

## Root and shoot attributes of indigenous perennial accessions of the wild mungbean (*Vigna radiata* ssp. *sublobata*)

G. J. Rebetzke<sup>A</sup> and R. J. Lawn<sup>B,C</sup>

<sup>A</sup>Department of Agriculture, University of Queensland, St Lucia, Qld 4072; present address: CSIRO Plant Industry, PO Box 1600, Canberra, ACT 2601, Australia.

<sup>B</sup>School of Tropical Biology, James Cook University, Townsville, Qld 4811 and CSIRO Sustainable Ecosystems, Davies Laboratory, Townsville, Qld 4814, Australia.

<sup>C</sup>Corresponding author. Email: robert.lawn@jcu.edu.au

**Abstract.** Root and shoot attributes of 12 indigenous perennial accessions of the wild mungbean (*Vigna radiata* ssp. *sublobata*) were evaluated in early and late summer sowings in the field in SE Queensland. All but one of the accessions were obtained from the Townsville–Charters Towers region of NE Queensland. In both sowings, the accessions developed thickened tap and lateral roots, the taproot thickening extending to a depth of 0.20–0.30 m below the soil surface, depending on accession. The thickened lateral roots emerged from the taproot within 0.10 m of the soil surface, and extended laterally up to 1.10 m, remaining close to the soil surface. Differences among the accessions in gross root morphology and phenology were relatively small. There were differences among the accessions in the production of seed, tuberised root, and recovered total plant biomass. Depending on accession and sowing date, the tuberised roots accounted for up to 31% of recovered plant biomass and among accessions, the root biomass was positively correlated with total plant biomass. In contrast, seed biomass represented only a small proportion of recovered plant biomass, up to a maximum of 14%, depending on accession and sowing date. Among accessions, the proportion of seed biomass tended to be negatively correlated with that of tuber biomass. The perennial trait appears to be unique to Australian accessions of wild mungbean obtained from coastal-subcoastal, speargrass-dominant woodlands of NE Queensland. Although the ecological significance of the trait remains conjectural, field observation indicates that it facilitates rapid plant re-growth following early summer rainfall, especially where dry-season fire has removed previous-season above-ground growth.

**Additional keywords:** bush tucker, environmental adaptation, legume germplasm, root tubers.

### Introduction

The wild mungbean (*Vigna radiata* ssp. *sublobata*) is one of several indigenous *Vigna* taxa found across tropical and subtropical Australia (Lawn and Watkinson 2002). The subspecies is the putative wild progenitor of the cultivated mungbean (*V. radiata* ssp. *radiata*) (Smartt and Hymowitz 1985). Australian forms of the subspecies are generally more gracile than those found in Asia and intervening islands. Nonetheless, Australian accessions can be hybridised readily with the cultivated mungbean, the progeny demonstrating normal inheritance for a range of qualitative and quantitative traits (James *et al.* 1999).

A study of wild mungbean accessions collected from a wide range of geographical locations in northern Australia and grown in the field in SE Queensland (Lawn and Rebetzke 2006), identified several perennial accessions possessing thickened tap and lateral roots, which contrasted with the

fine, fibrous root system normally observed in the species. In their natural habitat, the thickened tuberous roots have been observed to give rise to adventitious subterranean shoots that emerged with the first summer rains, or after fires towards the end of the dry season (Lawn and Cottrell 1988). The tuberous roots enable the plants to persist vegetatively from season to season.

The development of thickened tap and/or lateral roots to produce tubers or similar structures is a common adaptation among plants, enabling survival of environmental stresses caused by a range of biotic (e.g. predation, grazing) and abiotic (e.g. fire, frost, and drought) factors (Rundel 1983). The tuberous organs provide a source for adventitious buds and permit below-ground storage of assimilate to enable rapid regeneration after stresses are relieved. Although other indigenous *Vigna* species such as *V. lanceolata* and *V. vexillata* are tuberous rooted perennials (Grant *et al.* 2003;

Lawn and Holland 2003), root tuberisation in *V. radiata* appears to be unique to some indigenous Australian forms of the wild subspecies.

The purpose of the present study was to document variation in root and shoot morphological traits among several accessions of *V. radiata* ssp. *sublobata* that had been observed to perenniate through the development of thickened, tuberous roots.

## Materials and methods

### Germplasm

Twelve tuberous rooted accessions of *V. radiata* ssp. *sublobata* were selected (Table 1), based on observations on cultivated plants in south-eastern Queensland (Lawn and Rebetzke 2006). Although the entire collection sampled locations across northern Australia from northern coastal NSW to the Kimberley (Lawn and Watkinson 2002), all but one of the perennial accessions had been collected in the Charters Towers–Townsville region (Fig. 1). The exact collection location of ACC 30, the one accession not obtained from this region, is not known but was recorded as ‘Cape York somewhere’ when the seed was committed to storage in the 1960s.

### Experimental design and cultivation

The 12 perennial accessions were grown in the field at the CSIRO Samford Pasture Research Station, at 2 sowing dates (15 December and 16 February) to examine their growth and development in response to climatic conditions experienced by plants emerging in early and late summer. Plots were arranged in a randomised complete block design with 2 replicates of each of the 2 sowings. Each plot was 2.2 by 2.2 m in size, with 2 guard rows of black gram (*V. mungo*) cv. Regur around the perimeter of each sowing.

Cultural details of the plots are available in Rebetzke (1994). Briefly, the experimental area was cultivated and treated with superphosphate fertiliser (40 kg P/ha). Scarified seeds were inoculated with commercial rhizobium inoculant strain CB1015 (cowpea strain) and sown at a depth of 0.01 m in a row centred down the middle of each plot to allow for the trailing nature of the plants. The plots were irrigated immediately after sowing to promote germination, and seedlings thinned to 10 plants per linear m after establishment. Plots were maintained free of weeds, irrigated during occasional dry periods, and sprayed as necessary to control insects and disease, to provide conditions favourable for plant

growth. The plants grew vigorously and were trimmed fortnightly to constrain their lateral spread to within the defined plot area.

### Attributes measured

Several attributes describing root morphology were measured, together with selected shoot and phenological traits. The following root traits were measured after final seed harvest on 3 random plants carefully excavated from each plot.

- (a) Tap root:
  - (i) diameter at ground level;
  - (ii) length of tap root exceeding 2 mm diameter.
- (b) Lateral roots:
  - (i) depth beneath the soil surface of the junction of the tap and the first thickened lateral root;
  - (ii) number of thickened lateral roots exceeding 2 mm diameter when measured 10 mm from the junction with the tap root;
  - (iii) length of thickened lateral roots exceeding 2 mm diameter.

Phenological traits recorded were the dates of flowering (50% of plants with at least 1 flower) and of pod maturity (95% of pods mature), whence the durations from sowing to flowering (the vegetative phase), from flowering to pod maturity (the reproductive phase), and sowing to pod maturity (total growth cycle) were calculated. Shoot traits were stem length (soil surface to uppermost node, mm) at 6 weeks after sowing, growth habit (rating scale of 1–4, where 1 = erect, 4 = prostrate), and the above-ground biomass ( $\text{g/m}^2$ ) and seed biomass ( $\text{g/m}^2$ ) at pod maturity.

Estimates of dry tuber biomass were obtained by excavating a 2.0 m by 0.5 m quadrat located randomly over the sowing row to a depth of 0.3 m, 198 and 134 days after sowing, for sowing 1 and 2, respectively. All tuberised roots were carefully removed, washed free of soil, dried at 60°C, and weighed. Finer roots were not recovered. The seed harvest index ( $\text{HI}_{\text{seed}}$ ) and the tuber harvest index ( $\text{HI}_{\text{tuber}}$ ) were calculated as the respective proportions of the recovered total plant biomass present as seed and tuber at pod maturity.

The tubers from a subset of the accessions harvested from the 16 February sowing were analysed for protein content using the Kjeldahl procedure, where protein content (% dry weight basis) was estimated as  $6.25 \times$  nitrogen concentration (% dry weight basis).

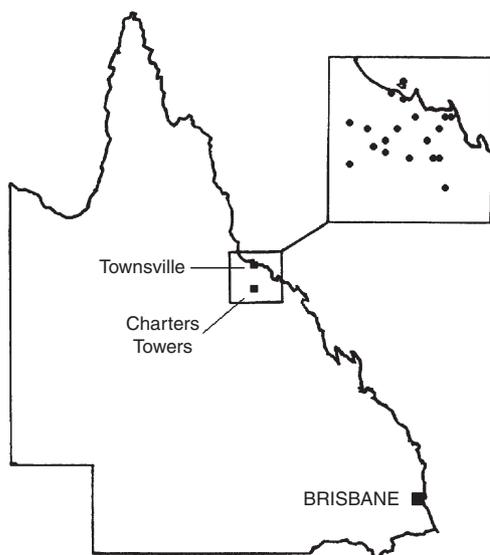
## Results and discussion

All accessions grew vigorously in the early summer sowing, and initially in the late summer sowing. However, growth was

**Table 1. Provenance information for 12 perennial accessions of *V. radiata* ssp. *sublobata* used in the study**

Accession	Location	Latitude	Longitude	Altitude (m)
ACC 2	Castle Hill, Townsville	19° 13'S	146° 48'E	100
ACC 3	Nelly Bay, Magnetic Island	18° 12'S	147° 25'E	2
ACC 22	Keelbottom Ck crossing, Hervey's Range Rd	19° 38'S	146° 17'E	400
ACC 25	Fanning River	19° 44'S	146° 26'E	250
ACC 26	Mingela Range	19° 53'S	146° 40'E	200
ACC 30	'Cape York'	_A	_A	_A
ACC 87	Woodstock, near Lansdown	19° 42'S	146° 50'E	170
ACC 88	Mingela Range	19° 53'S	146° 32'E	200
ACC 89	Mingela-Ravenswood Rd	19° 56'S	146° 42'E	200
ACC 90	Charters Towers	20° 03'S	146° 18'E	250
ACC 91	Near Townsville	19° 21'S	146° 52'E	10
ACC 92	Near Hillsborough Stud Station	20° 02'S	147° 00'E	100

<sup>A</sup>Exact provenance details not known for this accession.



**Fig. 1.** Sites from where indigenous perennial accessions of *V. radiata* ssp. *sublobata* were collected (based on the study of Lawn and Rebetzke 2006).

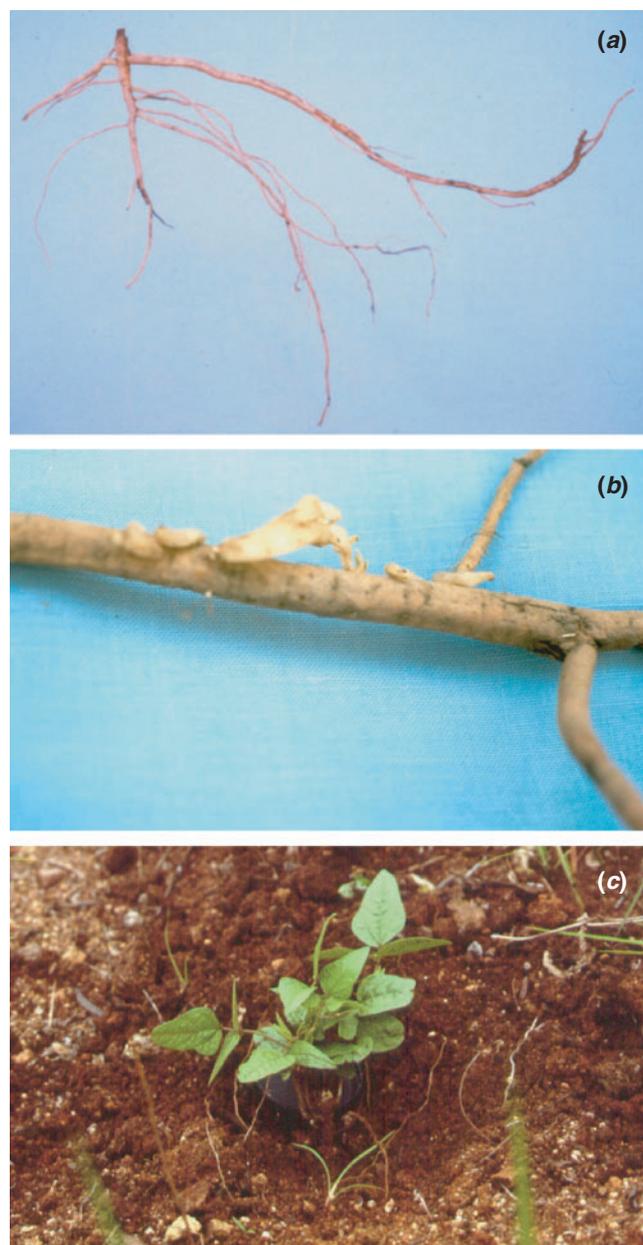
constrained towards the end of the growth cycle in the late summer sowing, presumably by cool autumn temperatures. A separate nearby study with a diversity of annual and perennial accessions (Rebetzke and Lawn 2006b) indicated that although leaf growth of all accessions was sensitive to the cooler autumn temperatures in the subtropics, the effect was most pronounced in accessions from the tropics.

#### Root morphology

All 12 accessions developed a strong, thickened tap root with well-developed lateral roots in the surface layers of the soil (Fig. 2a). Generally, the thickened lateral roots emerged from the taproot at relatively shallow depths and extended laterally just below the soil surface for some distance from the plant. By contrast, there was no evidence of any thickened roots in annual accessions sampled in immediately adjacent studies (data not shown).

All the accessions produced thickened tap and lateral roots in both the 15 December and 16 February sowings. There were significant differences between the 2 sowing dates for root traits except taproot length (Table 2). The magnitudes of most traits were larger at the first sowing date, as were the differences between accessions, presumably because the longer growth duration in the first sowing enabled the genotypic differences to be better expressed. There were significant accession  $\times$  sowing date interactions for some traits. However, these arose primarily because differences between accessions were compressed at the second sowing.

There were no significant genotypic differences in mean stem diameter at the soil surface, which declined from



**Fig. 2.** Root tuberisation in ACC 87, a perennial accession of *V. radiata* ssp. *sublobata* collected from Woodstock, west of Townsville. (a) Gross morphology showing thickened laterals; (b) close-up of a thickened lateral showing emerging adventitious shoot buds; (c) adventitious shoots emerging from the soil after fire and then early summer rain.

an average 9.0 mm at the first sowing to 5.9 mm at the second (Table 2). The average length of taproot exceeding 2 mm in diameter varied among accessions ( $P \leq 0.01$ ) from 204 mm in ACC 26 to 296 mm in ACC 2. However, it is not clear whether these differences were sufficient to be of adaptive significance, at least in terms of thickened lateral root development.

**Table 2. Stem diameter at ground level, length of thickened taproot, and attributes of the thickened lateral roots for 12 perennial accessions of *V. radiata* ssp. *sublobata***

Accession means are from 3 plants from each of 2 replicates at 2 sowing dates

Accession	Stem diam. (mm)	Tap root length (mm)	Depth of the 1st thickened lateral (mm)	Mean no. of thickened laterals (per plant)	Total length of thickened laterals per unit area (mm/m <sup>2</sup> )	Longest thickened lateral (mm)	Mean length of thickened laterals (mm)
ACC 2	7.2	296	38	3.9	1127	508	291
ACC 3	7.4	271	30	4.4	1158	533	257
ACC 22	7.5	260	26	4.6	1108	483	238
ACC 25	7.9	213	36	3.2	1131	625	350
ACC 26	8.0	204	42	3.9	990	425	248
ACC 30	7.9	248	27	4.2	1387	558	332
ACC 87	7.2	267	32	4.8	1930	667	400
ACC 88	6.9	265	27	3.8	941	377	248
ACC 89	7.0	269	26	3.6	1503	625	420
ACC 90	7.7	279	35	2.6	937	408	358
ACC 91	7.9	285	28	4.7	1955	642	412
ACC 92	7.1	238	27	4.8	1282	433	266
<b>15 Dec.</b>	<b>9.0</b>	<b>256</b>	<b>27</b>	<b>4.7</b>	<b>1921</b>	<b>724</b>	<b>426</b>
<b>16 Feb.</b>	<b>5.9</b>	<b>260</b>	<b>35</b>	<b>3.1</b>	<b>660</b>	<b>297</b>	<b>222</b>
Standard error of differences between:							
Accessions	0.67 n.s.	25**	7.0*	1.2**	284**	101**	62**
Dates	0.24**	10 n.s.	2.9*	0.20**	72**	22**	12**

\* $P \leq 0.05$ ; \*\* $P \leq 0.01$ ; n.s., not significant.

In all the accessions, the uppermost thickened lateral root originated close (between 0.026 and 0.042 m) to the soil surface (Table 2). With the delay in sowing, the average depth of the first thickened lateral root was slightly greater ( $P \leq 0.05$ ). There were no significant differences among accessions in the length of the zone of taproot from which thickened laterals emerged (data not shown). Most of the laterals emerged within 0.10 m of the soil surface and remained close to the soil surface throughout their length. Presumably, close proximity of the root to the soil surface facilitates the emergence and growth of adventitious shoots in subsequent seasons (cf. Fig. 2b).

There were significant differences ( $P \leq 0.01$ ) between accessions in the number of thickened laterals per plant, the length of thickened laterals per unit area, the longest thickened laterals, and the average length of the thickened laterals (Table 2). Those accessions with the greatest length per m<sup>2</sup> of thickened laterals (e.g. ACC91, ACC 87) tended to have more and longer thickened laterals, whereas those with the smallest length per m<sup>2</sup> (e.g. ACC 88, ACC 90) had fewer, shorter thickened laterals.

Indeed, the genotypic means for the length per m<sup>2</sup> of thickened lateral roots were positively correlated with genotypic means for the average length of the individual laterals ( $r = 0.75^{**}$ ), for the length of the longest laterals ( $r = 0.80^{**}$ ), and for the number of thickened laterals ( $r = 0.57^*$ ). That is, there was no evidence that genotypes with fewer thickened laterals had longer laterals. There was also no apparent association between genotypic differences in the taproot length and any of the lateral root traits.

The standard errors for the differences between means of the root traits were generally large (Table 2), reflecting large intra-plot variability among plants within each accession. For example, the coefficient of variation for the length of the zone of taproot from which the thickened lateral roots emerged was 43%. The length of the individual thickened lateral roots was highly variable from plant to plant (ranging from 10 to 1100 mm), in part because in some instances, the distal ends of the roots had died off by the time the plots were sampled.

Indeed, up to 10% of the plants in each plot had died before the roots were sampled. The dead plants had produced thickened roots similar to those of the surviving plants but these had failed to persist, presumably reflecting lack of adaptation to the cool, wet autumn of the subtropical environment where the study was conducted. Variable persistence between plants was noted for the related tuberous perennial species, *V. lanceolata*, when grown at the same location (Lawn and Holland 2003).

There was also no evidence of either above- or below-ground adventitious shoots in the current study, in contrast to previous studies in the same environment (Lawn and Rebetzke 2006) where adventitious shoots were abundant below ground on thickened tap and lateral roots (Fig. 2b), as well as above ground beneath the cotyledonary nodes. Presumably, the difference was due to the fact that sampling in the current study occurred in the early winter when plants were dormant and growth was suppressed by cool temperatures.

*Phenology and growth habit*

Averaged over sowing dates, the differences between accessions for time to flowering and for the durations of reproductive growth and the total growth cycle were small and non-significant ( $P > 0.05$ ). Nonetheless, all accessions were late flowering and of much longer growth duration than would be expected for mungbean cultivars. The relatively small overall variation among the accessions may have partly reflected their similar provenance (Fig. 1). Other studies

(Lawn and Rebetzke 2006; Rebetzke and Lawn 2006a) have shown that phenological differences among accessions, particularly in time to flowering, are due to differential sensitivity to photo-thermal environment, which in turn relates to their latitude of adaptation.

Later sowing generally extended the time to flowering but substantially reduced the duration of the reproductive phase (Table 3). The consequence was that without exception, later sowing shortened the duration of the growth cycle.

**Table 3. Phenology and growth habit of 12 perennial accessions of *V. radiata* ssp. *sublobata* for early- and late-summer sowings in SE Queensland**

Phenology: f, days to flowering; p, days from flowering to pod maturity; m, days from sowing to pod maturity. 1, erect; 4, prostrate; –, not measured for this sowing. Data are means across replicates in each sowing

Accession	Date of sowing	f (days)	p (days)	m (days)	Stem length (mm)	Growth habit (1-4)
ACC 2	15 Dec.	87.5	91.5	179.0	15.5	3.3
	16 Feb.	86.0	46.5	133.0	23.2	–
Mean over dates		86.8	69.0	156.0	19.4	
ACC 3	15 Dec.	84.0	96.0	180.0	17.7	4.0
	16 Feb.	86.0	44.0	130.0	22.7	–
Mean over dates		85.0	70.0	155.0	20.2	
ACC 22	15 Dec.	81.5	94.5	176.0	17.9	3.0
	16 Feb.	98.0	30.0	128.0	17.9	–
Mean over dates		89.8	62.3	152.0	17.9	
ACC 25	15 Dec.	80.5	99.5	180.0	20.0	3.0
	16 Feb.	102.0	40.5	143.0	22.5	–
Mean over dates		91.3	70.0	161.5	21.3	
ACC 26	15 Dec.	82.5	97.5	180.0	17.5	3.0
	16 Feb.	103.5	39.0	143.0	22.2	–
Mean over dates		93.0	68.3	161.5	19.9	
ACC 30	15 Dec.	80.0	98.0	178.0	19.2	3.0
	16 Feb.	98.5	34.5	133.0	22.9	–
Mean over dates		89.3	66.3	155.5	21.1	
ACC 87	15 Dec.	77.0	103.0	180.0	16.5	3.0
	16 Feb.	106.0	36.5	143.0	24.5	–
Mean over dates		91.5	69.8	161.5	20.5	
ACC 88	15 Dec.	74.5	104.5	179.0	17.5	3.0
	16 Feb.	102.5	22.5	125.0	20.0	–
Mean over dates		88.5	63.5	152.0	18.8	
ACC 89	15 Dec.	76.5	103.5	180.0	20.9	3.0
	16 Feb.	90.0	40.0	130.0	21.0	–
Mean over dates		83.3	71.8	155.0	21.0	
ACC 90	15 Dec.	78.5	101.5	180.0	16.7	3.3
	16 Feb.	96.0	41.5	138.0	18.5	–
Mean over dates		87.3	71.5	159.0	17.6	
ACC 91	15 Dec.	91.0	83.5	175.0	22.2	3.0
	16 Feb.	97.0	45.5	143.0	28.7	–
Mean over dates		94.0	64.5	159.0	25.5	
ACC 92	15 Dec.	80.0	94.5	175.0	19.4	3.3
	16 Feb.	95.0	47.5	143.0	19.3	–
Mean over dates		87.5	71.0	159.0	19.4	
<b>Date means</b>	<b>15 Dec.</b>	<b>81.1</b>	<b>97.3</b>	<b>178.5</b>	<b>18.4</b>	<b>3.2</b>
	<b>16 Feb.</b>	<b>96.7</b>	<b>39.0</b>	<b>136.0</b>	<b>22.0</b>	<b>–</b>
<b>Overall mean</b>		<b>88.9</b>	<b>68.1</b>	<b>157.3</b>	<b>20.2</b>	<b>–</b>
Standard errors of differences between:						
Accessions		6.7 n.s.	8.2 n.s.	5.2 n.s.	2.0*	0.2*
Sowing dates		2.7**	3.4**	2.1**	0.8*	–
Accessions within sowing dates		4.8**	7.9**	6.0**	2.6**	–

\* $P \leq 0.05$ ; \*\* $P \leq 0.01$ ; n.s., not significant.

Nonetheless, there was a large differential response to sowing date ( $P \leq 0.01$ ) among the accessions for the time to flowering and the duration of reproductive growth. The main difference was that flowering of the 3 coastal accessions, ACC 2, ACC 3, and to a lesser extent ACC 91, was not delayed by the later sowing, whereas flowering of some of the accessions obtained further inland, e.g. ACC 25, ACC 26, ACC 27, and ACC 88, was delayed considerably. The three coastal accessions were among the latest flowering in the first sowing, but were relatively earlier flowering at the second sowing.

The tendency for early-summer sowings of inland accessions to be earlier flowering than coastal accessions from the same latitude has been observed in other *Vigna* species (Grant *et al.* 2003; Lawn and Holland 2003). This may reflect the fact that the duration of the wet season is usually shorter and more variable further inland, so that late flowering genotypes are potentially more vulnerable in drier years. The adaptive significance of the differential responses to sowing date between the coastal accessions and those obtained further inland was not readily apparent but may reflect differential genotypic responses to photo-thermal conditions.

There was some variation ( $P \leq 0.05$ ) among the 12 accessions for stem length and growth habit, measured at 6 weeks after sowing (Table 3). Stem length at 6 weeks was greater for ACC 91 than for the other accessions, and in the second than the first sowing. The growth habit of ACC 3 was more prostrate than of the other accessions. The terminal leaflet of ACC 3 was also deeply lobed (data not shown), contrasting to the more common sublobate leaflet shape observed in the other accessions.

#### *Plant, tuber, and seed dry matter production*

Averaged over sowing dates, the recovered total plant biomass (above + below-ground dry matter), and tuberised root and seed dry matter varied significantly ( $P \leq 0.01$ ) among accessions and between sowing dates (Table 4). At the first sowing date, average biomass production was equivalent to 3.4 t/ha, with a 60% range among accessions. The variation in biomass was greater than that observed for phenology (Table 3), but was smaller than the range in biomass production for the collection of Australian accessions as a whole, when grown under generally similar conditions (Lawn and Rebetzke 2006). Average seed production was small, especially from the late summer sowing when most accessions produced only traces of seed. Average tuber biomass was 3 times that for seed, with an average of 20% of the final biomass in the tubers in the first sowing date (Table 4).

Among accessions, those producing greater total biomass also produced more tuber biomass and a greater proportion of tuber biomass. Indeed, averaged over sowing dates, there were positive correlations between tuber biomass

and total biomass ( $r = 0.76^*$ ) and between tuber biomass and  $HI_{\text{tuber}}$  ( $r = 0.95^{**}$ ). Seed production was correlated with  $HI_{\text{seed}}$  ( $r = 0.61^*$ ), but not total biomass. There was a trend for accessions with higher  $HI_{\text{seed}}$  to have lower  $HI_{\text{tuber}}$  ( $r = -0.52$ ,  $P < 0.10$ ).

The effect of sowing date on seed yield, tuberised root, and total biomass (Table 4) was large and highly significant ( $P < 0.001$ ). Of the 3 traits, total biomass was least affected by sowing date, decreasing approximately 40% on average when sowing was delayed. In contrast, average seed yield was reduced by 98% with later sowing. The reduction in seed yield coincided with the shortening in the duration of reproductive growth as sowing was delayed (cf. Table 3). The delay in sowing reduced tuber biomass by up to 85%, reflecting reductions in both total biomass and in  $HI_{\text{tuber}}$  (Table 4). There were small but significant accession  $\times$  sowing date interaction effects for most traits, largely because differences among accessions were compressed in the later sowing.

The relatively greater reduction in tuber biomass than total biomass with delayed sowing may arise because tuberisation is not initiated until plants have been growing for some time. This interpretation was supported by data from a separate study in which the perennial accession ACC 87 was sown at approximately 3-week intervals from November to April (see Rebetzke and Lawn 2006b for experimental details). As sowing was delayed and growth duration was shortened, tuber biomass declined from a maximum 126 to 0.2 g/m<sup>2</sup> when sown 138 days later. When tuber biomass was expressed as a function of growth duration at the different sowing dates, it appeared that little tuber biomass was accumulated for growth durations of less than 90 days, whereas beyond about 115 days, tuber biomass increased almost linearly with longer growth duration (Fig. 3).

This pattern would be broadly consistent with species such as potato (*Solanum tuberosum*) and yam (*Dioscorea rotundata*), where following initiation tuber weight increases curvilinearly (potatoes, Milthorpe 1967) or sigmoidally (yam, Sobulo 1972) with the duration of growth. Additionally, the observed reductions in tuber biomass (Table 4, Fig. 1) may have arisen because later sowing(s) delayed tuber growth into cooler autumn temperatures. While shorter days enhanced tuber initiation and development in yam beans (*Pachyrhizus* spp.), cool aerial temperatures substantially reduced tuber dry weight (Paull *et al.* 1988; Alvarenga and Valio 1989).

Whatever the cause, the reduction in tuber biomass with delayed sowing was relatively smaller than that in seed biomass (Table 4), which may indicate that tuber formation is relatively more important for survival and reproductive success of the perennial accessions when emergence occurs later, e.g. in seasons where the monsoonal summer rains arrive late. Consistent with this interpretation, a comparison of the responses of the 12 perennial accessions in this study with the responses of 10 annual accessions sown at the same

**Table 4. Production of seed, tuber, and recovered total biomass (above + below ground) of 12 perennial accessions of *V. radiata* ssp. *sublobata* for early- and late-summer sowings in SE Queensland**

The harvest indices for seed (HI<sub>seed</sub>) and tuber (HI<sub>tuber</sub>) are the respective proportions of these components in the recovered total plant biomass, which excludes finer roots and fallen leaves. – Indicates not measured. Data are means across replicates in each sowing

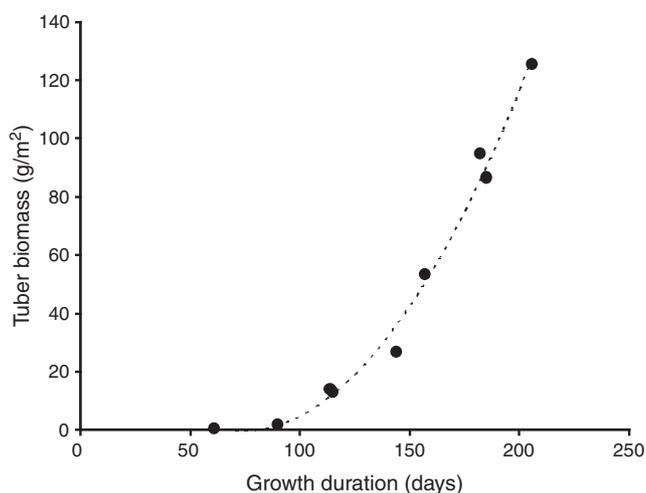
Accession	Date of sowing	Seed biomass (g/m <sup>2</sup> )	Tuber biomass (g/m <sup>2</sup> )	Recovered total biomass (g/m <sup>2</sup> )	HI <sub>seed</sub> (%)	HI <sub>tuber</sub> (%)	Tuber protein content (% w/w)
ACC 2	15 Dec.	28.8	80.4	355	8.0	23.0	–
	16 Feb.	1.4	19.3	239	1.0	8.0	11.1
Mean over dates		15.1	49.9	297	4.5	15.5	
ACC 3	15 Dec.	21.7	64.8	318	7.0	21.0	–
	16 Feb.	1.8	22.0	252	1.0	9.0	12.9
Mean over dates		11.8	43.4	285	4.0	15.0	
ACC 22	15 Dec.	20.0	96.9	315	6.0	31.0	–
	16 Feb.	0.3	12.3	200	0.0	6.0	10.8
Mean over dates		10.2	54.6	258	3.0	18.5	
ACC 25	15 Dec.	32.3	85.0	347	9.0	24.0	–
	16 Feb.	0.0	3.3	142	0.0	2.0	–
Mean over dates		16.2	44.2	245	4.5	13.0	
ACC 26	15 Dec.	34.8	97.8	409	9.0	24.0	–
	16 Feb.	0.0	5.3	231	0.0	2.0	–
Mean over dates		17.4	51.6	320	4.5	13.0	
ACC 30	15 Dec.	24.8	68.0	338	7.0	20.0	–
	16 Feb.	0.3	8.0	219	0.0	4.0	13.7
Mean over dates		12.6	38.0	279	3.5	12.0	
ACC 87	15 Dec.	17.3	65.5	316	5.0	21.0	–
	16 Feb.	0.0	9.2	204	0.0	5.0	13.8
Mean over dates		8.7	37.4	260	2.5	13.0	
ACC 88	15 Dec.	22.9	17.5	250	9.0	7.0	–
	16 Feb.	0.2	3.6	195	0.0	2.0	–
Mean over dates		11.6	10.6	223	4.5	4.5	
ACC 89	15 Dec.	29.0	39.1	347	8.0	11.0	–
	16 Feb.	0.4	12.2	198	0.0	6.0	–
Mean over dates		14.7	25.7	273	4.0	8.5	
ACC 90	15 Dec.	24.1	46.1	293	8.0	16.0	–
	16 Feb.	0.9	3.2	119	1.0	3.0	10.8
Mean over dates		12.5	24.7	206	4.5	9.5	
ACC 91	15 Dec.	18.8	129.2	411	5.0	31.0	–
	16 Feb.	0.0	18.0	232	0.0	8.0	–
Mean over dates		9.4	73.6	322	2.5	19.5	
ACC 92	15 Dec.	45.9	53.1	322	14.0	16.0	–
	16 Feb.	0.0	6.6	189	0.0	3.0	11.5
Mean over dates		23.0	29.9	256	7.0	9.5	
<b>Date means</b>	<b>15 Dec.</b>	<b>26.7</b>	<b>70.3</b>	<b>335</b>	<b>7.9</b>	<b>20.4</b>	–
	<b>16 Feb.</b>	<b>0.4</b>	<b>10.3</b>	<b>202</b>	<b>0.3</b>	<b>4.8</b>	–
<b>Overall mean</b>		<b>13.6</b>	<b>40.3</b>	<b>268</b>	<b>4.1</b>	<b>12.6</b>	–
Standard errors of differences between:							
		3.2**	10.9**	28.9**	0.29**	0.94**	–
		1.3**	4.4**	11.8**	0.12**	0.38**	–
		4.6**	15.4**	40.8**	0.41**	1.32**	–

\*\* $P \leq 0.01$ .

time in an adjacent serial sowing study suggested differential responses in seed production (Table 5).

On average, the perennial accessions produced significantly ( $P < 0.001$ ) less seed biomass when sown on 15 December than the annual accessions sown at the same time (Table 5), although the proportion of total biomass partitioned into seed was similar for the 2 groups. Later sowing reduced seed yields in both the annual and

the perennial growth types, but relatively less so in the annual types. However, the reduced partitioning of biomass into seed in the perennial forms at the later sowing was compensated by the accumulation of ~5% of biomass in tuberised roots (cf. Table 4). Thus the proportion invested in 'regenerative' biomass (i.e. seeds + tubers) in the perennial accessions (Table 4) was more than double that invested in seed alone by the annual accessions (Table 5).



**Fig. 3.** Relationship between the duration of the growth cycle and the accumulated tuber biomass for the perennial *V. radiata* ssp. *sublobata* accession ACC 87, for 9 sowing dates in south-eastern Queensland. The equation for the fitted least squares relation is given by  $y = 39.6 - 1.084x + 0.0073x^2$  ( $R^2 = 0.99^{**}$ ). Data from the study of Rebetzke and Lawn (2006b).

**Table 5. Comparison of mean seed yield and seed harvest index ( $HI_{seed}$ ) for the 12 perennial accessions in the present study with those for similar sowings of 10 annual accessions of *V. radiata* ssp. *sublobata***

The annual forms were collected from a range of geographic locations and grown in a serial sowing study at the same location as the present study (see Rebetzke and Lawn 2006b for details)

Growth cycle	Sowing date			
	15 December		16 February	
	Seed biomass (g/m <sup>2</sup> )	$HI_{seed}$ (%)	Seed biomass (g/m <sup>2</sup> )	$HI_{seed}$ (%)
Annual	33.2	8.0 <sup>A</sup>	2.2	2.0 <sup>A</sup>
Perennial	26.7	7.9 <sup>B</sup>	0.4	0.3 <sup>B</sup>
Standard errors of differences between growth cycle types within sowing dates	1.3 <sup>**</sup>	0.3 n.s.	1.3 n.s.	0.3 <sup>**</sup>

<sup>\*\*</sup> $P \leq 0.01$ ; n.s., not significant.

<sup>A</sup>Excludes root biomass.

<sup>B</sup>Includes tuber biomass.

The limited measurements of protein content taken in the second sowing (Table 4) indicated that on a dry weight basis, the protein content of the thickened tap and lateral roots averaged 12%. The observed concentrations were not as large as recorded for some tuberous legumes but are at least twice those reported for commonly grown non-leguminous root crops (Anon. 1979).

#### Summary and possible adaptive significance

The gross morphology of the root system of the 12 perennial accessions differed substantially from the normal fine, fibrous

root system of annual accessions of wild and cultivated mungbean. However, the differences in root morphology between the perennial accessions were relatively small. All developed a thickened tap root to a depth of 0.20–0.30 m, and thickened lateral roots that emerged from the taproot near the soil surface. The thickened side roots extended laterally for up to 1100 mm from the plant, remaining close to the soil surface.

There were statistically significant differences among accessions in tuber, seed, and total plant biomass production. Among the accessions, average tuber biomass production, but not seed production, was positively correlated with recovered total plant biomass. On average, tuber biomass represented 12.6% of total plant biomass at pod maturity, compared with only 4.4% for seed biomass. Among accessions, the trend was for accessions with higher proportions of tuber biomass to have lower proportions of seed biomass.

All but one of the perennial accessions were collected in the Townsville–Charters Towers region. This apparent discrete distribution of the perennial accessions, combined with their general morphological similarity, suggests that the accessions are part of a local geographic population, which shares a unique growth habit and generally similar phenologies.

The region where the accessions were collected is part of the seasonally arid tropics. Most of the rainfall (85–90%) occurs during the wet season, December–March, with only sporadic showers during the long dry season (April–November). The predominant habitat where the wild mungbean is found is lightly to moderately wooded savannah grassland, dominated in the natural state by eucalypts and the perennial grasses, speargrass (*Heteropogon contortus*) and kangaroo grass (*Themeda triandra*). The area is susceptible to fire especially during the dry season, and most of the woody and herbaceous species are well adapted to a fire regime.

Although the ecological significance of the trait remains conjectural, it is possible that the development of the perennial trait in wild mungbean was favoured by fire. In the absence of fire, some of the above-ground stems remain alive over the dry season, to give rise to new re-growth after the first summer rains. In these situations, competition from the dominant grasses is strong. However, where fire during the dry season has removed the aboveground biomass, the perennial mungbean regenerates from the below-ground adventitious buds that develop on the thickened taproot and shallow thickened laterals (Fig. 2b, c). In these situations, the re-growth is more vigorous than in the absence of fire, perhaps because of reduced initial competition from the grasses.

Alternatively or perhaps additionally, the tendency to divert more reproductive effort into tuber than seed biomass may reflect an adaptive response to seed predation. Field observation indicates that seed predation by a range of

organisms including pod-sucking and pod-chewing insects, seed-eating birds (especially parrots), and marsupials, is prevalent.

There is historical evidence that the existence of tuberous rooted ecotypes of wild mungbean in the Townsville region was known to the local Aborigines and that the tubers were used as 'bush tucker'. A report by the 19th century botanist Anthelme Thozet stated that 'the Cleveland Bay natives' baked the thickened roots of *Phaseolus mungo* L. for food (Thozet 1866). Although *Phaseolus mungo* L. (*sensu stricto*) does not occur naturally in Australia, the name was a common misnomer for *V. radiata* ssp. *sublobata* in the 19th Century (e.g. Bentham and Mueller 1864).

Some of the perennial accessions used in this study were among those shown to hybridise readily with the cultivated mungbean (James *et al.* 1999). However, the inheritance of the perennial trait has not yet been established. In the context of modern agriculture, it is unlikely that the perennial trait would be of immediate interest for development of commercial mungbean cultivars, given the low propensity of the perennial accessions to produce seed.

However, it is possible that the perennial accessions could be of interest for development as a forage legume adapted to the seasonally arid coastal and subcoastal grasslands of northern Australia. The invasive spread of exotic pasture species into non-pastoral areas has led to concerns about their effect on natural ecosystems (e.g. Lonsdale 1994). As part of the existing natural system, the perennial wild mungbean would avoid many of these environmental concerns. Even improved varieties specifically bred for enhanced productivity in managed forage or grazing systems would be of minimal concern, since escapes would likely fail to persist or would rapidly revert to wild type though introgression with the naturally occurring wild forms.

### Acknowledgments

The research reported here was supported by the Grains Research and Development Corporation and the CSIRO Division of Tropical Crops and Pastures, and was undertaken in partial fulfillment of the requirements of the MAgSc degree awarded to GJR by the University of Queensland.

### References

Alvarenga AA, Valio IF (1989) Influence of temperature and photoperiod on flowering and tuberous root formation of *Pachyrrhizus tuberosus*. *Annals of Botany* **64**, 411–414.  
 Anon. (1979) 'Tropical legumes: Resources for the future.' (National Academy of Science: Washington, DC)  
 Bentham G, Mueller F (1864) '*Flora Australiensis*. A description of the plants of the Australian Territory. II. Leguminosae to Commbretaceae.' (Lovell Reeve & Co: Covent Garden, London)

Grant T, Lawn RJ, Bielig LM (2003) Variation among Australian accessions of *Vigna vexillata* for traits of agronomic, adaptive or taxonomic interest. *Australian Journal of Agricultural Research* **54**, 243–250. doi: 10.1071/AR02147  
 James AT, Lawn RJ, Williams RW, Lambrides CJ (1999) Cross fertility of Australian accessions of wild mungbean (*Vigna radiata* ssp. *sublobata*) with green gram (*V. radiata* ssp. *radiata*) and black gram (*V. mungo*). *Australian Journal of Botany* **47**, 601–610. doi: 10.1071/BT97068  
 Lawn RJ, Cottrell A (1988) Wild mungbean and its relatives in Australia. *Biologist* **35**, 267–273.  
 Lawn RJ, Holland AE (2003) Variation in the *Vigna lanceolata* Benth. complex for traits of taxonomic, adaptive or agronomic interest. *Australian Journal of Botany* **51**, 295–308. doi: 10.1071/BT02105  
 Lawn RJ, Rebetzke GJ (2006) Variation among Australian accessions of the wild mungbean (*Vigna radiata* ssp. *sublobata*) for traits of agronomic, adaptive or taxonomic interest. *Australian Journal of Agricultural Research* **57**, 119–132. doi: 10.1071/AR05215  
 Lawn RJ, Watkinson AR (2002) Habitat, morphological diversity and distribution of the genus *Vigna* Savi in Australia. *Australian Journal of Agricultural Research* **53**, 1305–1316. doi: 10.1071/AR02065  
 Lonsdale WM (1994) Inviting trouble: introduced pasture species in northern Australia. *Australian Journal of Ecology* **19**, 345–354.  
 Milthorpe FL (1967) Some physiological principles determining the yield of root crops. In 'Proceedings of the International Symposium on Tropical Root Crops. Vol. 1'. (Eds EA Tai, WE Charles, EF Iton, PH Haynes, KA Leaslie) pp. 1–15.  
 Paull RE, Chen NJ, Fukuda SK (1988) Planting dates related to tuberous root yield, vine length and quality attributes in yam bean. *HortScience* **23**, 326–329.  
 Rebetzke GJ (1994) Attributes of potential adaptive and agronomic significance in the wild mungbean (*Vigna radiata* (L.) ssp. *sublobata* (Roxb.) Verdc.). MAgSc thesis, The University of Queensland, Australia.  
 Rebetzke GJ, Lawn RJ (2006a) Adaptive responses of wild mungbean (*Vigna radiata* ssp. *sublobata*) to photo-thermal environment. I. Phenology. *Australian Journal of Agricultural Research* **57**, (In press).  
 Rebetzke GJ, Lawn RJ (2006b) Adaptive responses of wild mungbean (*Vigna radiata* ssp. *sublobata*) to photo-thermal environment. II. Growth, biomass, and seed yield. *Australian Journal of Agricultural Research* **57**, (In press).  
 Rundel PW (1983) Fire as an ecological factor. In 'Encyclopaedia of physiological plant ecology. Vol. 12A'. (Eds OL Lange, PS Nobel, CB Osmond, H Zeigler) pp. 501–538. (Springer-Verlag: Berlin)  
 Smartt J, Hymowitz T (1985) Domestication and evolution of grain legumes. In 'Grain legume crops'. (Eds RJ Summerfield, EH Roberts) pp. 37–72. (Collins: London)  
 Sobulo RA (1972) Studies on white yam (*Dioscorea rotundata*). I. Growth analysis. *Experimental Agriculture* **8**, 99–106.  
 Thozet A (1866) 'Notes on some of the roots, tubers, bulbs and fruits used as vegetable food by the Aborigines of Northern Queensland, Australia.' (JH Buzacott, 'Bulletin' Office: Rockhampton, Qld.)

Manuscript received 17 October 2005, accepted 2 March 2006