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Light interception and utilization of four grain legumes sown at different plant populations and depths

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SUMMARY

Canopy development, radiation absorption and its utilization for yield was studied in four grain legume species *Cicer arietinum*, *Lens culinaris*, *Lupinus angustifolius* and *Pisum sativum*. The grain legumes were grown at different plant populations and sowing depths over two seasons in Canterbury, New Zealand. The green area index (GAI), intercepted radiation, radiation use efficiency (RUE) and total intercepted photosynthetically active radiation (PAR) increased significantly ($P < 0·001$) with increased plant population. Narrow-leafed lupin produced the highest maximum biomass (878 and 972 g/m^2, averaged over all populations during 1998/99 and 1999/2000, respectively) and intercepted more radiation (600 and 714 MJ/m^2, averaged over all populations during 1998/99 and 1999/2000, respectively) than the other three legumes. In all four species, in both trials, the highest plant populations reached their peak GAI about 7–10 days earlier than legumes sown at low populations. Cumulative intercepted PAR was strongly associated with seed yield and crop harvest index (CHI).

The RUE increased (from 1·10 to 1·46 and from 1·04 to 1·34 g/MJ during 1998/99 and 1999/2000, respectively) as plant population increased and was highest in the highest yielding species (e.g. 146 and 1·36 g/MJ for narrow-leafed lupin in both experiments). The larger leaf canopies produced at the higher plant populations reduced the extinction coefficient (k).

The results suggest that in the subhumid temperate environment of Canterbury, grain legume species should be selected for the development of a large GAI. This should maximize PAR interception, DM production and, consequently, seed yield.

INTRODUCTION

In Canterbury, grain legumes have the potential to produce high seed yields but yield varies from species to species, and from season to season. In grain legumes differences in total dry matter (TDM) production were due to differences in both their light utilization efficiency and the amount of light intercepted (Pilbeam *et al.* 1991). Total dry matter production in lentil (*Lens culinaris*) (McKenzie & Hill 1991) and seed yield in faba bean (*Vicia faba*) (Husain *et al.* 1988) were both directly related to intercepted solar radiation.

The green area index (GAI) and leaf angle of a crop determines the amount of radiation absorption, which is decisive in determining TDM production (Ashraf *et al.* 1994). A large GAI is required to fully intercept incident solar radiation (Thomson & Siddique 1997). In several crops seed yield is closely related to TDM production (Loss *et al.* 1998*a*). For many crops this is proportional to the amount of intercepted radiation (Thomson & Siddique 1997). Therefore, high TDM production is associated with a high GAI (Ashraf *et al.* 1994). Greater GA development, radiation absorption and TDM production have been reported in faba bean sown at high plant populations in both temperate and in Mediterranean environments by Stützel & Aufhammer (1992) and in lentil in Canterbury (McKenzie & Hill 1991).

The fraction of light interception (F_i) by a crop is a function of its GAI and the extinction coefficient (k). This is governed by a number of factors such as plant species, leaf size, leaf shape, elevation of the sun and the proportion of direct and diffused solar radiation (Hay & Walker 1989; Thomson & Siddique 1997).

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Table 1. *MAF soil quick test for 0–30 cm depth for the Horticultural Research area (1998/99) and the Henley Research farm (1999/2000) of Lincoln University, Canterbury. Ca, K, P, Mg, Na and S and* NH_4^+, NO_3^- *are expressed as μg/g soil, and total N (TN) and C as mg/g soil*

Season	pH	Ca	K	P	Mg	Na	S	C	NH_4^+	NO_3^-	TN
1998/1999	5·4	7	8	27	16	5	9	24	–	1	2·0
1999/2000	5·8	10	9	12	28	8	9	–	5	<1	2·7

In Canterbury, reported *k* values for field bean (*Vicia faba*) are 0·36–0·48 (Husain *et al.* 1988). McKenzie & Hill (1991) found a *k* value of 0·26 for lentil. However, there is no published data for the *k* value of narrow-leafed lupin (*Lupinus angustifolius*) or *desi* chickpea (*Cicer arietinum*) in a subhumid temperate environment like Canterbury. Thomson & Siddique (1997) reported *k* values of 1·06 for pea and 0·91 among the lupin species *Lupinus albus*, *L. angustifolius*, *L. atlanticus* and *L. pilosus* and 0·76 for lentil. Thomas & Fukai (1995) reported a value of 1·10 in chickpea, in Australia, and there was a range of 0·47–0·61 in Syria (Hughes *et al.* 1987).

Different grain legumes have different leaf sizes, growth patterns and photosynthetic functions. This provides a range of differences in their radiation use efficiency (RUE; the ratio of TDM to total intercepted photosynthetically active radiation (PAR)). It also gives different GAIs at which radiant energy interception approaches a maximum (Hipps *et al.* 1983).

The RUE is a key determinant of crop yield. In Canterbury it ranges from 2·0–2·5 g/MJ in pea (*Pisum sativum*) (Zain *et al.* 1983), and 1·6–1·8 g/MJ in lentil (McKenzie & Hill 1991). In other environments, the highest RUE values reported in grain legumes were 1·15–1·26 g/MJ for soybean (*Glycine max*), and in pea it ranged from 0·98–1·12 g/MJ (Sinclair & Muchow 1999). Faba bean had a highly variable RUE, which ranged from 1·03 g/MJ (Silim & Saxena 1992) to 2·04 g/MJ (Fasheun & Dennett 1982).

Lentils and *desi* chickpeas have much smaller leaflets (Singh 1997) than narrow-leafed lupin and pea, and it is of interest to know their basic response to solar radiation. Birch *et al.* (1998) reported that more, and larger, leaves in maize (*Zea mays*) had a higher PAR interception which consequently gave a higher TDM production. Similar results have been reported in rice (*Oryza sativa*) (Ashraf *et al.* 1994).

There is limited information on grain legumes, which compares their canopy development, canopy geometry and RUE when sown at different plant populations and depths in subhumid temperate environment such as Canterbury. The present study was designed to investigate the effects in four grain legumes sown at different plant populations and depths on (1) radiation interception, DM production and the relationship between them; and (2) the extinction coefficient and its relationship with RUE, in an attempt to explain variations in RUE through differences in canopy structure.

MATERIALS AND METHODS

Details of the experimental design, crop species, crop husbandry, standard measurements and procedures are described in Ayaz *et al.* (2004).

Briefly, in 1998/99, the design used was a split plot with four grain legumes (*desi* chickpea, *Cicer arietinum*; lentil, *Lens culinaris* cv. Rajah; narrow-leafed lupin, *Lupinus angustifolius* cv. fest; and field pea *Pisum sativum* cv. Beacon) as main plots. Subplots were four plant populations: 0·1 × optimum, 1·0 × optimum, 2·0 × optimum and 4·0 × optimum. Optimum populations were 50 plants/m^2 for chickpea, 150 plants/m^2 for lentil and 100 plants/m^2 for both lupin and pea.

The experiment was located at the Horticultural Research Area in 1998/99 and at the Henley Research Farm in 1999/2000, of Lincoln University, Canterbury, New Zealand (43°38′S, 172°30′E).

In 1999/2000, the experiment was a split–split plot design with the same four legumes as main plots. The subplots were three plant populations (10, 100 and 400 plants/m^2) and three sowing depths (2, 5 and 10 cm) were sub-subplots. Experiment 1 was given 75 mm of water by sprinkler irrigation. No irrigation was applied to Expt 2. Both sites were a Wakanui silt loam soil (Hewitt 1992). A Ministry of Agriculture and Fisheries (MAF) soil quick test was done each season to determine available soil nutrients (Table 1).

Details of the climate in both seasons are given in Fig. 1. The data were from the Broadfields Meterological station located at about 1 km from both trial sites.

Measurements

The green area index (GAI) and the amount of radiation transmitted through the canopy (T_i) were measured in both experiments using a LICOR LAI 2000 Plant Canopy Analyser (LICOR Inc., Lincoln, Nebraska, USA). The GAI and T_i were measured weekly from 35 days after sowing (DAS) until

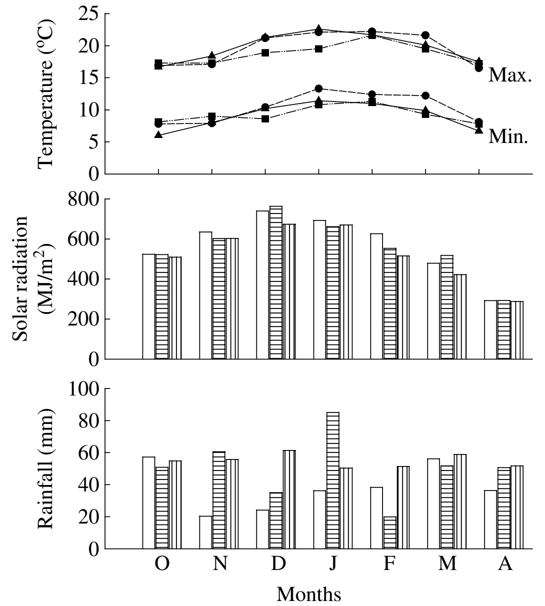

Fig. 1. Climate data for the 1998/99 (□, ●) and 1999/2000 (⊟, ◆) growing seasons and long-term means (▥, ▲) for Lincoln University, Canterbury, New Zealand. (Long-term means for rainfall and temperature 1944–99; solar radiation 1975–99.)

physiological maturity of each species in 1998/1999 and at 10–12 days' interval from 31 DAS until physiological maturity in 1999/2000. Four above and below canopy measurements were taken per plot per session. The proportion of radiation intercepted (F_i) by the canopy was calculated using the technique of Gallagher & Biscoe (1978).

$$F_i = 1 - T_i \tag{1}$$

The amount of photosynthetically active radiation (PAR) absorbed by the crop (S_a) was calculated from (Szeicz 1974):

$$S_a = F_i \times S_i \tag{2}$$

where S_i is the total incident PAR.

The extinction co-efficient (k) of the canopy was calculated from the slope of the regression line between $\ln(1-F_i)$ and GAI (Monteith 1965).

$$k = -\ln(1-F_i) \tag{3}$$

Statistical analysis

All variates were analysed using analysis of variance. The statistical package used was Genstat. Standard errors (S.E.), coefficient of variation (CV as a %) and percentage variation accounted for, the correlation coefficient (r), were also calculated.

RESULTS

Climate

The weather from October 1998 to April 1999 was dry and rainfall was about 40 % less than the long-term average (Fig. 1). Mean temperature and solar radiation were higher than the long-term average by 5 and 7 %, respectively, from January to March 1999. In the second year, rainfall was about 90 % of the long-term average (385 mm). The mean monthly maximum temperatures during December 1999 and January 2000 were lower, at 18·9 and 19·5 °C, than the long-term averages values of 21·3 and 22·6 °C respectively (Fig. 1). Solar radiation from December 1999 to March 2000 was about 10 % higher than the long-term mean.

Green area index

There was a significant trend for GAI to increase at higher plant populations from about 45 DAS until close to physiological maturity in both seasons. In 1998/99, the plant population of 0·1 × optimum reached a peak GAI of 2·38 in chickpea, 2·63 in lentil, 3·72 in narrow-leafed lupin and 3·58 in field pea, compared with 4·20, 4·33, 6·10 and 5·62 at 4·0 × optimum population, respectively (Fig. 2*a–d*). In 1999/2000, the highest populations achieved their maximum GAI about 10 days earlier than the lowest population (Fig. 2*e–h*). The maximum GAIs at 400 plants/m² in chickpea, lentil, narrow-leafed lupin and field pea were 4·73, 4·56, 6·00 and 5·83, respectively.

In both seasons, GAI declined rapidly at the higher populations after peak GAI was achieved. However, it remained constant or increased at 0·1 × optimum population in the first year and at 10 plants/m² in the second year. All four legumes showed similar trends. As crops senesced, GAI decreased.

Radiation interception

In 1998/99, field pea intercepted 95 % of incident solar radiation by 56 DAS. Comparable values were 75 % for lentil, 70 % for narrow-leafed lupin and 58 % for chickpea (Fig. 3*a–d*). Similarly in 1999/2000, field pea intercepted 90 % of the incident radiation by 62 DAS, while lentil, narrow-leafed lupin and chickpea intercepted 70, 78 and 80 %, respectively, by the same time (Fig. 3*e–h*). Similar trends to those in GAI were evident in the proportion of intercepted radiation (F_i).

Significantly ($P < 0·001$) more radiation was intercepted at the highest plant population in both seasons (Fig. 3). The maximum F_i was about 95 % in both seasons and generally it coincided with peak GAI. The F_i did not decline as rapidly as the GAI. However, radiation interception generally followed similar patterns in all species and F_i was strongly affected by

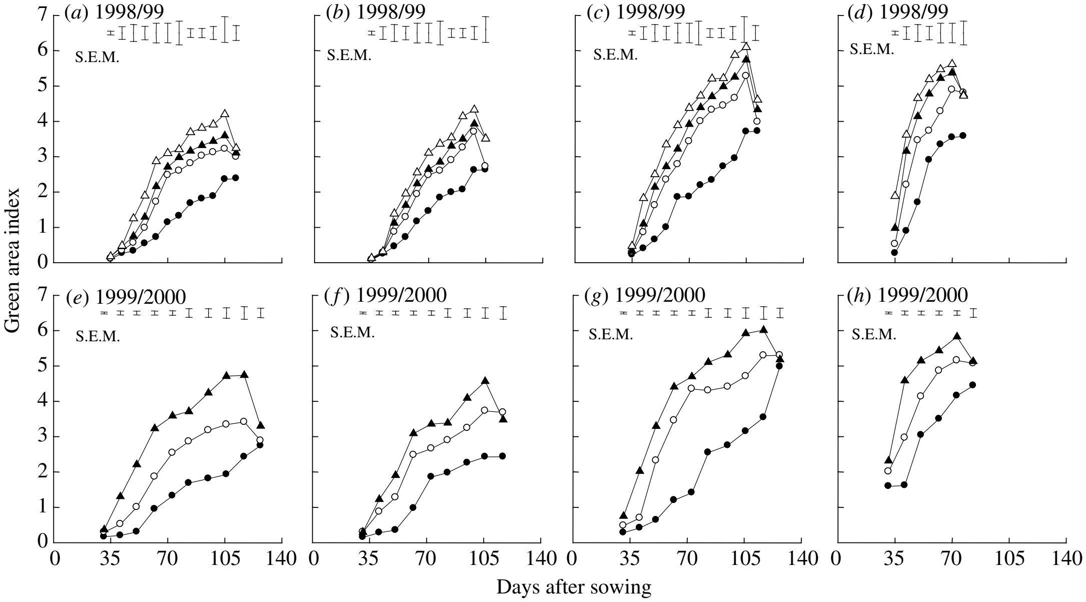

Fig. 2. The Green area index over the growing seasons of four grain legumes sown at different plant populations, (i) 1998/1999 (*a–d*): 0·1 × optimum (●), 1·0 × optimum (○), 2·0 × optimum (▲), 4·0 × optimum (△), (ii) 1999/2000 (e–h): 10 plants/m² (●), 100 plants/m² (○), 400 plants/m² (▲). (*a*, *e*) chickpea, (*b*, *f*) lentil, (*c*, *g*) narrow-leafed lupin, (*d*, *h*) pea.

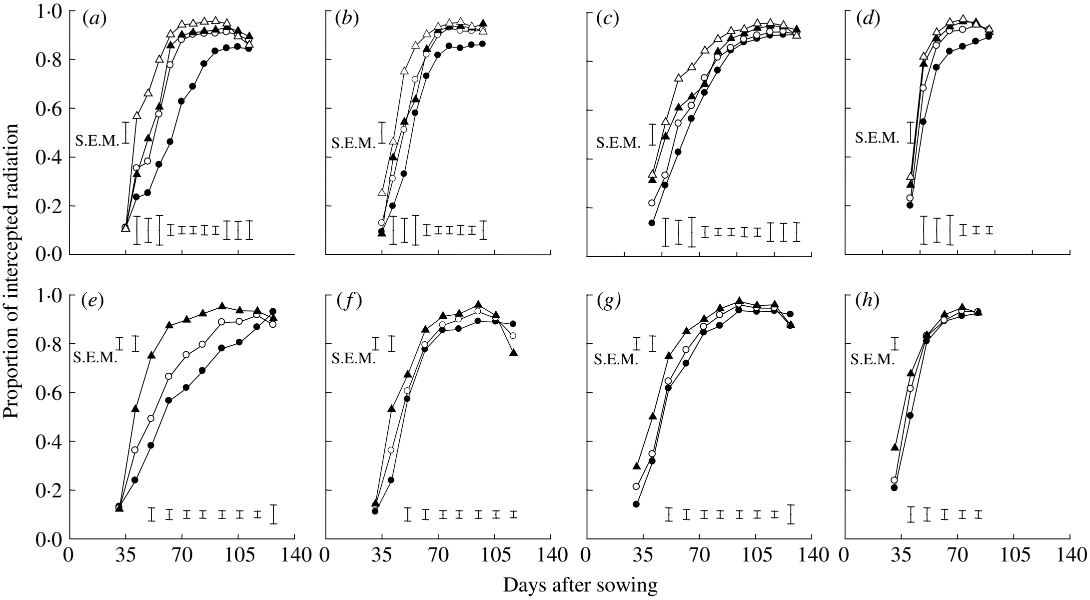

Fig. 3. The proportion of intercepted radiation (F_i) up to maximum green area index over two growing seasons of four grain legumes sown at different plant populations, (i) 1998/1999 (*a–d*): 0·1 × optimum (●), 1·0 × optimum (○), 2·0 × optimum (▲), 4·0 × optimum (△), (ii) 1999/2000 (*e–h*): 10 plants/m² (●), 100 plants/m² (○), 400 plants/m² (▲). (*a*, *e*) chickpea, (*b*, *f*) lentil, (*c*, *g*) narrow-leafed lupin, (*d*, *h*) pea.

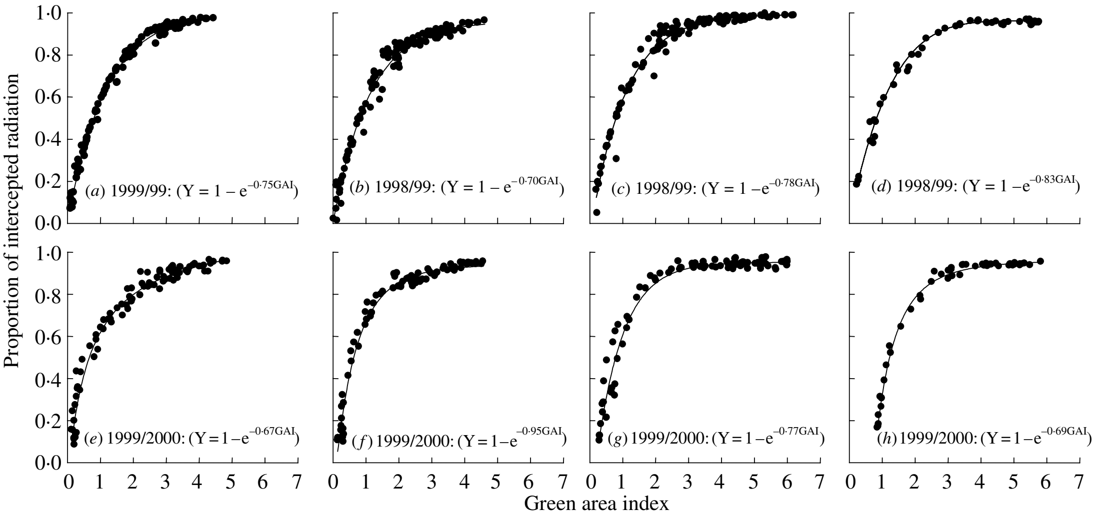

Fig. 4. The relationship between green area index and the proportion of intercepted radiation in four grain legumes sown at different plant populations, 1998/1999 and 1999/2000. (*a*, *e*) chickpea, (*b*, *f*) lentil, (*c*, *g*) narrow-leafed lupin, (*d*, *h*) pea.

GAI, which showed a typical exponential function (Fig. 4). A GAI of 3·5–4·0 was required to intercept 90–95% of incident radiation in chickpea. To intercept the same amount of incident radiation in lentil, narrow-leafed lupin and field pea required GAIs of 4·2–4·5, 3·1–3·5 and 3·1–3·8, respectively.

Total intercepted PAR

In both seasons total intercepted photosynthetically active radiation (PAR) varied significantly among species ($P < 0{\cdot}001$) and populations ($P < 0{\cdot}001$). However, their interactions were also significant ($P < 0{\cdot}05$). In 1998/99, narrow-leafed lupin intercepted the most PAR at 600 MJ/m^2. Lowest interception of 366 MJ/m^2 was in pea (Table 2). The species by population interaction (Table 3) ($P < 0{\cdot}05$) shows that chickpea, lentil and field pea responded in the same way to increased plant population by intercepting about 50% more intercepted PAR. However, there was only a 25% increase in intercepted PAR when plant population increased from 0·1 × optimum to 4·0 × optimum in narrow-leafed lupin. In 1999/2000, narrow-leafed lupin had a 60% higher total intercepted PAR than pea (Table 2). In all four species higher populations intercepted more PAR than the lower populations (Table 4).

In 1999/2000, different sowing depths also gave significant differences ($P < 0{\cdot}05$) in light interception. However, intercepted PAR was only increased by 5% as sowing depth increased from 2 to 10 cm. On average, in 1999/2000 all four species intercepted 25% more PAR than in 1998/99 (Table 2).

The extinction coefficient

The extinction coefficient (k) of field pea ($k = 0{\cdot}83$) was higher than that of the other three species in 1998/99. The k of lentil (0·69) was lowest in this season (Fig. 5*a–d*). In 1999/2000, the k of narrow-leafed lupin was higher ($k = 0{\cdot}76$) than in the other three species (Fig. 5*e–h*). Averaged over both seasons, the k of chickpea, lentil, narrow-leafed lupin and field pea was 0·70, 0·67, 0·77 and 0·76, respectively. The value of k, among the different plant populations, decreased slightly with increased plant population. Therefore only pooled data for all populations in each year are shown.

Radiation use efficiency

In 1998/99 radiation use efficiency (RUE) varied significantly among legume species ($P < 0{\cdot}001$) and populations ($P < 0{\cdot}001$) (Fig. 6). The RUE tended to increase with DAS to a maximum level in each species at each population density and then the RUE declined to that of the lowest population. Field pea at 4·0 × and 2·0 × optimum population had the highest RUE of 1·68 g DM/MJ intercepted PAR, at 49 DAS. In narrow-leafed lupin, the highest RUE was 1·40 g DM/MJ intercepted PAR at 4·0 × optimum population at 63 DAS.

Species, population and their interactions all significantly affected the final RUE. In both seasons the RUE of lentil was lower than in the other three species (Table 2). In 1998/99, RUE tended to increase in all four species, as population increased up to

Table 2. *The effect of legume species, plant population and sowing depth on total seasonal intercepted photosynthetically active radiation (PAR) and radiation use efficiency (RUE) in Canterbury in 1998/1999 and 1999/2000*

Treatments	Total PAR_i (MJ/m^2)	RUE (g/MJ)
1998/99		
Species (S)		
Chickpea	489	1·25
Lentil	368	1·11
Lupin	600	1·46
Pea	366	1·42
S.E. (D.F. = 3)	4·73	0·017
Population (P)		
0·1 × optimum	364	1·10
1·0 × optimum	454	1·42
2·0 × optimum	479	1·46
4·0 × optimum	527	1·31
S.E. (D.F. = 3)	5·64	0·028
CV %	4·3	7·2
1999/2000		
Species (S)		
Chickpea	634	1·24
Lentil	522	0·90
Lupin	714	1·36
Pea	447	1·32
S.E. (D.F. = 3)	9·59	0·021
Population (P)		
10 plants/m^2	466	1·04
100 plants/m^2	594	1·25
400 plants/m^2	678	1·34
S.E. (D.F. = 2)	6·58	0·017
Depth (D)		
2 cm	565	1·23
5 cm	581	1·22
10 cm	588	1·22
S.E. (D.F. = 2)	9·25	0·010
CV %	5·3	5·8

2·0 × optimum population (Table 3). In 1999/2000 their interaction (Table 4) showed that RUE was directly related to plant population from 10 to 400 plants/m^2. Averaged over all, the RUE was about 15% higher in 1998/99 than in 1999/2000 (Table 2). In both seasons k was inversely related to RUE (Fig. 7).

Correlations

The relationship between total intercepted PAR and TDM production at final harvest in all four species in both years was linear (Fig. 8*a*, *b*). In both seasons, the regression accounted for about 90% of the variance and the slopes indicated RUE values of 1·5, 2·0, 1·5 and 2·0 g DM/MJ of intercepted PAR for chickpea, lentil, narrow-leafed lupin and field pea, respectively. In 1998/99, seed yield was linearly correlated with total intercepted PAR (Fig. 8*c*) ($R^2 > 0{\cdot}77$) ($P < 0{\cdot}01$). Averaged over all four species, the relationship showed that 1·21 g of seed was produced per MJ of intercepted PAR. In 1999/2000, seed yield was again highly correlated with total intercepted PAR, and the regression accounted for 88% of the variance. The slope indicated 1·23 g of seed was produced per MJ of intercepted PAR (Fig. 8*d*). There were also strong associations ($P < 0{\cdot}01$) between intercepted PAR and CHI (Fig. 8*e*,*f*). In 1998/99 the R^2 values accounted for > 80% of the variance in all species, except in chickpea ($R^2 = 63\%$).

DISCUSSION

The quantity of solar radiation available to a plant determines its potential TDM production within the constraints imposed by other limiting factors such as water supply and nutrient availability. The quantity of PAR intercepted by a crop can be increased by rapid attainment of complete ground cover and by increasing the amount of canopy cover at any time, up to a definable threshold. Either mechanism can account for greater TDM production at high plant populations. Conversely, lower plant populations yielded less TDM, had lower GAIs and intercepted less PAR. All four legume species showed the same trend of increased GAI, intercepted PAR and biomass production as plant population increased. At the same time k values decreased as population increased.

Different legume species had the ability to intercept different amounts of PAR. In the present study the highest total seasonal intercepted PAR was by narrow-leafed lupin and the lowest was in lentil and field pea. This is consistent with work on lentil by McKenzie & Hill (1991) and chickpea by Anwar (2001) in Canterbury. In other environments, high yielding genotypes of *Lens culinaris* (Silim *et al.* 1993) and *Pisum sativum* (Martín *et al.* 1994) intercepted more solar radiation than lower yielding genotypes.

Plant population substantially influenced the proportion of intercepted radiation (F_i), and this followed a consistent pattern to the GAIs (Figs 2 and 3) as reported in other legume species (Loss *et al.* 1998*a*; Anwar 2001). This is a major factor in high radiation interception, as a large vegetative plant frame increased PAR interception in peanut (*Arachis hypogaea*) (Gardner & Auma 1989). Singh (1991) found that a decrease in chickpea GAI caused a corresponding reduction in F_i by the canopy and TDM production.

Generally, F_i has been related to crop GAI by an exponential function (Trapani *et al.* 1992). In the present study, the best fit of an exponential function between F_i and GAI (Fig. 4) showed that the amount of radiation intercepted (pooled data of all populations)

Table 3. *The species by population interaction of total seasonal intercepted PAR (MJ/m²) and final RUE (g/MJ) in Canterbury, 1998/99*

	Plant population			
Species	0·1 × optimum	1·0 × optimum	2·0 × optimum	4·0 × optimum
Total intercepted PAR (MJ/m²)				
Chickpea	366	503	515	572
Lentil	290	362	373	445
Lupin	531	583	621	664
Pea	270	368	405	425
S.E. (D.F. = 9)		10·86		
Final RUE (g/MJ)				
Chickpea	1·10	1·35	1·38	1·21
Lentil	0·66	1·31	1·33	1·15
Lupin	1·40	1·47	1·48	1·46
Pea	1·10	1·53	1·65	1·41
S.E. (D.F. = 9)		0·052		

Table 4. *The species by population interaction of total seasonal intercepted PAR (MJ/m²) and final RUE (g/MJ) in Canterbury, 1999/2000*

	Population		
Species	10 plants/m²	100 plants/m²	400 plants/m²
Total intercepted PAR (MJ/m²)			
Chickpea	482	641	779
Lentil	412	543	610
Lupin	620	727	796
Pea	349	464	529
S.E. (D.F. = 6)		14·40	
Final RUE (g/MJ)			
Chickpea	1·10	1·32	1·33
Lentil	0·62	0·96	1·10
Lupin	1·34	1·32	1·41
Pea	1·10	1·38	1·47
S.E. (D.F. = 6)		0·035	

increased exponentially up to about 90–95% with increased GAI. An exponential function describing the relationship between F_i and GAI, has been found in other grain legumes in Canterbury (McKenzie & Hill 1991; Anwar 2001).

Compared with 1998/99, in 1999/2000 all four legumes covered the ground more slowly and there was lower PAR absorption during the growing season. Species differences in TDM depended more on growth duration. Narrow-leafed lupin and chickpea had a much higher duration than pea and lentil. Again, this would give greater intercepted radiation. However, they all had higher yields (see Ayaz *et al.* 1999, 2001). In 1998/99, the crops took less time to reach their maximum GAI (Fig. 2). This may have been due to the slightly higher mean temperature and moisture stress caused by low rainfall (200 mm). In contrast, in 1999/2000 rainfall was well distributed (350 mm) and conditions were cooler early in the growing season. Haloi & Baldev (1986) found a chickpea crop attained a GAI of 7·5 with prolonged soil moisture availability.

Plant population had a significant positive effect on GAI, which had a sigmoid response over time. In all four legume species, in both seasons, GAI tended to increase with increased plant population. The highest populations reached their maximum GAIs earlier than the low plant population. This was consistent with the results of Loss *et al.* (1998*b*) who reported early canopy closure of faba beans when they were sown at high densities. McKenzie & Hill (1991), working with lentil, also considered that high plant population gave earlier canopy closure. This increased GAI, radiation absorption and DM accumulation (Ayaz *et al.* 1999). The GAIs at high plant densities fell earlier but they remained constant at the low plant population. This might have been due to internal competition and leaf senescence at the higher plant populations (Herbert 1977). As expected, leaf senescence increased with increased plant population (data not presented).

Intercepted PAR and yield

In both years highest total intercepted PAR was in narrow-leafed lupin and the lowest was in lentil and field pea. This was due to the large lupin canopy, which led to increased PAR interception (Table 2). Different species have the ability to intercept different amounts of PAR and this is consistent with work on lentil (284–582 MJ/m², McKenzie & Hill 1991) and chickpea (284–562 MJ/m², Verghis 1996) in Canterbury. In the present study, high population density gave significantly earlier canopy closure; a high GAI, more radiation absorption, greater TDM

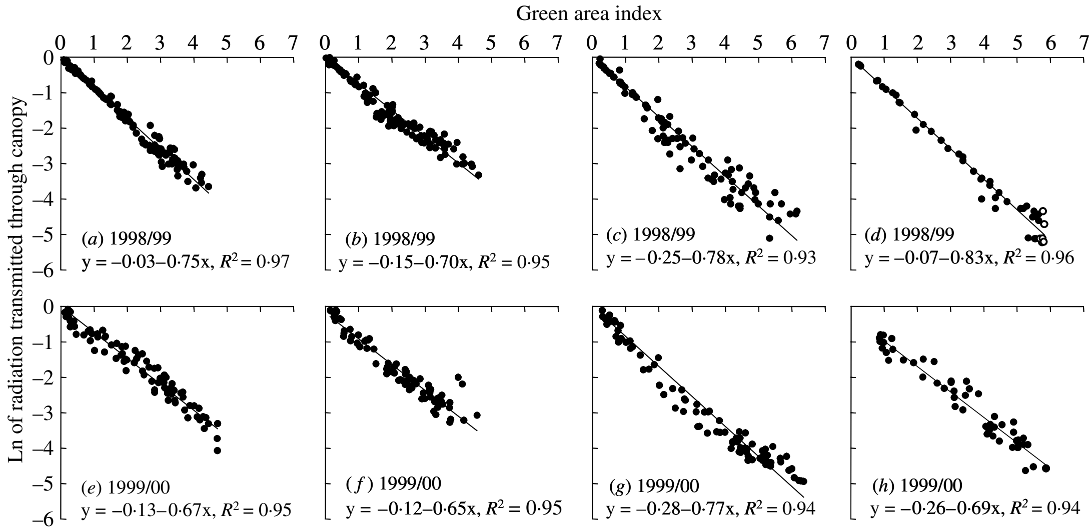

Fig. 5. The relationship between green area index and *ln* of radiation transmitted through canopy of four grain legumes at different plant populations in 1998/99 and 1999/2000. (*a*, *e*) chickpea, (*b*, *f*) lentil, (*c*, *g*) narrow-leafed lupin, (*d*, *h*) pea.

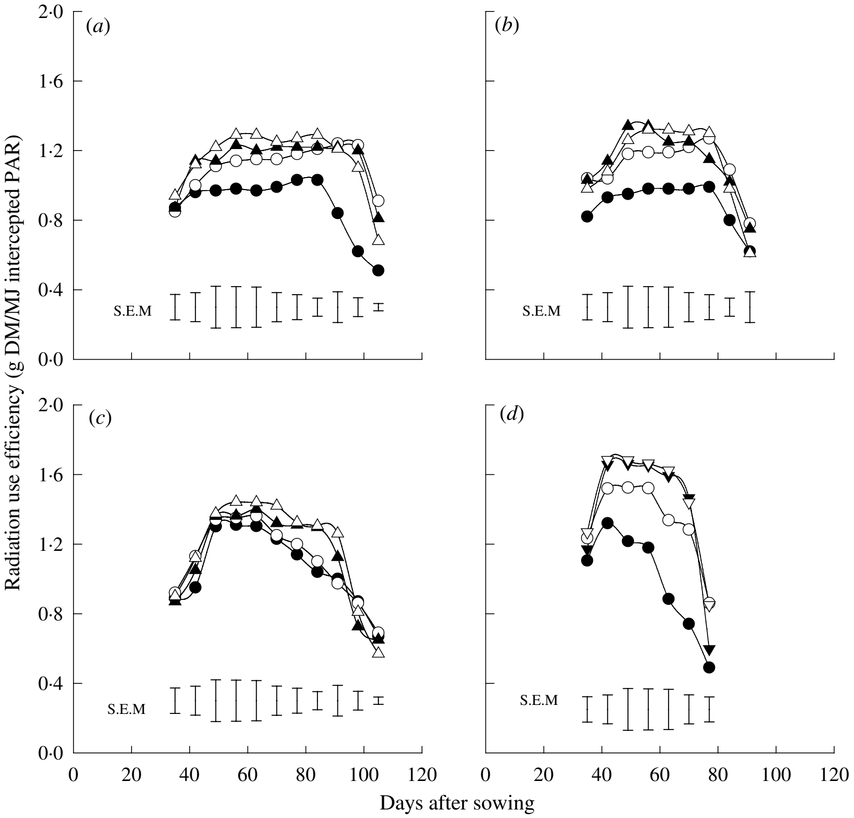

Fig. 6. The change in radiation use efficiency over the growing season in four plant populations of four grain legumes grown in Canterbury in 1998/99. (*a*) Chickpea, (*b*) lentil, (*c*) narrow-leafed lupin, (*d*) pea. 0·1 × optimum (●), 1·0 × optimum (○), 2·0 × optimum (▲), 4·0 × optimum (△).

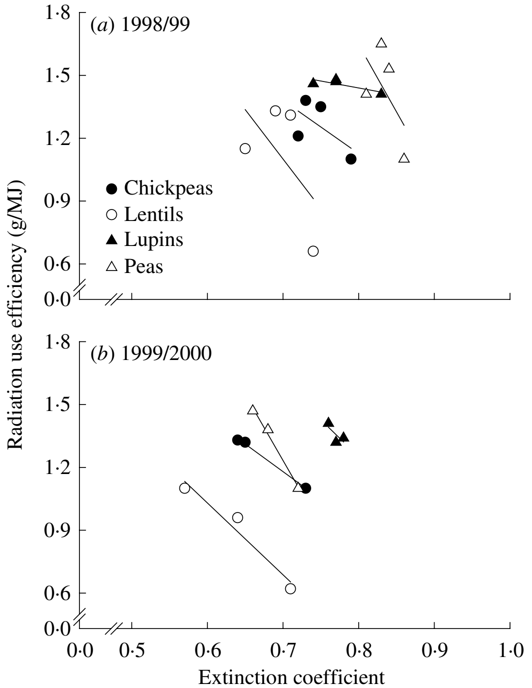

Fig. 7. The relationship between the extinction coefficient (*k*) and radiation use efficiency (RUE) of four grain legumes sown at different plant populations in (*a*) 1998/99 and (*b*) 1999/2000.

production and seed yield than the low population treatments. Increasing plant population from 0·1 × optimum to 4·0 × optimum, increased intercepted PAR by about 45%. There was a 30% increase in total intercepted PAR when lentil plant population increased from 1·0 × optimum to 4·0 × optimum (McKenzie & Hill 1991).

In these experiments in 1999/2000, GA development, radiation absorption, TDM production and crop harvest index (CHI) increased with increased plant population. However, in 1998/99, the CHI and yield of chickpea and field pea were relatively constant or declined at the highest plant population (Ayaz *et al.* 1999). This decline may have been due to pod dehiscence in the peas (Knott 1987), interplant competition or lower rainfall (Schulz *et al.* 1999).

In 1999/2000 sowing depth also affected total intercepted PAR. This may have been due to plants sown at the greatest depth having access to more available soil moisture (Wilson & Thurling 1996). However, the difference, although significant, was small (4%) and will not be discussed further.

Variation in crop yield can also be related to differences in radiation use efficiency (RUE) within species. Variations have been reported in RUE among four cereal species and in sunflower (*Helianthus annuus*) by Kiniry *et al.* (1989) and among different genotypes of *Vicia faba* by Stützel & Aufhammer (1992). This is strongly supported by data from the present study, where RUE varied among species. It was also influenced by plant population and by growing season. This suggests that the aim of crop modellers to use a universal value for each species to convert intercepted PAR into DM production is unrealistic. The final RUE value in 1998/99 was higher than in 1999/2000. As RUE is sensitive to minimum temperatures (Bell *et al.* 1993) the lower minimum temperatures in 1999/2000 might have contributed to the lower RUE values than in 1998/99 (Fig. 1). However, the highest yielding species had the highest RUE and these were closely related to the CHI for each species during each year of the present study. Stützel & Aufhammer (1992), working with *Vicia faba*, reported that RUE cannot be expected to remain constant throughout the life cycle of a crop, during which growing conditions and the intensities of physiological processes may change. This is especially so late in the growing season when crop biomass is high and maintenance respiration demand will high.

There is no published information on the relationship between RUE and the extinction coefficient (*k*), and between PAR and HI in the Canterbury environment. The present study showed that variation in RUE was inversely related to differences in *k*. This is to be expected, as canopies with erect leaves will spend less time with highly light saturated leaves than a canopy of flat leaves. Stützel & Aufhammer (1992), in *Vicia faba*, also found that *k* decreased with increased GAI. Data from the present study on four grain legumes sown at different plant populations with both mechanical and hand sowing confirm this.

The relationship of TDM and seed yield, at final harvest, with total intercepted PAR was strong (Fig. 8). The slope of the TDM and total intercepted PAR regression indicate comparatively high RUE values in both seasons in all four legume species. These values are higher than the mean RUE values (Tables 3 and 4) because the lines did not pass through the origin (Fig. 8*a*, *b*). This is identical with results from lentil (McKenzie & Hill 1991) and pea (Zain *et al.* 1983). However, in the RUE 1999/2000 was lower. The lower minimum temperatures in 1999/2000 (Fig. 1) may have contributed to the lower RUE values than in 1998/99. Gardner & Auma (1989) and Bell *et al.* (1993) in peanut and Andrade *et al.* (1993) in maize all reported that RUE was sensitive to low minimum temperatures.

Seed yield was linearly related to total intercepted PAR ($R^2 = 0·77$ to 0·98) and the slopes show that from 0·90 to 1·50 g seed/m^2 was produced from each MJ of absorbed PAR in the different legume species. The highest yielding species had the highest final RUE. This was closely related to TDM, seed yield and HI, but was inversely related to *k* in all four

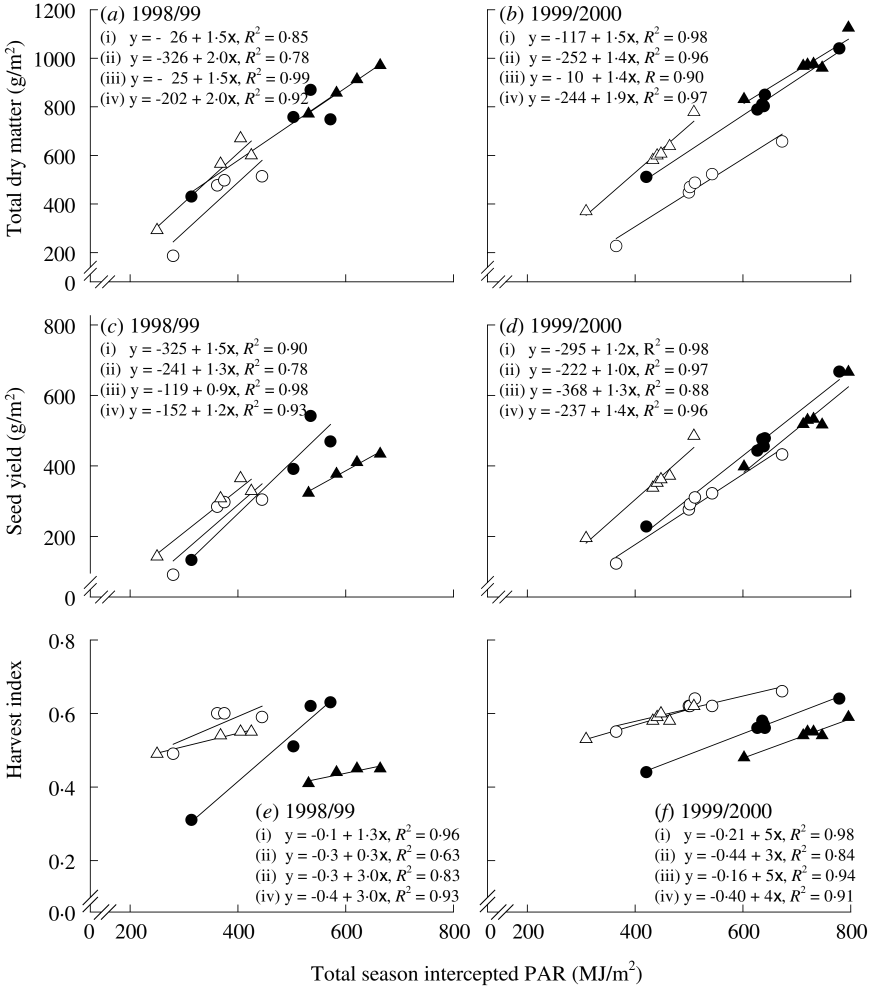

Fig. 8. The relationships of total seasonal intercepted photosynthetically active radiation (PAR) with total DM production, seed yield and crop HI of four grain legumes at final harvest in 1998/99 and 1999/2000. Chickpea (eqn i, ●) lentil (eqn ii, ○), narrow-leafed lupin (eqn iii, ▲), pea (eqn iv, △).

species in the present study. These variations might affect HI. As RUE is a key determinant of crop yield, HI can be stabilized by stabilizing the RUE.

The results show that higher plant populations gave increased GAIs when compared with the lower plant population in all four legumes. Total dry matter, seed yield and crop HI were strongly correlated with total seasonal intercepted PAR. The RUE was directly related to TDM production, seed yield and CHI. The RUE increased with increased plant population up to 2·0 × optimum in the first trial and up to 400 plants/m^2 in the second experiment. It was stable over different sowing depths. The differences in RUE were inversely related to differences in the extinction coefficient. The results also suggest that in a subhumid temperate environment such as Canterbury, grain legumes should primarily be selected for the development of a large GAI, which will maximize interception of PAR, DM production and consequently crop seed yield.

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