Journal of Agricultural Science, Cambridge (1999), **133**, 141–150. *Printed in the United Kingdom*

© 1999 *Cambridge University Press*

Seed and pod development of autumn-sown, determinate white lupins (*Lupinus albus*) in relation to the assimilation and distribution of dry matter and nitrogen in crops grown at different densities

G. F. J. MILFORD*, I. F. SHIELD, H. J. STEVENSON, T. SCOTT AND J. E. LEACH

IACR-Rothamsted, Harpenden, Hertfordshire AL5 2JQ, UK

(*Revised MS received 13 May 1999*)

SUMMARY

Pod and seed growth were studied in two experiments in which the plant's source-sink relationships were modified by (a) manually pruning an autumn-sown, indeterminate white lupin variety, Lunoble, to a determinate form, and (b) by growing a determinate variety, Lucyane, at densities ranging from 7 to 35 plants/m². The pruning experiments indicated that the faster pod growth rate of determinate genotypes was not an inherent genetic trait but an indirect physiological consequence of the plant's changed architecture. In the density experiment, crop dry matter (DM) and nitrogen (N) were maximum at the end of pod extension in late July and similar across the plant density range at *c.* 12 t DM and 320 kg N/ha. Therefore, the amount of dry matter per plant decreased proportionately with the increase in plant number. The DM and N contents of the pod walls were also maximum at the end of pod extension, but seeds contained only a third of their final DM and a quarter of their final N. Protein accumulation during the final stages of seed growth, therefore, depended on the remobilization of nitrogen from other plant organs, primarily the leaves and pod walls. Nitrogen withdrawn from the leaves accounted for 44% of the gain in the pods, and N withdrawn from pod walls for 50–60% of the gain in the seed.

Seed number/m² was the major yield component. Seeds and pods mainly aborted during early development, but seed number per pod was also decreased by some seed abortion after full pod extension, especially in first-order pods of plants grown at high density. The number of late-aborted seeds was negatively correlated with the amount of N remobilized from the pod wall. In determinate lupins, which have highly synchronous flowering and pod development, the large and sudden remobilization of nitrogen from leaves and pod walls for seed growth and protein accumulation triggered crop senescence.

INTRODUCTION

The white lupin has long been regarded as a candidate protein crop for Europe with the potential to rival imported soyabeans, but the spring-sown, indeterminate genotypes so far tested in the UK have not been successful because, although they sometimes yielded well, they usually produced excessive vegetative growth and ripened late (Williams 1979; Heath 1987; McEwen 1989). However, new, autumn-sown, determinate white lupin genotypes have been bred recently (Julier & Huyghe 1993) and the determinate character shown to be monogenic and recessive (Julier 1994). The main features of the determinate growth habit are that plant structure is restricted to a mainstem plus one order of branches, that the vegetative and reproductive growth phases are distinctly separated, and that flowering and pod development on the mainstem and branches are near synchronous with all pods being borne at the same level within the canopy (Julier & Huyghe 1992). It has been suggested that determinate genotypes set more pods and maintain faster rates of pod growth than indeterminates because they have better radiation profiles within the canopy (Milford *et al.* 1993*a*) and less competition for resources between the vegetative and reproductive growth (Julier 1994). Because of these features, determinate genotypes potentially have a higher yield potential, better yield stability and

* To whom all correspondence should be addressed.
Email: george.milford@ukgateway.net

https://doi.org/10.1017/S0021859699006826 Published online by Cambridge University Press

earlier ripening compared with indeterminate genotypes, especially in the cooler maritime climates of northern Europe (Julier *et al.* 1994). Potential disadvantages are that they have fewer branch leaves which might limit light interception during the early stages of growth (Julier 1994) and, unlike indeterminate genotypes, their seed yield is strongly and positively correlated with DM production (Harzic *et al.* 1997). Seed yield and grain protein content in determinate genotypes may also be more strongly influenced by the nitrogen status of the plant than in indeterminates. During the later stages of pod development in determinate genotypes, the large number of synchronously developing seeds is likely to create a large demand for nitrogen to sustain seed growth and protein accumulation. To meet this demand, the plant either has to rely on the fixation of atmospheric N by root nodules or soil supplies, or has to remobilize internal reserves of previously accumulated nitrogen which could, according to the hypothesis of Sinclair & de Wit (1976), lead to premature senescence. The extent to which determinate lupins remobilize N to maintain grain growth and protein content is examined in this paper, using unpublished data from previously reported experiments.

MATERIALS AND METHODS

The experiments were done on a clay loam with flints of pH 6·5–7·2 at Rothamsted Experimental Station in Hertfordshire between 1990 and 1993. Full details of the experiments and descriptions of indeterminate and determinate lupin structures have been given by Milford *et al.* (1993*b*) and Shield *et al.* (1996). Briefly, Expt 1 (1990/91) compared the growth of pods of a determinate variety (Lucyane) with that of an indeterminate variety (Lunoble), and with Lunoble manually pruned to the determinate structure. In Expt 2 (1991/92), pod and seed growth was compared in Lucyane grown at a range of plant densities (7, 14, 21, 28 and 35 plants/m^2).

The lupins were sown with a Nodet drill on 25 September 1990 and 9 September 1991 using seed treated with an iprodione + carbendazim fungicide mixture, and inoculated with *Bradyrhizobium lupini* (MicroBio, Hemel Hempstead). The three treatments of Expt 1 were randomized within three replicate blocks in 2·4 × 3·0 m plots drilled with 22 seeds/m^2 in rows 0·6 m apart. The five density treatments of Expt 2 were randomized within four replicate blocks on 6·0 × 2·9 m plots containing eight rows spaced 0·36 m apart. Plots were drilled at twice the required seed rate and thinned to the final populations in the following March. Appropriate herbicides and pesticides were applied to both experiments to control weeds, pests and diseases.

The dates of flowering on the mainstem and branches were recorded as the day on which at least one floret was open on the relevant inflorescence on 50% of the plants. The total number of florets and the maximum number of pods set on the mainstem and the upper three first-order branch inflorescences were counted in two subplots within each plot of the lowest and highest density treatments. In Expt 1, the lengths of five marked pods on the mainstem and five on the first-order branches were measured *in situ* on ten plants per plot at intervals of 3–7 days. Generalized logistic equations were fitted to the pod growth curves and the parameters used to calculate the weighted mean rates and durations of growth were as described by Milford & Riley (1980) for sugarbeet leaves. In Expt 2, plants were sampled from an area of 1·3 m^2 in each plot (1·5 m × 3 rows) at the start of spring growth (23 April), at emergence of the mainstem inflorescence (19 May), at full pod set (17 June), at full pod extension (29 July), and at final harvest (28 August). Plants were separated into leaves, mainstem plus branches, and the different orders of pods. In addition, intermediate samples of pods were taken from ten plants per plot at 10-day intervals from pod set. On each sampling occasion, the total number of pods was counted, and pod length, seed number, and seed and pod wall weights were determined on a subsample of 20 pods of median length from each order. The dry matter of each plant part was weighed, the samples milled, and their nitrogen contents determined by Kjeldahl analysis. The final number of mainstem leaves, the number of florets produced by the mainstem inflorescence, and the total number of florets produced by the three uppermost first-order branches were measured *in situ* during flowering on five plants per plot in the 7 and 35 plants/m^2 density treatments. Plants were harvested by hand when fully mature (i.e. seed moisture was below 20%) from a 5 m length of the central six rows of each plot. One fifth of the plants was used to measure the branching structure and components of yield within each pod order, and the remainder threshed in a stationary combine. Accumulated day degrees above 3 °C (°C days) were calculated using weather data collected at an official meteorological station within 0·5 km of the experiments.

RESULTS

Expt 1, 1990/91

Flowering

The mainstem inflorescence of the indeterminate variety, Lunoble, flowered on 22 May 1991 (1590 °C days after sowing), and inflorescences on the first- and second-order branches on 23 June (1855 °C days) and 10 July (2075 °C days), respectively. The mainstem inflorescence of the determinate variety, Lucyane, flowered on 29 May (1650 °C days after sowing and 1 week later than in Lunoble), and the first-order inflorescences within 5 days of the mainstem on

https://doi.org/10.1017/S0021859699006826 Published online by Cambridge University Press

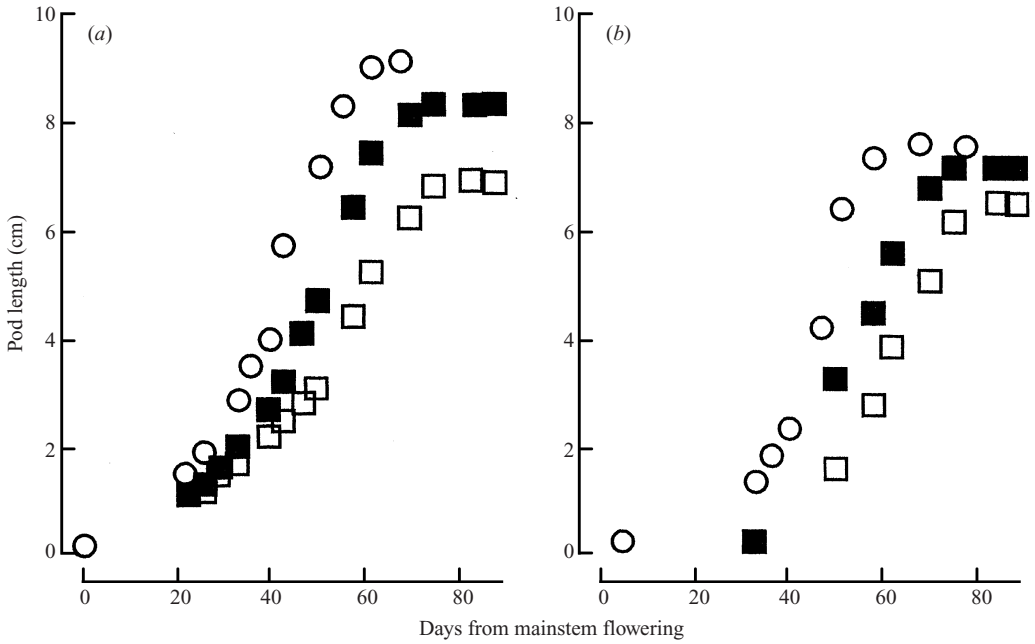

Fig. 1. Growth in length of (*a*) mainstem and (*b*) first-order pods of the determinate white lupin variety Lucyane (○), the indeterminate variety Lunoble (□), and Lunoble pruned to a determinate form (■). The respective weighted mean growth rates were 0·19, 0·12 and 0·15 cm/day for mainstem pods, and 0·21, 0·22 and 0·21 cm/day for first-order pods (S.E. = 0·008, 15 D.F.).

Table 1. *The effects of planting density on the structure, yield and components of yield of the determinate white lupin variety, Lucyane*

	Plants/m²					S.E. (D.F.)
	7	14	21	28	35	
Plants/m² at harvest	4·8	12·8	17·1	22·4	28·8	1·17 (12)
No. mainstem leaves	30·0	—	30·6	—	31·5	0·45 (10)
First-order branches/plant	6·1	5·2	4·5	4·1	2·9	0·15 (12)
Pods/plant						
Mainstem	27	24	20	18	13	1·0 (12)
First-order	34	21	16	12	6	2·4 (12)
Total No. pods/m²	393	684	620	676	557	34·8 (12)
Seeds/pod						
Mainstem	4·0	4·0	4·2	3·7	3·5	0·16 (12)
First-order	3·1	2·8	2·7	2·3	2·1	0·09 (12)
Mean seed weight (mg)						
Mainstem	231	242	242	241	251	7·9 (12)
First-order	229	259	257	254	269	9·4 (12)
Seed yield						
t/ha	2·21	4·32	4·46	4·27	4·12	0·170 (12)
% on mainstem	34	44	54	58	65	

3 June (1680 °C days after sowing and almost 3 weeks earlier than in Lunoble).

Pod growth

The mainstem pods of Lucyane grew, completed their growth sooner, and reached a greater final length than those of Lunoble. The growth rate and final length of the mainstem pods of Lunoble were increased by pruning plants to a determinate form. First-order pods grew faster than mainstem pods but

https://doi.org/10.1017/S0021859699006826 Published online by Cambridge University Press

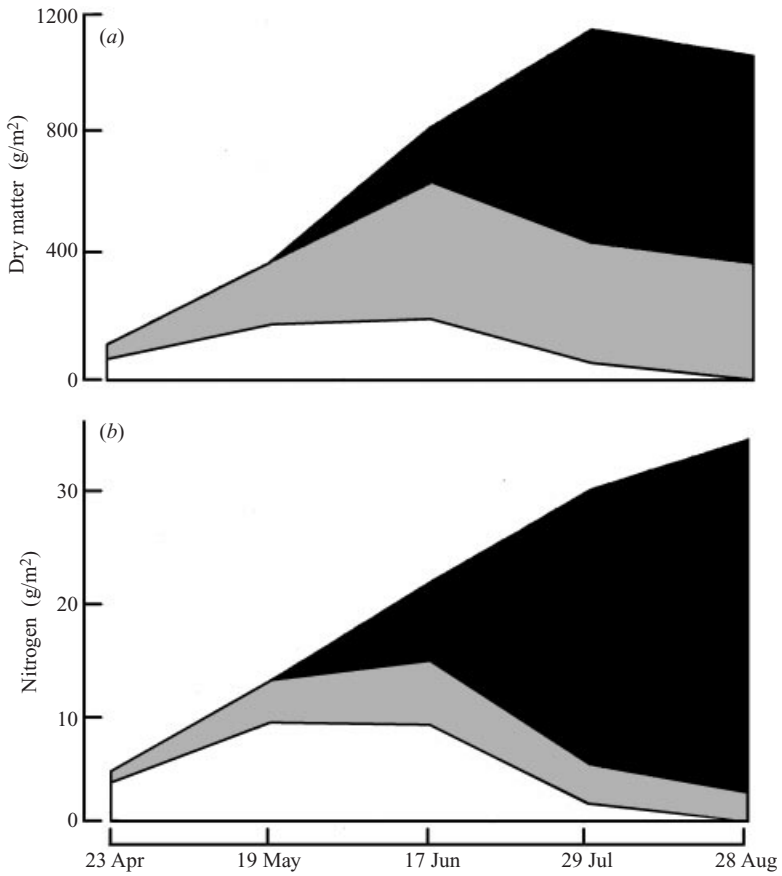

Fig. 2. Patterns of (*a*) dry matter production and (*b*) N assimilation and distribution to the leaves (□), stems plus branches (▨) and pods (■) of the determinate white lupin variety Lucyane grown at a density of 21 plants/m².

the duration of growth and final length were shorter. The effect of pruning the indeterminate genotype was also smaller (Fig. 1).

Expt 2, 1991/92

Plant structure and final pod numbers

Increasing the planting density of the determinate variety Lucyane decreased the number of first-order branches and the number of pods per plant. It did not affect the number of mainstem leaves or seeds per mainstem pod but decreased seed number in first-order pods. A similar number of pods/m² was obtained over much of the density range because pod number per plant decreased proportionately with the increase in plant number. Mean seed weight was not affected by plant density, except in first-order pods of plants grown at the lowest density. A significantly smaller grain yield (2·2 t/ha) was obtained with only 7 plants/m² compared with the rest of the density range within which a similar yield was produced (*c.* 4·3 t/ha) but with an increasing proportion on the mainstem at the higher densities (Table 1).

Distribution of dry matter and nitrogen

The patterns of above-ground DM production and N assimilation and their distribution between the plant organs are shown for crops grown at the median density of 21 plants/m² in Fig. 2. Plants overwintered as a rosette of leaves, and spring growth and stem extension commenced in early March. Dry matter and N initially accumulated in the leaves and stems, reaching a maximum in leaves by mid-May and in the stems and branches by mid-June. As they developed from June onwards, pods rapidly became the major location of both DM and N, and maximum crop DM was achieved toward the end of July and maximum N soon after. Leaves started to relocate N and senesce in mid-June; dead leaves contained less than 0·2 % N. Increasing the plant density only affected crop DM and N between 7 and 14 plants/m²; maximum DM was increased from *c.* 0·9 to 1·3 kg/m² and N from

https://doi.org/10.1017/S0021859699006826 Published online by Cambridge University Press

Table 2. *Maximum above-ground crop dry matter (DM) and nitrogen (N) contents (measured on 29 July) of the determinate white lupin variety Lucyane grown at different planting densities*

	Plants/m²					S.E.
	7	14	21	28	35	(12 D.F.)
			g/m²			
Crop DM	862	1299	1149	1115	1207	89·1
Crop N	22·4	35·9	29·3	30·2	31·8	3·48
			g/plant			
Plant DM	154·2	86·2	64·7	49·2	47·6	10·20
Plant N	4·40	2·38	1·78	1·33	1·23	0·291

c. 22 to 36 g/m² (Table 2). There was no further increase in DM or N/m² with densities above 14 plants/m², but the amounts per plant progressively decreased so that plants grown at the highest density had only a third of the DM and N of plants grown at lowest density (Table 2).

Flowering and pod numbers

Changing the planting density did not affect the flowering date of Lucyane in 1992; the mainstem inflorescence flowered on 24 May 1992 (1220 °C days after sowing), and those on the first-order branches on 30 May (1288 °C days). Floret numbers were measured only at the two extreme densities. At low density, the mainstem inflorescence produced 65 florets and those on the three uppermost first-order branches a total of 157 florets compared with 56 and 86 florets, respectively, at high density (S.E. for mainstem florets = 2·6 with 10 D.F. and for first-order florets S.E. = 8·8 with 10 D.F.). Not all florets set pods, and the number set was greatly affected by the planting density. At the end of flowering, plants grown at low density had set 38 pods per plant on the mainstem inflorescence and a total of 64 on the first-order branches, compared with 22 and 27 pods per plant, respectively at the highest density (Table 3). Most of the pods that aborted were shed within a month of flowering, whereas the number of seeds/m² decreased sharply soon after flowering and continued to decrease gradually through to harvest, particularly on the branches rather than the mainstem and at high rather than low plant densities (Table 3). Plants grown at high density retained to harvest only 62% of the pods set on the mainstem and 22% of those on the first-order branches, compared with 70% and 53%, respectively, for plants grown at low density.

Pod and seed development

At the standard density of 28 plants/m², mainstem pods grew to a longer length than the first-order pods (Fig. 3*a*). Mainstem and first-order pods were also longer when plants were grown at lower densities (Table 3). Pods completed their growth by the end of July and, at this stage, wall DM was at its maximum with more wall DM being present in mainstem than first-order pods. Pod-wall DM subsequently decreased as the seeds grew and the pods matured (Fig. 3*d*). Although initially smaller, first-order seeds achieved the same size at maturity as mainstem seed (Fig. 3*b*), and the effects of density on seed size at maturity were small (Table 3). Seed growth ceased at the beginning of August, and at this time seed weight per pod was at its maximum, mainstem pods contained a much greater weight of seed than first-order pods (Fig. 3*c*), and the weight of seeds in first-order, but not mainstem, pods was decreased by high planting densities (Table 3). First-order pods contained a smaller weight of seed because there were fewer seeds per pod, the numbers having decreased substantially after the end of pod extension (Fig. 4*a*).

Pod and seed nitrogen

The amount of N per seed increased progressively during growth. First-order seed initially contained less N than mainstem seed, in line with their dry-matter growth, but there was no difference between the two categories in the amount of N per seed at maturity (Fig. 4*b*). The amount of N per seed was slightly greater in both mainstem and first-order pods at the higher plant densities (Table 3). There was a greater total amount of N per pod in the seed of mainstem pods than in first-order pods, especially when seed number in first-order pods declined during the later stages of growth (Fig. 4*c*). However, the changes in seed N were largely matched by corresponding changes in seed DM, so there was only a small difference in the protein concentrations of mainstem and first-order seed at harvest (34·7 *cf.* 33·6%; S.E. = 0·22, 27 D.F.), and there was no effect of planting density (Table 3). Wall N increased during pod extension, and was maximal at the end of pod extension. There was less N in the walls of first-order than mainstem pods at the end of pod extension, and less in the walls of first-order pods from plants grown at high as compared to low densities (Table 3). In all cases, pod wall N decreased during the second half of

https://doi.org/10.1017/S0021859699006826 Published online by Cambridge University Press

https://doi.org/10.1017/S0021859699006826 Published online by Cambridge University Press

Table 3. *Effect of plant density on pod and seed characteristics of the determinate white lupin variety, Lucyane.* (* *S.E. for comparing density × pod hierarchy effect*)

		Mainstem pods					First-order pods					
Plants/m²:		7	14	21	28	35	7	14	21	28	35	*S.E. (27 D.F.)
Pod characteristics												
Pod no./plant	End of flowering	38·4	27·5	23·5	25·6	21·5	63·9	46·7	41·8	30·4	26·9	3·45
	End pod extension	30·0	23·2	18·9	16·4	13·8	40·7	14·2	14·2	8·6	10·5	1·91
	Maturity	26·8	23·6	20·1	17·9	13·3	33·8	20·6	16·1	11·6	6·0	1·90
Pod length, cm	End pod extension	9·5	9·2	9·1	9·0	8·8	8·5	7·4	7·5	7·2	6·9	0·21
No. seeds/pod	End pod extension	4·5	4·5	4·4	4·3	4·3	4·4	4·1	4·2	4·0	4·0	0·21
	Maturity	4·0	4·0	4·2	3·7	3·5	3·1	2·8	2·7	2·3	2·1	0·14
Seeds/m²	End of flowering	1002	2128	1994	3033	2894	2696	3623	3376	3541	3130	356·8
	End pod extension	1026	1635	1251	1548	1708	1624	1072	890	872	890	175·3
	Maturity	513	1153	1384	1457	1323	664	726	723	634	377	74·6
Seed and pod wall DM												
Mean DM/seed, mg	Maturity	232	242	242	241	251	229	259	257	255	269	8·3
Seed DM, mg/pod	End pod extension	480	513	484	476	511	350	291	302	211	286	42·0
	Maturity	1053	1037	1015	962	1012	868	716	696	729	654	67·7
Wall DM, mg/pod	End pod extension	804	829	799	778	836	698	575	582	468	518	54·7
	Maturity	491	494	495	422	405	394	389	356	320	307	17·7
Seed and pod wall N												
Seed N, mg/seed	Maturity	13·0	13·1	13·5	13·4	14·1	12·1	13·9	13·8	13·7	14·6	0·55
Seed protein, %	Maturity	34·9	33·9	34·9	34·6	35·0	33·1	33·6	33·4	33·8	34·0	0·50
Seed N, mg/pod	End pod extension	22·8	23·7	22·8	23·8	23·8	14·9	12·2	13·9	9·4	12·8	2·01
	Maturity	55·2	55·7	56·5	52·4	53·2	45·3	38·5	37·3	39·3	33·5	0·86
Wall N, mg/pod	End pod extension	22·9	24·2	23·7	21·6	22·7	19·8	16·2	15·7	12·8	12·7	1·11
	Maturity	5·3	5·5	5·3	4·0	3·3	4·1	3·6	2·9	2·8	2·3	1·34

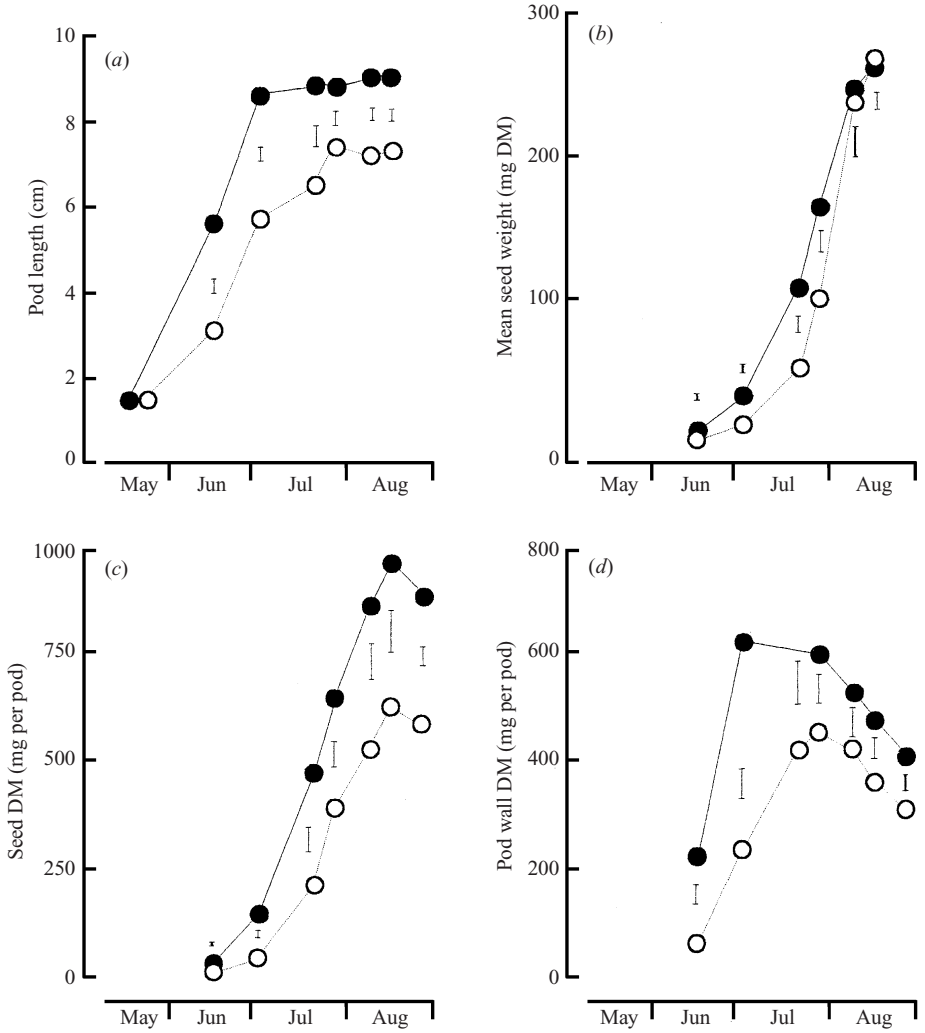

Fig. 3. Changes in (*a*) length, (*b*) mean dry matter per seed, (*c*) seed dry matter per pod and (*d*) wall dry matter during growth of mainstem (●) and first-order (○) pods of the determinate white lupin variety, Lucyane, grown at a density of 28 plants/m^2. Vertical bars indicate the S.E.D. (27 D.F.) for differences between the pod hierarchies.

seed development to very low levels at harvest (Fig. 4*d*). The decrease in seed number per pod between the end of pod extension and harvest was more strongly negatively correlated with amount of nitrogen withdrawn from the pod wall than with the quantity of remobilized DM (Fig. 5).

DISCUSSION

These studies were done on well-grown and productive crops which, at densities above 14 plants/m^2, produced over 10 t DM/ha[1], assimilated over 300 kg N/ha, and yielded close to the ceiling of 5·0 t grain/ha expected from these varieties. The grain yields and yield components of Expt 2 are not considered here as they have already been considered by Shield *et al.* (1996) as part of a wider evaluation of the effects of agronomy and seasonal weather on the performance of determinate lupins in different regions of the UK. Many of the compensatory effects of plant population on crop growth were as described by Herbert (1977) for spring lupins.

The physiology and genetics of modifications to plant architecture in grain legumes has recently been reviewed by Huyghe (1998). The determinate growth habit in *L. albus* was discovered as a monogenic recessive mutation, *epl*, in an early-flowering spring-sown genotype (Mikolajczyk *et al.* 1984) and

https://doi.org/10.1017/S0021859699006826 Published online by Cambridge University Press

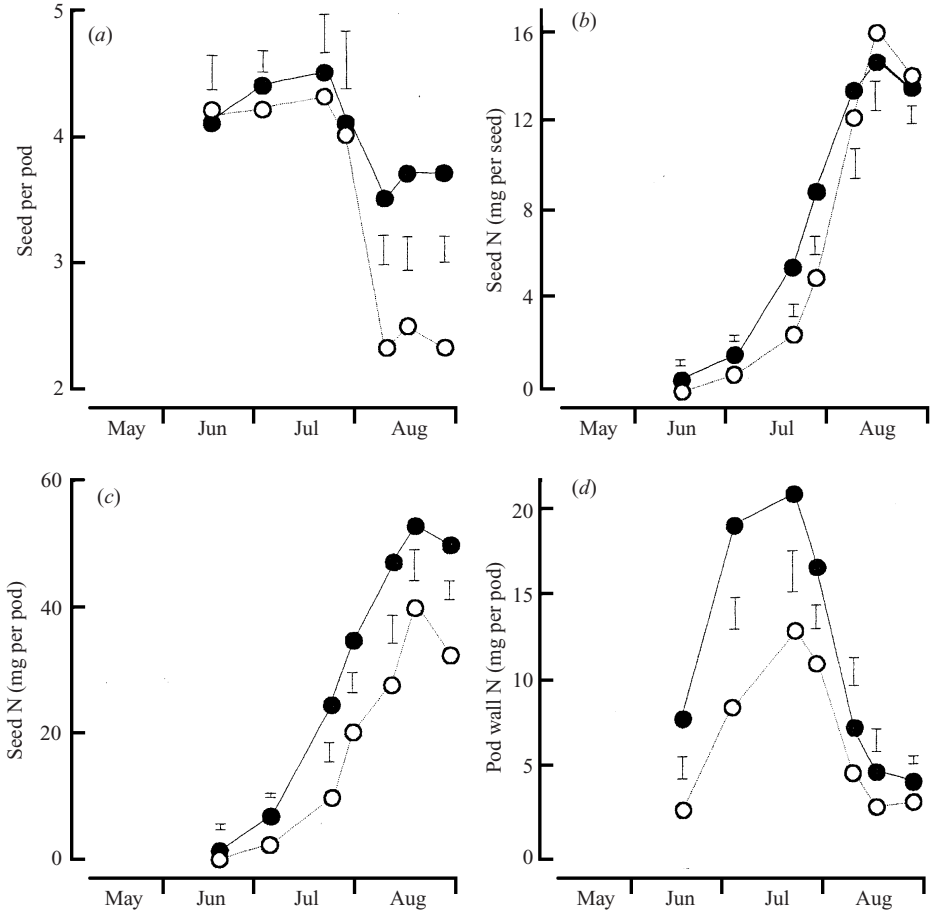

Fig. 4. Changes in (*a*) seed number, (*b*) N per seed, (*c*) seed N per pod and (*d*) wall N per pod during growth of mainstem (●) and first-order (○) pods of the determinate white lupin variety, Lucyane, grown at a density of 28 plants/m². Vertical bars indicate the S.E.D. (27 D.F.) for differences between the pod hierarchies.

transferred by crosses to the autumn-sown genotypes used in this study. The latter genotypes are characterized by a restricted number of branch orders and their ability to set and retain a large number of pods, especially on the mainstem inflorescence. The interdependence of these two characteristics is not clear. The ability to set a large number of pods may be a consequence of the diminished competition between vegetative and reproductive growth conferred by the *epl* gene, or controlled by independent genes. The observation that the pruning of indeterminate plants to a determinate form increased pod set (Milford *et al.* 1993*b*) and the growth rate of mainstem pods favours the physiological rather than the genetic explanation.

There was no significant difference in crop DM production or N assimilation per unit area within the density range of 14–35 plants/m², so both DM and N per plant decreased proportionately with the increase in plant number. The DM and N contents of the plant and pods walls were at their maximum at the end of pod extension, but seeds contained only a third of their final DM and a quarter of their final N. During the final 3–4 weeks of growth, the gains in seed N greatly exceeded the gain in the whole plant, implying that the final stages of seed protein accumulation depended on the remobilization of nitrogen from other plant organs. Some was withdrawn from the leaves, inducing them to senescence and die prematurely, and some from the pod walls. Pate *et al.* (1977) have suggested previously that the pod wall of legumes acts as an important temporary storage site for nitrogen that is later used in seed protein accumulation. Sinclair & de Wit (1976) described the remobilization of large amounts of nitrogen to support grain growth in legumes, and consequent loss of physiological activity and ultimate senescence of the deprived organs, as 'self-destructive'. Munier-Jolain

https://doi.org/10.1017/S0021859699006826 Published online by Cambridge University Press

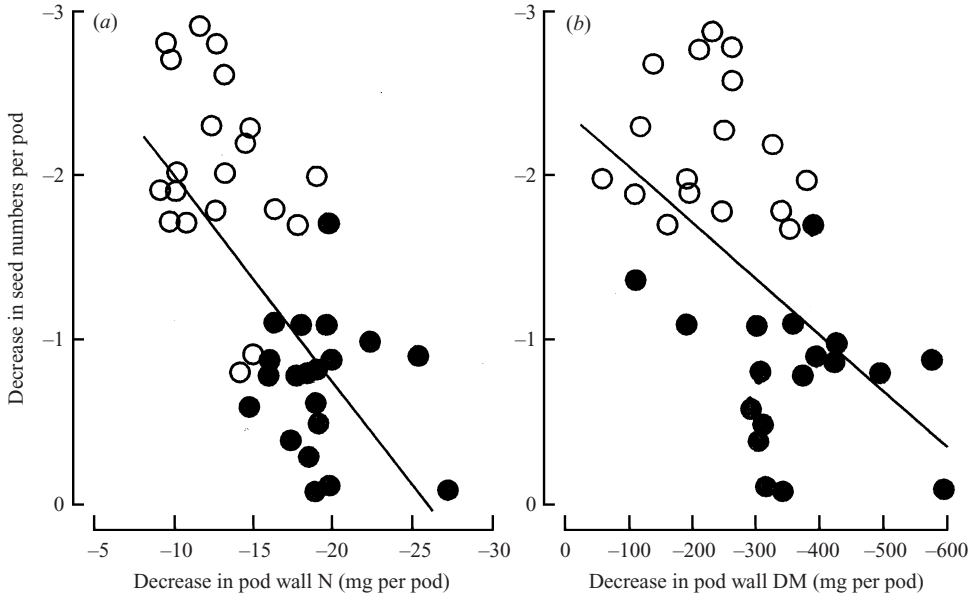

Fig. 5. Relationship between the decrease in seed number per pod between the end of pod extension and harvest and the decrease in (*a*) pod-wall N ($y = 3{\cdot}5–0{\cdot}13x$; % variance = 44·7) and (*b*) pod-wall DM ($y = 2{\cdot}5–0{\cdot}0037x$; % variance = 25·6) in mainstem (●) and first-order (○) pods of the determinate white lupin variety, Lucyane grown at different plant densities.

et al. (1996) showed that the duration of seed filling in indeterminate soyabeans is determined by the amount of available remobilizable N within the plant, seed growth finishing when N reserves are exhausted. In our studies, calculations based on the gross changes in crop N during the final 4 weeks of growth indicate that N withdrawn from the leaves could have accounted for 44% of the N gain in the pods; and those based on changes within pods (Table 3) that withdrawal of N from the wall could have accounted for 50–60% of the gain in the seed. These values are comparable to those published by Duthion *et al*. (1987) for spring-sown lupins grown in France.

Jeuffroy & Ney (1997) concluded that seed number per pod is determined early in seed development at the stage of final seed abortion. This coincides with the start of the linear phase of seed growth (Duthion & Pigeaire 1991). Our work shows that seeds also abort at relatively late stages in their development to leave shrivelled grain from which the constituents have almost completely been re-absorbed. It also shows that the number that aborted late was strongly influenced by the amount of N remobilized from other parts of the plant. Because of their more highly synchronised flowering and seed development, the demand for nitrogen for seed protein accumulation is more concerted and intense in determinate than indeterminate lupin genotypes. One consequence of the 'self-destruct' mechanism of Sinclair & de Wit (1976) in determinate lupins, is that it physiologically triggers early ripening which is crucial in making determinate genotypes better suited to the cooler climates of northern Europe. The intensive relocation of N from other plant organs is also the reason why determinate lupins have a high nitrogen harvest index for N (grain N/total crop N) of 0·82–0·86.

This research was supported by the Biotechnology and Biological Sciences Research Council and the Ministry of Agriculture, Fisheries and Food.

REFERENCES

Duthion, C., Amarger, N. & Mariotti, A. (1987). Accumulation potentielle de matire seche et d'azote chez le lupin blanc de printemps (*Lupinus albus* L.). *Agronomie* **7**, 585–593.

Duthion, C. & Pigeaire, A. (1991). Seed lengths corresponding to the final stage in seed abortion of three grain legumes. *Crop Science* **31**, 1579–1583.

Harzic, N., Shield, I., Huyghe, C. & Milford, G. F. J. (1997). *Lupinus albus* as a European crop. *Proceedings of the 3rd International Food Legume Research Conference*, *Adelaide*, *Australia*.

Heath, M. C. (1987). Grain legumes in UK agriculture. *Outlook on Agriculture* **16**, 2–7.

Herbert, S. J. (1977). Growth and yield of *Lupinus albus* at

https://doi.org/10.1017/S0021859699006826 Published online by Cambridge University Press

different plant populations. *New Zealand Journal of Agricultural Research* **20**, 459–465.

HUYGHE, C. (1998). Genetics and genetic modifications of plant architecture in grain legumes: a review. *Agronomie* **18**, 383–411.

JEUFFROY, M. H. & NEY, B. (1997). Crop physiology and productivity. *Field Crops Research* **53**, 3–16.

JULIER, B. (1994). *Etude génétique et physiologique de l'architecture déterminée chez le lupin blanc d'hiver. Conséquences agronomiques et en sélection*. PhD thesis, L'Ecole Nationale Superieure Agronomique de Rennes.

JULIER, B. & HUYGHE, C. (1992). Heredity of determinate growth in winter white lupin (*Lupinus albus* L.). Influence of the sowing time on architecture. In *Proceedings of the 1st European Conference on Grain Legumes*, *Angers*, *France*, pp. 47–48. Paris: AEP.

JULIER, B. & HUYGHE, C. (1993). Description and model of the architecture of four genotypes of determinate autumn-sown white lupin (*Lupinus albus* L.) as influenced by location, sowing date and density. *Annals of Botany* **72**, 493–501.

JULIER, B., HUYGHE, C. & PAPINEAU, J. (1994). Dry matter and N accumulation in indeterminate autumn-sown white lupin (*Lupinus albus*) *cv*. Lunoble. *European Journal of Agronomy* **3**, 153–160.

MCEWEN, J. (1989). Alternative crops and land use: lupins. In *Report of the Arable Crops Research Institute for 1988*, p. 61. Harpenden: Lawes Agricultural Trust.

MIKOLAJCZYK, J., STAWINSKI, S. & WIZA, M. (1984). Directions actuelles de l'amèlioration et l'état actuel des recherches sur l'acclimatation du lupin blanc en Pologne. In *Proceedings of the 3rd International Lupin Conference*, *La Rochelle*, *France*, pp. 570–571. Paris: International Lupin Association.

MILFORD, G. F. J. & RILEY, J. (1980). The effects of temperature on leaf growth of sugarbeet varieties. *Annals of Applied Biology* **94**, 431–443.

MILFORD, G. F. J., DAY, J. M., HUYGHE, C. & JULIER, B. (1993*a*). Floral determinacy in autumn-sown white lupins (*Lupinus albus*): the development of varieties for cooler European climates. *Aspects of Applied Biology* **34**: *Physiology of varieties*, 89–97.

MILFORD, G. F. J., DAY, J. M., LEACH, J. E., STEVENSON, H. J., HUYGHE, C. & PAPINEAU, J. (1993*b*). The effect of modifying plant structure on the yield and maturity of the white lupin (*Lupinus albus*). *Annals of Applied Biology* **122**, 113–122.

MUNIER-JOLAIN, N. M., NEY, B. & DUTHION, C. (1996). Analysis of branching in spring-sown white lupins (*Lupinus albus* L.): the significance of the number of axillary buds. *Annals of Botany* **77**, 123–131.

PATE, J. S., SHARKEY, P. J. & ATKINS, C. A. (1977). Nutrition of a developing legume fruit. *Plant Physiology* **59**, 506–510.

SHIELD, I. F., STEVENSON, H. J., LEACH, J. E., SCOTT, T., DAY, J. M. & MILFORD, G. F. J. (1996). The effects of sowing date and planting density on the structure and yield of autumn-sown, florally-determinate white lupins (*Lupinus albus*) in the United Kingdom. *Journal of Agricultural Science*, *Cambridge* **127**, 183–191.

SINCLAIR, T. R. & DE WIT, C. T. (1976). Analysis of the carbon and nitrogen limitations to soybean yield. *Agronomy Journal* **68**, 319–324.

WILLIAMS, W. (1979). Studies on the development of lupins for oil and protein. *Euphytica* **28**, 481–488.

https://doi.org/10.1017/S0021859699006826 Published online by Cambridge University Press