species	Family	Seed Predator Species [1]	Family	Subfamily	Order
Pavetta australiensis	Rubiaceae	"morpho sp. 129"	?	?	Hymenoptera
Phaleria octandra	Thymelaeaceae	*Calliphara imperialis*	Scutelleridae	?	Hemiptera
Phaleria octandra	Thymelaeaceae	"morpho sp. 134"	?	?	Hymenoptera
Sarcopteryx montana	Sapindaceae	"morpho sp. 39"	?	?	Lepidoptera
Schizomeria whitei	Cunoniaceae	*Haplonix sp*?	Curculionidae	Haplonychini	Coleoptera
Senna occidentalis [2]	Caesalpiniaceae	*Isotenes* (Meyrick, 1938) *sp. miserana* (Walker, 1863)?	Tortricidae	Tortricinae	Lepidoptera
Siphonodon membranaceus	Celastraceae	*Isotenes* (Meyrick, 1938) *sp. miserana* (Walker, 1863)?	Tortricidae	Tortricinae	Lepidoptera
Siphonodon membranaceus	Celastraceae	"morpho sp. 92"	Eurytomidae?	?	Hymenoptera
Syzygium alatoramulum	Myrtaceae	*Microcolona characta* (Meyrick, 1897)	Blastodacnidae	?	Lepidoptera
Syzygium sayeri	Myrtaceae	*Baris sp.* 1	Curculionidae	Baridinae	Coleoptera
Toechima erythrocarpum	Sapindaceae	"morpho sp. 14"	Curculionidae	?	Coleoptera
Zanthoxylon ovalifolium	Rutaceae	? (Tribe: Eucosmini)	Tortricidae	Olethreutinae	Lepidoptera
Zanthoxylum veneficum	Rutaceae	?	?	?	Hymenoptera

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[1] Specimens of the Lepidoptera and Hymenoptera are lodged with the Australian National Insect Collection, Canberra and specimens of the Coleoptera are lodged at the Natural History Museum, London and Queensland Department of Primary Industries, Mareeba.

[2] Introduced species

Appendix 2.

The adult insect predispersal seed predators reared from the plants sampled for Chapter 6.

Host species	Family	Seed Predator Species*	Family	Subfamily	Order
Exotics					
Crotalaria pallida	Fabaceae	"morpho sp. 35"			Hemiptera
Crotolaria pallida	Fabaceae	*Brachyacma palpigera* (Walsingham, 1891)	Gelechiidae	Dichomeridinae	Lepidoptera
Delonix regia	Caesalpiniaceae	*Cryptophlebia ombrodelta* (Lower, 1898)	Tortricidae	Olethreutinae	Lepidoptera
Delonix regia	Caesalpiniaceae	"morpho sp. 91"			Hymenoptera
Desmodium uncinatum	Fabaceae	*Hypena conscitalis* (Walker, 1866)	Noctuidae	Hypeninae	Lepidoptera
Senna occidentalis	Caesalpiniaceae	"morpho sp. 97"			Hymenoptera
Senna X floribunda	Caesalpiniaceae	*Cryptophlebia ombrodelta* (Lower, 1898)	Tortricidae	Olethreutinae	Lepidoptera
Natives					
Alpinia caerulia	Zingiberaceae	"morpho sp. 104"			Hymenoptera
Daphnandra repandula	Monimiaceae	"morpho sp. 8"	Curculionidae		Coleoptera
Glochidion harveyanum	Euphorbiaceae	*Conogethes haemactalis* (Snellen, 1890)	Pyralidae	Pyraustinae	Lepidoptera
Glochidion harveyanum	Euphorbiaceae	"morpho sp. 86"	Tortricidae	Olethreutinae	Lepidoptera
Glochidion harveyanum	Euphorbiaceae	"morpho sp. 162"			Diptera
Glochidion harveyanum	Euphorbiaceae	"morpho sp. 165"			Diptera
Helichrysum rupicola	Asteraceae	"morpho sp. 65"	Gracillariidae?		Lepidoptera
Pavetta australis	Rubiaceae	"morpho sp. 129"			Hymenoptera
Pavetta australis	Rubiaceae	"morpho sp. 133"			Hymenoptera

Appendix 2. Continued…

Host species	Family	Seed Predator Species*	Family	Subfamily	Order
Ripogonum papuanum	Smilaceae	*Batrachedra* (Herrich-Schaffer, 1853) *sp.* 2		Batrachedridae	Lepidoptera
Toona ciliata	Meliaceae	*Hypsipyla robusta* (Moore, 1886)	Pyralidae	Phycitinae	Lepidoptera
Toona ciliata	Meliaceae	*Eucosma' aellaea* (Turner,1916) (Eucosma)	Tortricidae	Olethreutinae	Lepidoptera
Zanthoxylum veneficum	Rutaceae	?			Hymenoptera

* Specimens of the Lepidoptera and Hymenoptera are lodged with the Australian National Insect Collection, Canberra and specimens of the Coleoptera are lodged at the Natural History Museum, London and Queensland Department of Primary Industries, Mareeba.

Appendix 3.

A list of the adult insect predispersal seed predators reared from plants sampled for other studies additional to that of Chapters 4 and 6.

Host Species	Family	Seed Predator Species[1]	Family	Subfamily	Order
Acmena resa	Myrtaceae	*Coscinoptycha improbana* (Meyrick, 1881)	Carposinidae	?	Lepidoptera
Acmena resa	Myrtaceae	*Haplonix sp?*	Curculionidae	Haplonychini	Coleoptera
Acmena resa	Myrtaceae	*Cryptospasma sordida* (Turner, 1945)	Tortricidae	Olethreutinae	Lepidoptera
Alpinia modesta	Zingiberaceae	"morpho sp. 103"	?	?	Hymenoptera
Breynia stipitata	Euphorbiaceae	*Lampromicra senator* (Fabricius)	Scutelleridae	?	Hemiptera
Breynia stipitata	Euphorbiaceae	"morpho sp. 81"	Gracillariidae	?	Lepidoptera
Calamus moti	Arecaceae	"morpho sp. 77"	Oecophoridae	Stathmopodinae	Lepidoptera
Calamus moti	Arecaceae	"morpho sp. 112"	?	?	Hymenoptera
Corynocarpus cribbianus	Corynocarpaceae	"morpho sp. 22"	Curculionidae	Anthribidae	Coleoptera
Dendrocnide photinophylla	Urticaceae	"morpho sp. 141"	?	?	Hymenoptera
Dendrocnide photinophylla	Urticaceae	"morpho sp. 152"	?	?	Diptera
Emmenosperma alphitonioides	Rhamnaceae	"morpho sp. 161"	?	?	Diptera
Euodia sp. (Mountain Euodia)	Rutaceae	"morpho sp. 18"	Curculionidae	?	Coleoptera
Glochidion harveyanum	Euphorbiaceae	"morpho sp. 12"	Curculionidae	?	Coleoptera
Glochidion harveyanum	Euphorbiaceae	"morpho sp. 81"	Gracillariidae	?	Lepidoptera
Glochidion harveyanum	Euphorbiaceae	"morpho sp. 95"	?	?	Hymenoptera
Glochidion harveyanum	Euphorbiaceae	"morpho sp. 122"	?	?	Hymenoptera
Guettardella tenuiflora	Rubiaceae	"morpho sp. 127"	?	?	Hymenoptera
Guettardella tenuiflora	Rubiaceae	"morpho sp. 132"	?	?	Hymenoptera
Harpullia pendula	Sapindaceae	"morpho sp. 19"	Curculionidae	Anthribidae	Coleoptera
Harpullia pendula	Sapindaceae	*Isotenes* (Meyrick, 1938*) sp. miserana* (Walker, 1863)?	Tortricidae	Tortricinae	Lepidoptera

Appendix 3. Continued…

Host Species	Family	Seed Predator Species [1]	Family	Subfamily	Order
Mallotus mollissimus	Euphorbiaceae	*Physopelta familica?*	Largidae	?	Hemiptera
Mallotus phillipensis	Euphorbiaceae	*Calliphara imperialis*	Scutelleridae	?	Hemiptera
Mallotus phillipensis	Euphorbiaceae	*Cantao parentum* (White)	Scutelleridae	?	Hemiptera
Melicope elleryana	Rutaceae	"morpho sp. 106"	?	?	Hymenoptera
Melicope elleryana	Rutaceae	"morpho sp. 1"	Curculionidae	?	Coleoptera
Melicope elleryana	Rutaceae	"morpho sp. 106"	?	?	Hymenoptera
Mischocarpus lachnocarpus	Sapindaceae	"morpho sp. 74.2"	Cosmopterigidae	?	Lepidoptera
Mischocarpus lachnocarpus	Sapindaceae	"morpho sp. 90"	Cosmopterigidae	Cosmopteriginae	Lepidoptera
Polyalthia nitidissima	Annonaceae	"morpho sp. "	?	?	Hymenoptera
Prunus turneriana	Rosaceae	*Coscinoptycha improbana* (Meyrick, 1881)	Carposcinidae	?	Lepidoptera
Prunus turneriana	Rosaceae	"morpho sp. 22"	Curculionidae	Anthribidae	Coleoptera
Senna X floribunda [2]	Caesalpiniaceae	*Riptortis sp.*	Elididae	?	Hemiptera
Syzygium alatoramulum	Myrtaceae	*Microcolona characta* (Meyrick, 1897)	Blastodacnidae	?	Lepidoptera
Tetracera nordtiana	Dilleniaceae	"morpho sp. 22"	Curculionidae	Anthribidae	Coleoptera
Toona ciliata	Meliaceae	"morpho sp. 40"	?	?	Lepidoptera
Zanthoxylon ovalifolium	Rutaceae	"morpho sp. 68"	Tortricidae	Olethreutinae	Lepidoptera

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[1] Specimens of the Lepidoptera and Hymenoptera are lodged with the Australian National Insect Collection, Canberra and specimens of the Coleoptera are lodged at the Natural History Museum, London and Queensland Department of Primary Industries, Mareeba.

[2] Exotic species.