An Examination of Vegetative and Reproductive Growth Habits and Their Contribution to Seed Yield in 'Grasslands Maku' Lotus (*Lotus uliginosus* Schk.)

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ABSTRACT

Growth analysis of 'Grasslands Maku' lotus (*Lotus uliginosus* Schk.) was conducted at Massey University, Palmerston North, New Zealand to investigate the morphological characteristics which may limit seed yield potential. In addition to the crop's long indeterminate flowering and pod shattering, one major factor influencing seed yield was the competition which developed between vegetative and reproductive growth for photosynthetic assimilate. The plant continuously produced new main shoots which, along with the growth and development of lateral shoots, cumulatively added to the dense vegetative canopy during the early summer because of increasing daylength and temperature. Intense lateral branching occurred at the same locations where umbels ultimately appeared in November. Intensive vegetative and reproductive growth continued simultaneously during the flowering months (December and January). As a result, physiological compensation became important and was expressed in flower bud, floret and pod abortion which decreased potential seed yield. Main shoots which originated in the period from September to December contributed most to seed yield. Other details of the morphological structure of the plant are also discussed.

Additional index words: **seed yield components, pod shatter, assimilate, abortion, main shoots.**

INTRODUCTION

'Grasslands Maku' lotus (*Lotus uliginosus* Schk. syn. *Lotus pedunculatus* Cav.) is a tetraploid herbage legume bred in New Zealand and released for commercial use in 1975. It has high potential for use in acidic (pH < 5.2), phosphate-deficient soils and is often seen growing in swampy areas and wet hollows. Traditionally it has been widely sown on moist, acid, low-fertility hill country, but lately it has also performed very well in subtropical areas in Queensland, Australia (Cook and Jones, 1985). Maku lotus tolerates high levels of soil aluminium and is efficient in absorbing soil phosphate under low phosphate conditions. It has greater feeding and nutritive value for animals than lucerne, red clover and perennial ryegrass as well as being non-bloating (John and Lancashire, 1981). Maku lotus has a valuable characteristic in its tolerance to damage by grass grub (*Costelytra zealandica* White) (Kain and Atkinson, 1975) and porina (*Wiseana cervinata* Walker) (Farrell and Sweney, 1974).

Despite these agronomic advantages, the comparatively poor seed yield often obtained from Maku lotus is one factor limiting its more widespread use. It has an indeterminate flowering habit which may extend over 3-4 months within the period from November to April in New Zealand (Neal, 1983). This, together with the crop's pod shattering behaviour (Lancashire, Gomez and McKellar, 1980) makes it difficult to select the most appropriate time for seed harvesting. Optimum time for harvest was found to be two to four days after seed maturity when the seeds had 35% moisture content, the pods were light brown in colour, and only about 3-4% pod shatter had occurred (Hare and Lucas, 1984). In their study, 27 days were required after pollination for the crop to reach seed maturity in 1982 and 35 days in 1983. Hampton, Li and Hare (1989) implicated competition for assimilates as one factor limiting seed yield. However, there is little evidence as to why and how such competition takes place. A better understanding of the vegetative and reproductive growth habit of Maku lotus is needed in order to improve seed production through management practices such as mechanical or chemical manipulation.

This study monitored the growth habit of Maku lotus to assess the relationship between vegetative and reproductive growth, to determine how each contributes to seed yield and to evaluate how competition for assimilates may occur.

MATERIALS AND METHODS

The 'Grasslands Maku' lotus seed used in this study was supplied by the Grasslands Division of the New Zealand Department of Scientific and Industrial Research (DSIR). The experiment was carried out from May 1989 to February 1990 at Massey University, Palmerston North, New Zealand (Latitude 40°S, Longitude 170°E). Ten plants were taken from a one-year old Maku lotus crop on April 20 1989, and transplanted individually into plastic pots 29 cm in diameter by 29 cm in height. The soil used was taken from a field of Tokomaru silt loam (an aeric frafiaqualf {gleyed yellow-grey earth}). Plants selected were of uniform average size. The pots were arranged at a 1.5 m spacing in an open field

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and buried to ground level. Existing stems were retained and the plants were watered only when initial signs of leaf wilting appeared throughout the cropping season, especially when there was no rain. No fertiliser was applied. Mavrik aquaflow insecticide (fluvalinate) was applied at 40 ml per 100 l of water three times (on 1 and 20 November and 16 December) as a protection against insects. Application was in the evening when bees were absent. Hand weeding was done at the end of each month to control weeds around the plants.

Tagging of all main and primary lateral shoots was carried out at the end of each month starting in May 1989 and continuing until January 1990. Different coloured fine wire rings were used for tagging. A new shoot was tagged when it had at least one unfolded leaf. The number of main and lateral shoots, number of nodes per main shoot and their month of occurrence were recorded. Flower bud initiation was determined with the aid of a stereoscopic dissecting microscope at a magnification of X 40. The dates of flower bud occurrence and flower opening were noted. The number of flowers (umbels) from the start of flowering until the end of flowering was also recorded. Umbel counting was done every seven days to avoid repeated or missed countings, since it took 4-5 days for a new umbel (with at least one yellow floret open) to reach full bloom, and a further 2 days for the florets to show withering. The flowering period was divided into three time stages (Li and Hill, 1988) according to the profuseness of flowering (i.e. early, middle and late flowering stages). Monthly development of node numbers was recorded by examining the number of nodes which developed between coloured rings of the same shoots tagged on successive months. The number of umbels contributed by the main shoots formed each month and their laterals were noted at harvest. Number of floret buds, florets and pods per umbel were determined at the three flowering stages. Number of seeds per pod (using x-ray photography), thousand seed weight and seed yield for all monthly shoot age groupings were also determined at harvest, which was 37 days after peak flowering when the majority of pods were brown (Hare and Lucas, 1984). The thousand seed weights and seed yields were corrected to 8% moisture content and cleaned to 99.9% or higher seed purity. Climate data were collected from the DSIR, Palmerston North, New Zealand (approximately 1 km from the trial site) and from the Carter Observatory, Wellington, New Zealand (approximately 100 km from the trial site, but used for daylength records only).

RESULTS

Vegetative Growth

There was a continued increase in the number of main shoots from July on, but with November, December and January shoots showing the most intensive growth (Table 1). The May shoots occurred early, replacing the April shoots present at transplanting. However, none of these survived until harvest. Shoots which originated in June, July and August had 67, 75 and 80% survival respectively, while shoots formed from September to January were still present at harvest.

Table 1. Mean main shoot occurrence and survival per plant.

Date of tagging	Time of main shoot occurrence								
	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan
May 31	6.7	-[1]	-	-	-	-	-	-	-
June 30	6.0	5.2	-	-	-	-	-	-	-
July 31	5.5	5.0	4.0	-	-	-	-	-	-
Aug 31	4.6	4.2	4.0	5.0	-	-	-	-	-
Sept 30	2.0	3.9	4.0	5.0	7.5	-	-	-	-
Oct 31	0.0	3.9	3.8	5.0	7.5	10.5	-	-	-
Nov 30	0.0	3.9	3.5	4.6	7.5	10.5	22.5	-	-
Dec 31	0.0	3.8	3.2	4.3	7.5	10.5	22.5	26.5	-
Jan 31	0.0	3.5	3.0	4.0	7.5	10.5	22.5	26.5	30.5
Feb 10[2]	0.0[g]	3.5[f]	3.0[f]	4.0[f]	7.5[e]	10.5[d]	22.5[c]	26.5[b]	30.5[a]
% survival	0	67.4	75.0	80.0	100.0	100.0	100.0	100.0	100.0

[1] New main shoots not yet produced.

[2] Harvest date.

Means having the same letters are not significantly different at $P < 0.05$.

June formed shoots showed minimal growth during the winter months of June, July and August with very few new nodes developing per main shoot (Table 2). However, as temperatures increased in spring (September, October and November) and summer (December and January) (Fig. 1), more rapid growth occurred on all main shoots, irrespective of month of origin. This was reflected in increases in the number of nodes formed per month up until December, when node production declined markedly. Nodes formed in November and December were the locations from which flowers emerged on June to October formed main shoots, but main shoots originating in November, December and January produced reproductive nodes only after the fifth node. Late December and January shoots continued growing even beyond harvest.

Table 2. Number of nodes per plant formed each month on main shoots (assessed at harvest, 10 February).

	Time of node occurrence per main shoot								
MS by month of origin	**June**	**July**	**Aug**	**Sept**	**Oct**	**Nov**	**Dec**	**Jan**	**Total**
June	2.0	2.0	3.0	5.0	6.0	8.0[2]	0.0	0.0	26.0
July	-[1]	2.0	3.0	4.5	5.0	6.0[2]	2.5[2]	0.0	23.0
August	-	-	3.4	5.9	7.4	6.8[2]	2.5[2]	0.0	25.9
September	-	-	-	5.3	7.3	6.6[2]	2.7[2]	0.0	21.8
October	-	-	-	-	5.1	7.6[2]	3.8[2]	0.0	16.5
November	-	-	-	-	-	6.9[3]	4.5[2]	0.8[2]	12.2
December	-	-	-	-	-	-	8.9[3]	1.0[2]	9.9
January	-	-	-	-	-	-	-	9.2[3]	9.2

MS - main shoots.
1 nodes not yet produced.
2 nodes from which flowers emerged.
3 flowers emerged only after the 5th node.

Maku lotus produced primary lateral shoots (PLS) from all the main shoot groups. However, most of the PLS were borne in September, October and November main shoots (Table 3, right hand Total PLS). Main shoots formed in these months provided over 70% of the primary lateral shoot population present at harvest. PLS on main shoot nodes were located on the nodes formed each month by the main shoots from July to January. However, 83 and 55 primary lateral shoots (about 62.3%) originated at nodes which were formed in November and December respectively (see Total PLS at the bottom of Table 3). These November and December formed nodes were the main sites at which flowers were produced (Table 2). The plant produced most primary lateral shoots and flowers at the same location.

Table 3. Location of primary lateral shoots per plant at the main shoot group by month of origin and at the main shoot nodes (assessed at harvest, 10 February).

	Nodes by month of formation where PLS emerged								
MS by month of origin	**June**	**July**	**Aug**	**Sept**	**Oct**	**Nov**	**Dec**	**Jan**	**Total PLS[2]**
June	-	-	0.5	1.0	0.5	-[1]	-	-	2.0[f]
July	-	0.5	2.5	3.0	5.0	1.5	-	-	12.5[e]
August	-	-	5.5	5.5	6.5	2.5	-	-	20.0[d]
September	-	-	-	10.5	16.0	19.5	-	-	46.0[b]
October	-	-	-	-	23.0	29.0	1.0	-	53.0[a]
November	-	-	-	-	-	30.5	26.0	-	56.5[a]
December	-	-	-	-	-	-	28.0	-	28.0[c]
January	-	-	-	-	-	-	-	3.5	3.5[f]
Total PLS[3]	0[g]	0.5[fg]	8.5[e]	20.0[d]	51.0[c]	83.0[a]	55.5[b]	3.5[f]	221.5

MS - main shoots, PLS - primary lateral shoots
1 no primary lateral shoots occurred.
2 total primary lateral shoots contributed by the main shoot groups.
3 total primary lateral shoots which emerged at the main shoot nodes formed at different times.
Total values having the same letter are not significantly different at $P < 0.05$.

Secondary lateral shoots (SLS) emanating from primary lateral shoots came from the main shoot groups originating from July to November only (Table 4). The SLS were classified as reproductive (flowering) and vegetative (non-flowering) shoots. About 78% of reproductive SLS occurred on earlier main shoots formed during July, August and September. This compared with a corresponding occurrence of about 84% vegetative SLS in the same groups of main shoots, making the percentage ratio of reproductive against vegetative SLS lower than the general average at 59.4%, especially in August and September shoots.

Table 4. Number of secondary lateral shoots per plant and their main shoot origin (assessed at harvest, 10 February).

MS by month of origin	No. of repSLS	No. of vegSLS	% of repSLS to vegSLS
June	0.0^{c}	0.0^{c}	0.0
July	8.5^{ab}	3.5^{bc}	70.8
August	8.5^{ab}	8.0^{ab}	51.5
September	15.0^{a}	12.0^{a}	55.6
October	6.0^{bc}	2.5^{bc}	70.6
November	3.0^{bc}	2.0^{bc}	60.0
December	0.0^{c}	0.0^{c}	0.0
January	0.0^{c}	0.0^{c}	0.0
Total	41.0	28.0	59.4%

MS - main shoots.
repSLS - reproductive secondary lateral shoots.
vegSLS - vegetative secondary lateral shoots.
Mean values having the same letters are not significantly different at $P < 0.05$.

Reproductive Growth

The time of occurrence of the plant shoots and reproductive parts and the monthly mean daylength and temperature which prevailed during the cropping season are shown in Fig. 1. The mean daily temperature for the 1989-90 cropping season did not differ from the normal mean temperature except for November and February which were higher by about 2°C (Fig. 1). Main shoots occurring in June and July, when the mean daylength and temperature were low (9.2 hr - 9.3 hr daylength and 7.7 - 8.8°C, respectively) remained mostly vegetative because 25 and 20% respectively died before flowering, while the

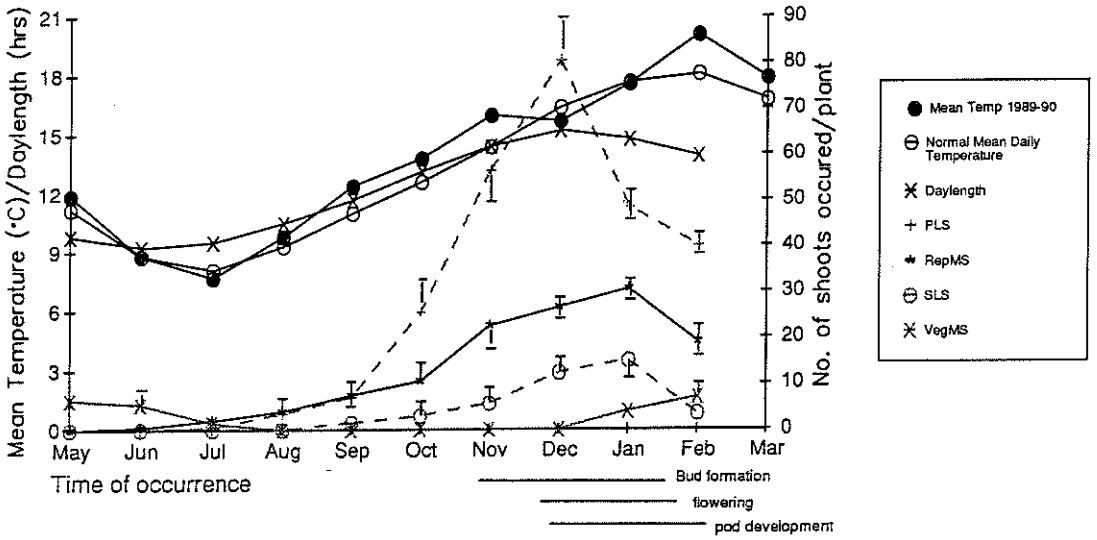


Figure 1: Shoot occurrence and reproductive stages in relation to temperature, rainfall and daylength, 1989/90. PLS = primary lateral shoots, RepMS = reproductive main shoots, SLS = secondary lateral shoots, VegMS = vegetative main shoots, I = standard error of means.

survivors were shaded by the more vigorous and upright younger shoots. Those formed from August to December became highly reproductive when conditions for floral induction became favourable (14 to more than 15 hours daylength and 12.4 to 17.6°C mean temperature). The most intense growth of main shoots occurred in the months of November, December and January when mean temperatures were favourably high (16.0, 15.7 and 17.6°C, respectively) and daylengths were at their peak (14.4, 15.2 and 14.8 hours, respectively), although rainfall was abnormally low in November and December, being only 76 and 37% of the normal rainfall respectively (data not shown). The plants resumed vegetative main shoot growth in late January when daylength began decreasing below 14 hours (Fig. 1) and when rainfall was about 32% higher than normal (data not shown). The primary lateral shoots composed the greatest bulk of vegetative growth contributing to reproductive potential. Their pattern of growth followed that of the reproductive main shoots. Secondary lateral shoots while comparatively less than the MS and PLS, exhibited the same pattern of growth as the reproductive main shoots. The most intense growth of all plant shoots occurred in November, December and January, coinciding with bud formation, flowering and pod-filling. Early flower buds were initiated in late October (when daylengths were about 13.6 to 13.9 hours) but only became visible at the shoot apex in early November. Flowering started in the third week of November when daylength was about 14.6 hours.

Umbels bearing mature pods (brown and ready to harvest) were contributed by both the main and lateral shoots. The main shoots, primary lateral shoots and the secondary lateral shoots contributed 37.9, 52.9 and 9.2% respectively of the umbels available at harvest (Table 5). While all the main monthly shoot groupings contributed to the umbel population, the biggest contribution was on MS formed in November, December and January, which collectively contributed about 81% of the total umbels available. However, 10% of the umbels from December MS and 80% from the January MS were immature at harvest (37 days after peak flowering - 10 February). At this time, open flowers and flower buds were still present on MS formed in December and January. These late MS groups were responsible for extending the flowering period beyond the optimum harvest date. Umbel production was greatest on PLS formed in September, October and November. The SLS however, produced most umbels from shoots formed in September. The major contribution to the total umbel population was from PLS and MS, with SLS having a relatively smaller influence on total umbel numbers. The majority (78.3%) of pod-bearing umbels available at harvest from all shoots occurred on those formed in September, October, November and December.

Table 5. Number of umbels per plant formed on different reproductive shoots (assessed at harvest, 10 February).

MS by month of origin	Number of umbels formed						
	MSpods	PLSpods	SLSpods	Totalpods	Flower[1]	Buds[2]	Total
June	1.5	3.0	0.0	4.5[f]	0.0	0.0	4.5
July	3.0	23.5	13.0	39.5[e]	0.0	0.0	39.5
August	3.5	18.0	13.0	34.5[e]	0.0	0.0	34.5
September	17.0	67.0	26.0	110.0[c]	0.0	0.0	110.0
October	26.0	94.0	10.0	130.0[b]	0.0	0.0	130.0
November	63.0	127.0	4.0	194.0[a]	1.5	0.0	195.5
December	84.5	44.0	0.0	128.5[b]	4.5	0.0	133.0
January	74.0	3.5	0.0	77.5[d]	11.0	10.5	99.0
Total	272.5	380.0	66.0	718.5	17.0	10.5	746.0
%	37.9	52.9	9.2	100.0			

MSpods - pod-bearing umbels from main shoots.
PLSpods - pod-bearing umbels from primary lateral shoots.
SLSpods - pod-bearing umbels from secondary lateral shoots.
[1] open flowers from main shoots.
[2] flower buds from main shoots.
10% of December pods were immature.
80% of January pods were immature.
Mean values having the same letters are not significantly different at $P < 0.05$.

Components of Seed Yield

Flowering pattern was influenced by daylength differences as the number of open flowers increased to a well pronounced peak as daylength increased to its maximum and subsequently decreased as daylength eventually decreased also (Fig. 2). The first open flowers appeared on 22 November when the daylength was 14.7 hours, and flowering ceased 91 days later on 21 February. Early flowers occurred during the first 21 days, from 22 November to 13 December (with daylengths from 14.7 to 15.1 hours). Middle flowers occurred from the 22nd to 56th day (14 December to 17 January with daylengths from 15.1 to 14.9 hours), a period characterised by a rapid increase in flowering with a well-pronounced peak on the 42nd day (January 3) and an abrupt decrease after 14 days. The late flowers occurred from the 57th to 91st day (18 January to 21 February with daylengths from 14.7 to 13.5 hours). Plants produced a mean total of 823 umbels, of which 96 (11.7%) came from the early flowers, 625 (76%) from the middle flowers and 102 (12.4%) from the late flowers. Major flower production was therefore concentrated into a comparatively short and intense period of only 35 days.

Early flowers had a mean of 10.7 floret buds per umbel on 22 November, which decreased to 8.1 florets per umbel at flower opening 14 days later (Table 6). After a further 30 days only 5.9 pods per umbel were present at seed maturity. These reductions represented an abortion loss of 24% from bud stage to flowering and a total 45% from floret bud stage to pod maturity. Middle flowers started with 11.9 floret buds per umbel which was reduced to 11.1 florets per umbel at flower opening and to 10.4 pods per umbel at maturity. These values represented a 7% abortion from flower bud stage to open flower stage and a total of 13% from bud stage to pod maturity. Late flowers bore 12.1 floret buds per umbel at the bud stage which reduced to 10.5 florets at flower opening and finally to 8.4 pods per umbel at maturity. This represents a loss through abortion of 13% from bud stage to open flower stage and a total abortion of 31% from bud stage to maturity. The mean percentage abortion for all flowering groups showed a loss of 14.5% of floret buds per umbel, 16.9% of florets per umbel and a total loss of 29.4% from the flower bud stage to pod maturity.

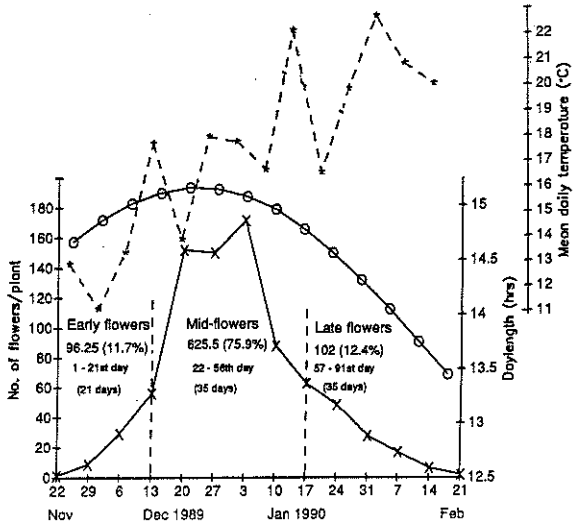


Figure 2.: The flowering pattern of 'Grasslands Maku' lotus in relation to daylength and temperature, 1989/90. O——O = daylength, *——* = temperature, X——X = flowering pattern.

Table 6. Number of floret buds, florets and pods per umbel at three different flowering stages.

Stages of flowering time	floret buds[1] per umbel	florets[2] per umbel	Abortion %	pods[3] per umbel	Total abortion[4]
1. Early flowers	10.7^{NS}	8.1^{c}	23.9	5.8^{c}	45.0^{a}
2. Mid-flowers	11.9	11.1^{a}	6.9	10.4^{a}	12.4^{c}
3. Late flowers	12.1	10.5^{b}	13.1	8.4^{b}	30.7^{b}
Means	11.6	9.9	14.5	8.2	29.4

1 flower bud (pre-yellow, about 14 days before opening).
2 flowering (opening of the florets).
3 matured pods (30 days after flowering).
NS - not significant. Means having the same letter within a column are not significantly different at $P < 0.05$.

There were significant differences between the number of seeds per pod in umbels formed each month from each main shoot group (Table 7). Seeds per pod varied from 6.1 to 8.8, rising to a peak in September formed shoots before declining again for December and January formed shoots. Seed weights showed small differences among the main shoot groupings. However, a similar trend was seen with increasing weight to a maximum on August to November formed shoots before a decline to January. Seed yields from main shoots formed in September, October, November and December were the greatest contributors (81.7%) to total seed yield. Main shoots developed in June, July and January made a relatively smaller contribution (18.3%) to total seed yield per plant.

Table 7. Number of seeds per pod, one thousand seed weight and seed yield.

MS by month of origin	seeds /pod	TSW (g)	seed yield /plant (g)	Percentage contribution
June	6.20^{f}	0.7635^{bc}	0.11^{e}	(0.39)
July	7.10^{d}	0.7630^{bc}	1.48^{d}	(5.20)
August	7.60^{c}	0.7787^{abc}	2.04^{d}	(7.17)
September	8.78^{a}	0.7875^{ab}	5.38^{b}	(18.90)
October	8.11^{b}	0.7809^{abc}	6.14^{b}	(21.57)
November	7.67^{c}	0.7995^{a}	7.85^{a}	(27.57)
December	6.60^{e}	0.7470^{c}	3.89^{c}	(13.66)
January	6.10^{f}	0.6483^{d}	1.58^{d}	(5.55)
Mean	7.27	0.7585		
Total			28.47	(100.00)

MS - main shoot.
TSW - One thousand seed weight in grams at 8% seed moisture content.
Values in parenthesis are percentage yield contribution per main shoot group by month of occurrence.

DISCUSSION

'Grasslands Maku' lotus responds readily to changes in daylength, temperature and rainfall. During the cool winter months of June and July (mean temperatures of 8.8 and 7.7°C, and daylengths of 9.3 and 9.5 hours, respectively) the plant formed few new shoots and nodes. However, increased growth rate was associated with increasing temperatures and daylengths in spring and summer. New main shoots produced each month cumulatively formed a dense vegetative bulk, resulting in the death of all the May and 33, 25 and 20% of the June, July and August formed main shoots respectively. Those shoots which originated during the early spring and into the summer (September to January) had a high survival percentage and more vigorously dominated the earlier formed shoots. This characteristic was also observed in a first year Maku lotus seed crop (Hill and Witchwoot, 1990) and in *L. corniculatus* (Li and Hill, 1988).

The number of main shoot nodes formed increased irrespective of the month of shoot origin from June to November, but abruptly decreased in December. If there is a 'determinate aspect' to this indeterminate plant, it is this situation where shoot growth slows coincident with the production of flowers and finally ceases during the period of pod-filling. Not all nodes of a reproductive shoot were fertile, as only those produced in November, December and January produced flowers. Hill and Witchwoot (1990) found that fertile nodes occurred from late October to December, an effect which may be due to differences in weather and soil conditions. However, the present study confirmed the observations of Li and Hill (1988) that in *L. corniculatus* older shoots bore flowers at higher nodes while younger shoots commenced flowering at lower nodes.

Flower-induction on June to November main shoots began in mid-November. The unusually low rainfall in November also probably helped induce the initiation of flower buds and flowering as observed in the same crop by Neal (1983) and Hill and Witchwoot (1990). Newly-formed December and most January shoots also became reproductive as they grew and developed. The same floral-inducing conditions also triggered flowering in *L. corniculatus* - a long-day plant grown at the same site (Li and Hill, 1988). The flowering responses to daylength reported here for Maku lotus are very similar to results obtained by Forde and Thomas (1966) in a north German variety of *L. pedunculatus* where the critical daylength for inflorescence initiation ranged from 14.5 to over 15 hours. Flowers were formed from axillary buds at the main shoot

apex in a similar manner to that observed by Hill and Witchwoot (1990), but the main shoots contributed only about 38% of the total number of umbels available at harvest. The greater majority of umbels (53%) were contributed by the primary lateral shoots while secondary lateral shoots had a relatively small influence (9%) on total umbel numbers.

This study indicates that competition for assimilate may be one of the causes of low seed yield in Maku lotus. There were two particular instances where intra-plant competition is likely to have occurred. Firstly, during the period of the most intense growth of main and lateral shoots (November to January) (Fig. 1), which coincided with bud formation, flowering and pod-filling. Vegetative main shoots were still forming in January when pod-filling was at its maximum. Secondly, the locations from which 62.3% of the primary lateral shoots emerged were also those nodes from which most flowers from the main shoots also developed. The time of flowering in the present study agrees with the observations of Hare and Lucas (1984), who found that flower buds were initiated 25-30 days before the opening of the flowers. With the formation and growth of vegetative and reproductive parts occurring simultaneously, available photo-assimilate must be partitioned between demands created by vegetative and reproductive sinks. Lower partitioning of assimilate to the reproductive sinks is possibly reflected in the occurrence of flower abortion. Similar results obtained in *L. corniculatus* (McGraw and Beuselinck, 1983), and soybeans (Chanprasert, 1988) have shown that under stress conditions (light, temperature or water stress) associated with an inadequate supply of essential assimilates, young flower buds constitute a weak sink in comparison with vegetative apices, developing leaves, fruits or storage organs, and compete poorly with them for the available assimilate. In one study with *L. corniculatus* McGraw and Beuselinck (1983) found that only 12% of the total assimilate went to the seeds, 28% to the peduncle, pedicel and pod walls, and 60% to the stems and lateral shoots. Flower abortion has been found to be aggravated when daylength below the critical number of hours, low light intensity, low or extremely high temperature or water stress during inflorescence development occur (Halevy, 1975; 1984; Forde and Thomas, 1966). In plants possessing young flower buds and open flowers, these environmental stresses promote abortion and blasting or abscission of the flower buds, while other organs may only be slightly affected (Kinet, 1977). In the present study, flower abortion was found to be less in middle season flowers, probably because daylength (14.5 to over 15 hr) from 14 December to 17 January was more favourable for floral initiation and development, a suggestion also made by Forde and Thomas (1966) in *L. pedunculatus*.

Stephenson (1984) observed that about 57% of all initiated *L. corniculatus* flowers and fruits aborted, and found that availability of resources rather than pollination limited production in this species. He further found that fertiliser-enriched plants produced more flowers per ramet, flowers per inflorescence, inflorescences per ramet, and seeds per ramet, than did both the control and partially defoliated plants (resource-limited treatment). However, he observed that the proportion of flower and fruit abortion in *L. corniculatus* was constant, whether in resource-deprived or resource-enriched treatments. This finding prompted Stephenson (1984) to propose two hypotheses to explain why *L. corniculatus* produces so many flowers which it may not be able to support until maturity. The first hypothesis states that surplus flower production allows plants to take advantage of the occasional "good years" when resources are plentiful. The other hypothesis states that the surplus flowers are selected for the male contribution to fitness (Stephenson, 1984 and references therein) so that the proportion of flowers that produce mature fruit will remain constant over a wide range of resource availability. Whether one or both of these hypotheses apply to *L. uliginosus* is not known. Further observation and experimentation is required.

CONCLUSIONS

Results from this study have shown the consistent major contributions of those main shoots which originate in September, October and November to the total number of primary lateral shoots, umbels, pods per umbel, seeds per pod, seed weight and final seed yield. Although earlier (June, July and August) and later-formed shoots (mid-December and January) added considerably to the total shoot population and consequently to the number of umbels, these shoots did not contribute significantly to the ultimate seed yield. Latest-formed shoots in particular (January), probably have deleterious effects on seed yield by competing with reproductive sinks developing simultaneously. This effect is likely to be most pronounced under high moisture conditions which encourage the continuation of vegetative growth.

Management strategies need to be examined to improve seed production in Maku lotus. These include techniques (e.g. dryland conditions with controlled irrigation) to encourage more main shoot growth in the months of September, October and November but also to suppress them in December and January. Any management which encourages the earlier occurrence of primary lateral shoots at a lower stem node location in order to avoid their simultaneous growth and development with flower buds, flowers and pods would be likely to allow improved partitioning of assimilates to the seeds during their development and to increased seed yield in this crop.

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