Screening pasture species for shade tolerance

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Abstract

The effects of shade on tillering ability as well as biomass production of hill pasture species which differed in morphology and for shade tolerance was evaluated. A split-plot design with four replicate blocks was employed for the experiment, in which five levels of shade were applied within 1.25 × 0.84 × 0.45 m metal frames covered by Sarlon cloth to shade light from all directions. The main plot treatments were 14, 18, 27, 43, and 73% of the ambient photosynthetically active radiation (PAR). Ten different pasture species: *Dactylis glomerata* L. cv. Grasslands Wana; *Lolium perenne* L. cv. Grasslands Nui, high endophyte; *Holcus lanatus* L. cv. Massey Basyn; *Plantago lanceolata* L. cv. Grasslands Lancelot; *Festuca arundinacea* Schreb. cv. Grasslands Advance; *Agrostis capillaris* L. cv. Grasslands Muster; *Poa trivialis* L. cv. Sabre; *Trifolium repens* L. cv. Grasslands Tahora, *Trifolium subterraneum,* L. cv. Karridale; and *Lotus uliginosus* Schkuhr cv. Grasslands Maku were grown in pots as subplots. Twelve to fourteen plants were maintained per pot, and plants were watered daily. Water and fertiliser were non- limiting. The experiment ran from 5 June to 6 September, 1996. Shoot dry weight, tillers/runners/stolons/number of branches per plant, and specific leaf area were determined at 15-day intervals for five harvests. At each harvest, plants were clipped to 5 cm height. Shade had a marked effect on tillering ability of all grass plants. However, mean tiller numbers per plant at the final harvest in the lowest PAR (14% ambient) were significantly higher (P<0.0001) for *Holcus lanatus* (4) and *Dactylis glomerata* (4) than for the other grass species. Similarly, *Lotus uliginosus* produced a higher (P<0.0001) number of branches (4) in 14% ambient PAR than other legumes. This trend was also observed for relative tiller numbers per plant (to that of 73% ambient PAR), where *Dactylis glomerata* had about 20% of its tiller production in the highest level of shade (14% ambient PAR) compared with *Lolium perenne* which had 5 %. The results are discussed in terms of the desired attributes of shade tolerant pasture species.

Additional key words: *growing points, cocksfoot, Yorkshire fog, lotus, perennial ryegrass, plantain, tall fescue, browntop, clover,* Poa trivialis.

Introduction

Large areas of land used for agriculture in New Zealand are susceptible to soil erosion (Clough and Douglas, 1993). One technology to cope with this situation has been the planting of conservation trees, particularly poplars and willows (Anonymous, 1995; Miller *et al.*, 1996). The impact of shading by these trees on the productivity and persistence of hill pastures has received little research attention (Hawke, 1991; Knowles, 1991; Pollock *et al.*, 1994). However, research with widely spaced *Pinus radiata* has suggested that *Holcus lanatus* L., *Dactylis glomerata* L. and *Lotus uliginosus Schkuhr* are more shade tolerant than other hill pasture species (Seo *et al.*, 1989; West *et al.*, 1991).

Shading is the most significant factor determining the output from pastures grown in plantations (Shelton *et al.*, 1987). Decreasing irradiance reduces the growth of pasture species and influences the outcome of competitive relations between plant species (Shelton *et al.*, 1987). Low irradiance also affects morphological attributes of pasture species, through altered partitioning of photosynthate which may impact on productive performance (Kephart and Buxton, 1993). The abilities of plants to regenerate leaf area to maximise interception of available radiation, and to generate tillers and stolons from main stems, are the critical factors that determine production and persistence of pasture species under low irradiance (Chen, 1993).

Tree shade also affects the quality of transmitted light, decreasing the ratio of red to far red wavelengths (R:FR). Effects of R:FR on the productive performance of pasture plants have been widely reported (Thomson, 1993; Murphy and Briske, 1994; Teuber and Laidlaw, 1996). In general, low R:FR stimulates morphological change, such as increased plant height and reduced tillering.

Despite research on the impact of shade on the performance of pasture species (Kephart and Buxton, 1993; Eriksen and Whitney, 1981; Samarakoon *et al.*,

1990) there is little information available on effects of a range of light intensities, particularly at low levels of transmitted light (high levels of shade) found under mature stands of conservation trees, on the growth and morphology of hill pasture species. This study aimed to screen hill pasture species for their biomass and morphological responses to a range of levels of photosynthetically active radiation (PAR) in glasshouse conditions. This was part of a programme to determine suitable pasture species for silvopastoral systems based on deciduous trees. Accordingly, three legume species, six grass species, and one forb species were chosen for their different morphological characteristics and observed responses to shade.

Materials and Methods

The experiment was conducted from June 5 to September 6, 1996 (95 days) at the Plant Growth Unit (PGU), Massey University. A split-plot design was used with four replicate blocks: the main plots were shade treatments and subplots were pasture species. Plants were grown under control conditions (without shade) and under a range of shade levels. Shade levels were imposed by differing densities of neutral shade cloth (Sarlon) supported on hollow metal frames (1.25 × 0.84 × 0.45 m) arranged on benches that were 0.9 m above the ground. The shade frames were aligned in a north-south direction and completely enclosed the pots. Five levels of transmitted photosynthetically active radiation (PAR; μ moles photons m^2/s, 400-700 nm) were created. The transmitted PAR for the five treatments was 73, 43, 27, 18, and 14% of the ambient PAR determined on a daily basis from 1200 to 1300 h throughout the experiment using a Licor quantum sensor. The treatment with 73% ambient PAR , or 27% shade, was not covered by shade cloth, as this was the percentage of ambient PAR transmitted through the glasshouse. PAR was measured inside and outside the glasshouse at the same time. Red:Far Red (R:FR) ratio during clear sky days was measured three times a day (morning, afternoon, and evening) with a Skye sensor, inside and outside the glasshouse, and under the shade cloth treatments.

Details of the pasture species and cultivars used are given in Table 1. Seeds of pasture species were sown on 4 June, 1996 in PB 5 (3 litre capacity) black polypots filled with potting mix (80% tree bark + 20% pumice), and always kept under their allocated shade treatments. Dolomite 300 g, agricultural lime 300 g, iron sulphate 50 g, and Osmocote plus (16 N-3.5 P-10.8 K) 400 g per 100 litre were blended with the potting mix, which was rated for medium to long term (< 9 months) greenhouse crops. Twelve to fourteen plants were maintained per pot, and plants were watered daily. The pots within cages were rerandomized weekly. Seeds of legumes were inoculated with the appropriate rhizobia.

The glasshouse temperature was maintained at 25°C until seeds of all plants were fully germinated. Thereafter, day temperature was 15-17°C and night temperature 8-10°C.

The first harvest was on July 10, 35 days after sowing. Subsequent harvests were on July 25, August 9 and 23, and September 6. At each harvest, all the plants were clipped to 50 mm above the media surface. Shoot material above 50 mm was dried at 70°C for 24 hours and weighed, and added to the above ground shoot mass at the final harvest. From the July 25 harvest onwards, five fully expanded leaves were randomly taken from each pot to measure leaf area, and leaf dry weight for estimation of specific leaf area. At each harvest, the

Table 1. Pasture species and cultivars used in the experiment

	Pasture species	Cultivar
1.	White clover (*Trifolium repens* L.)	Grasslands Tahora
2.	Lotus (*Lotus uliginosus* Schkuhr)	Grasslands Maku
3.	Subterranean clover (*Trifolium subterraneum* L.)	Karridale
4.	Browntop (*Agrostis capillaris* L.)	Grasslands Muster
5.	Cocksfoot (*Dactylis glomerata* L.)	Grasslands Wana
6.	Yorkshire fog (*Holcus lanatus* L.)	Massey Basyn
7.	Tall fescue (*Festuca arundinacea* Schreb)	Grasslands Advance
8.	Perennial ryegrass (*Lolium perenne* L.)	Grasslands Nui
9.	Poa trivialis (*Poa trivialis* L.)	Sabre
10.	Plantain (*Plantago lanceolata* L.)	Grasslands Lancelot

number of tillers per pot for grasses and branches per pot for legumes were counted. Tiller numbers and leaf area only at the final harvest are reported in this paper. Plant height and leaf/petiole length were measured but are not reported. Specific leaf area was analysed by considering harvests as repeated measures. Statistical analysis was by analysis of variance using the GLM model of a SAS package (SAS Institute Inc. 1989), and the linear regression of shoot weight and of relative shoot weight with the percent of transmitted PAR using SAS.

Results

Growth environment

Mean PAR at noon in the shade treatments was 318, 188, 117, 81, and 60 μ moles photons m^2/s resulting in 73, 43, 27, 18, and 14% ambient PAR, respectively. The mean ambient PAR outside the glasshouse was 432 μ moles photons m^2/s. R:FR ratio at noon inside the glasshouse was 1.33 to 1.49, while outside it was from 1.47 to 1.49. There was no effect of shade cloth on R:FR.

Plant growth

The shoot dry weight per plant of all legumes and grasses showed a significant ($P<0.0001$) linear increase with % ambient PAR, producing their highest yield at 73% ambient PAR and lowest at 14% ambient PAR (Fig. 1). At 27% shade, perennial ryegrass had the highest shoot dry weight per plant (1113.8 mg), and lotus the least (277.4 mg). However, at the lower level of PAR (86% shade), subterranean clover shoot dry weight (22.1 mg/plant) was higher ($P<0.0001$) than white clover (13.5 mg/plant), and comparatively better than that of lotus (17.4 mg/plant). Yorkshire fog produced the highest shoot dry weight (29.7 mg/plant) at low PAR (14% ambient, 86% shade) followed by perennial ryegrass (24.7 mg/plant), and cocksfoot (22.3 mg/plant), whereas browntop (6.3 mg/plant) and Poa (10.8 mg/plant) had the lowest shoot dry weight of the grasses (Fig. 1).

The response of relative shoot dry weight of the species to shading differed from that for absolute shoot dry weight. Relatively, the three legume species produced more shoot dry weight at all levels of shade than the grass species and plantain (Fig. 2). Within the legumes, the relative shoot dry weight of lotus increased in comparison to subterranean clover and white clover as the intensity of shade increased (Fig. 2a). Within the grass species, the relative shoot dry weight of cocksfoot and Yorkshire fog was greater than that of the other grass species at 14, 18 and 27% ambient PAR (Fig. 2 b,c).

Specific Leaf Area (SLA)

Specific leaf area over all harvests increased ($P<0.0001$) with decreasing PAR for all species. There was a significant interaction between shade level and species. The SLAs of subterranean clover and cocksfoot were comparatively unresponsive to the % ambient PAR, whereas the SLA of Yorkshire fog increased at only 14% ambient PAR (Fig. 3 a,b). On the other hand, the SLAs of Poa and browntop increased as PAR decreased, but at 14% ambient PAR their SLA was less than at 27% ambient PAR (Fig. 3c). The SLA's of white clover, lotus, ryegrass, tall fescue and plantain all increased with decreased PAR (Fig. 3).

Leaf area

Leaf area per plant over all harvests also increased significantly ($P<0.0001$) with increased PAR in all pasture species (Table 2). In 73% PAR, Yorkshire fog had the highest leaf area (118.7×10^{-4} m^2) followed by ryegrass (96.0×10^{-4} m^2) and cocksfoot (94.7×10^{-4} m^2) while Lotus had the lowest (41.5×10^{-4} m^2). However, under dense shade (14% PAR), the highest leaf area was produced by Yokshire fog (8.0×10^{-4} m^2) which was followed by lotus (6.3×10^{-4} m^2), plantain (5.0×10^{-4} m^2) and cocksfoot (3.8×10^{-4} m^2). Browntop, Poa and tall fescue produced the lowest leaf area (Table 2).

Tiller and branch numbers per plant

The main effects and the interaction between shade and species for tiller and branch numbers per plant were significantly different ($P<0.0001$) in absolute as well as in relative terms (Table 2). At final harvest, the highest number of tillers in 73% ambient PAR was produced by Yorkshire fog (39) followed by Poa (35) and browntop (30). Under the highest shade (14% ambient PAR), cocksfoot and Yorkshire fog and lotus produced the greatest number of tillers/branches (4), while subterranean clover, white clover, plantain and tall fescue did not produce any branches/tillers.

Grasses like Poa, browntop and Yorkshire fog produced a higher number of tillers than the number of branches produced by legumes in 73 and 43% ambient PAR. This trend continued for the cocksfoot, Yorkshire fog, and Poa, as PAR decreased to 27 and 18% ambient PAR (increased shade). However, at the lowest PAR level (14% transmission), lotus, Yorkshire fog, and cocksfoot all produced a similar number of branches or tillers, whereas the number of tillers produced by Poa was lower. Among the grasses, ryegrass produced one tiller per plant, and tall fescue none in 14% ambient PAR (Table 2).

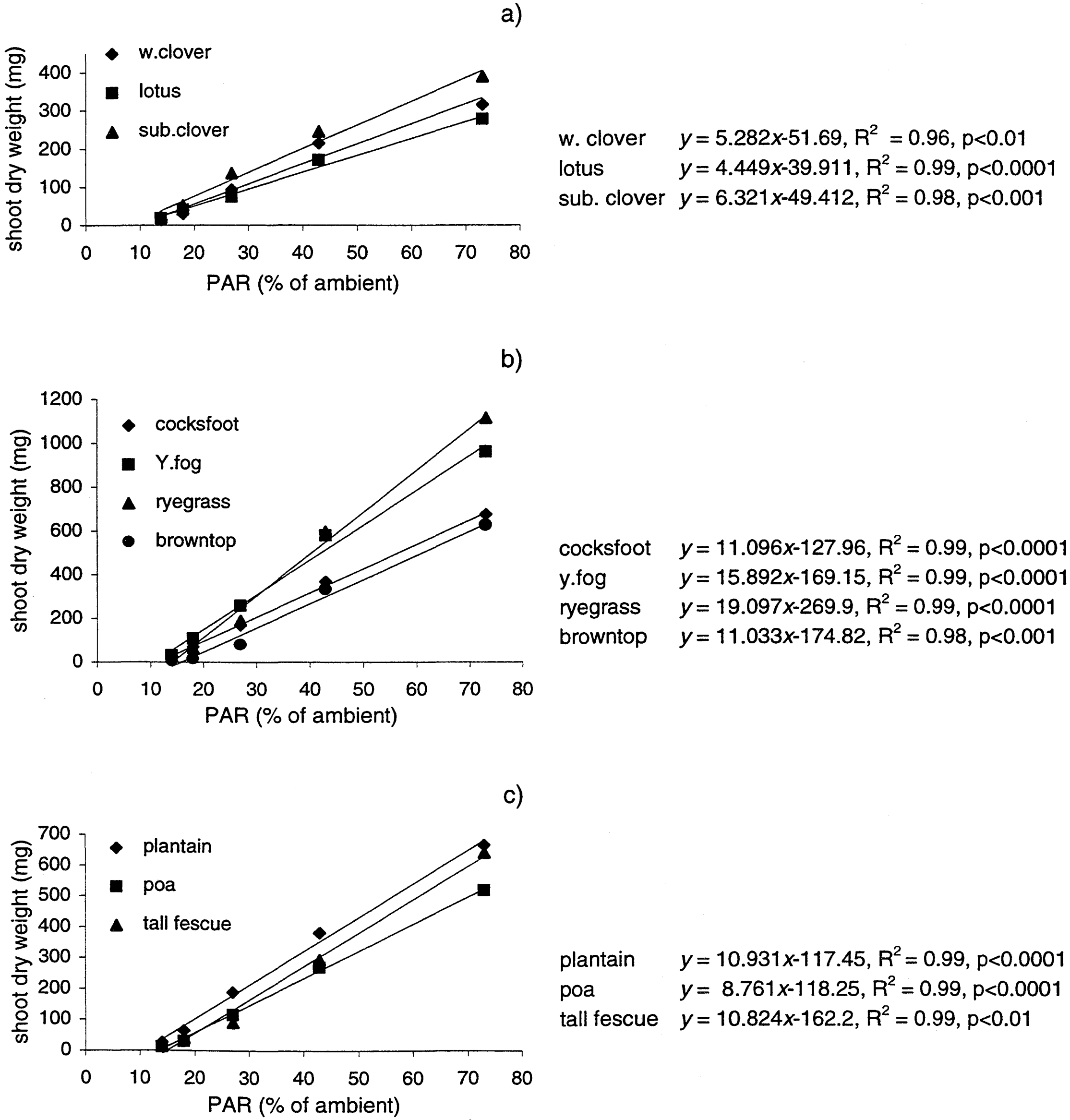
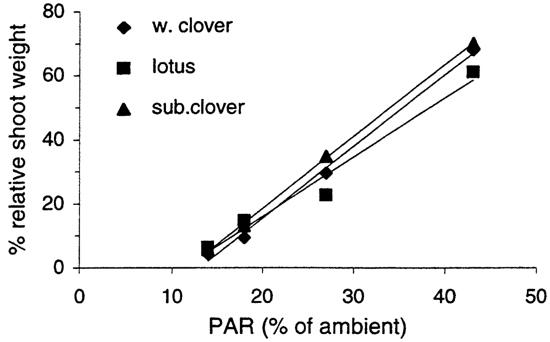


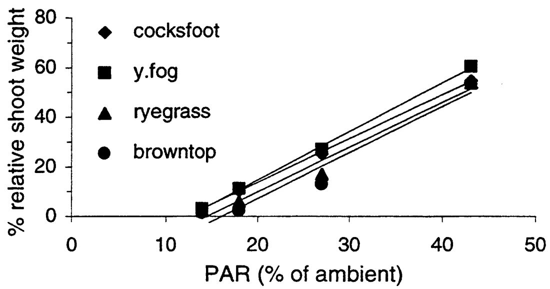
Figure 1. Effects of shade (level of PAR) on shoot dry weight of (a) legumes, (b) hill grass species, and (c) other species. Standard error of means for species = 2.06.

a)



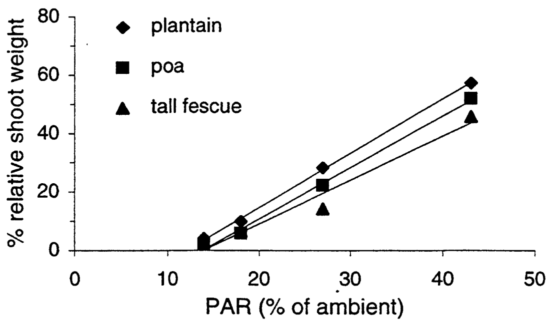
w.clover $y = 2.237x\text{-}29.264$, $R^2 = 0.097$, $p<0.001$
lotus $y = 1.849x\text{-}20.987$, $R^2 = 0.96$, $p<0.01$
sub.clover $y = 2.241x\text{-}26.295$, $R^2 = 0.99$, $p<0.001$

b)



cocksfoot $y = 1.768x\text{-}21.805$, $R^2 = 0.99$, $p<0.001$
y.fog $y = 1.964x\text{-}24.709$, $R^2 = 0.99$, $p<0.001$
ryegrass $y = 1.804x\text{-}26.34$, $R^2 = 0.97$, $p<0.01$
browntop $y = 1.859x\text{-}30.12$, $R^2 = 0.94$, $p<0.05$

c)



plantain $y = 1.880x\text{-}22.659$, $R^2 = 0.99$, $p<0.001$
poa $y = 1.758x\text{-}24.366$, $R^2 = 0.99$, $p<0.001$
tall fescue $y = 1.499x\text{-}20.968$, $R^2 = 0.96$, $p<0.01$

Figure 2. Effects of shade (level of PAR) on shoot dry weight of (a) legumes, (b) hill grass species, and (c) other species relative to their dry weights at 73% ambient PAR. Standard error of means for species = 0.3.

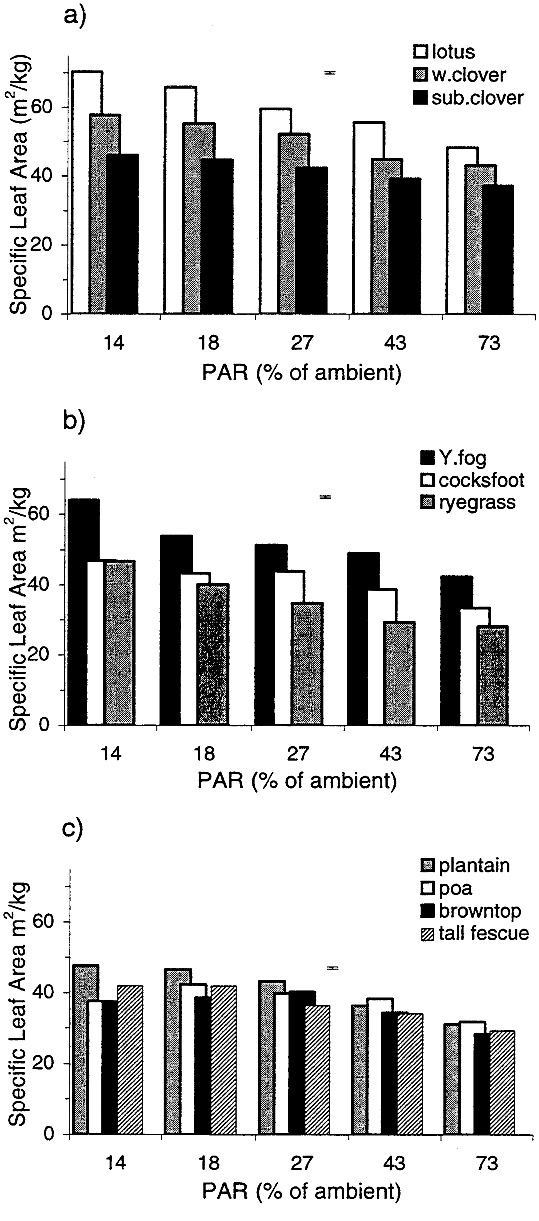


Figure 3. Specific leaf area (m^2/kg) of (a) legumes, (b) hill grass species, and (c) other species by repeated analysis over all harvest periods at different levels of PAR. Vertical bar represents standard error of means for species (0.29).

Table 2. Effects of shade on pasture species tiller or branch numbers per plant, their relative values (to that of 73% ambient PAR), and leaf area at final harvest under glasshouse conditions in Palmerston North, September, 1996.

PAR / species	Tillers or branches per plant	Relative tillers or branches per plant	Leaf area ($m^2 \times 10^{-4}$) per plant
73% ambient PAR			
White clover	14	-	42.7
Lotus	27	-	41.5
Sub. clover	9	-	52.4
Browntop	30	-	72.7
Cocksfoot	18	-	94.7
Yorkshire fog	39	-	118.7
Tall fescue	15	-	66.8
Plantain	4	-	82.6
Perennial ryegrass	24	-	96.0
Poa trivial is	35	-	81.3
43% ambient PAR			
White clover	11	76	33.5
Lotus	23	85	35.4
Sub. clover	7	78	35.7
Browntop	30	99	56.4
Cocksfoot	14	76	71.1
Yorkshire fog	28	71	130.4
Tall fescue	11	73	38.8
Plantain	2	58	71.3
Perennial ryegrass	16	65	70.5
Poa trivialis	24	69	40.0
27% ambient PAR			
White clover	7	50	20.1
Lotus	13	46	22.9
Sub. clover	4	47	16.5
Browntop	9	31	13.0
Cocksfoot	12	65	34.3
Yorkshire fog	18	45	55.2
Tall fescue	4	25	10.4
Plantain	2	55	39.0
Perennial ryegrass	5	20	23.1
Poa trivialis	15	43	20.9

continued next column

PAR / species	Tillers or branches per plant	Relative tillers or branches per plant	Leaf area ($m^2 \times 10^{-4}$) per plant
18% ambient PAR			
White clover	3	23	05.2
Lotus	6	23	13.6
Sub. clover	3	29	06.8
Browntop	3	11	01.8
Cocksfoot	7	36	17.1
Yorkshire fog	10	24	23.8
Tall fescue	3	22	03.8
Plantain	0	0	13.4
Perennial ryegrass	3	13	16.6
Poa trivialis	6	17	05.0
14% ambient PAR			
White clover	0	0	02.4
Lotus	4	16	06.3
Sub. clover	0	0	03.2
Browntop	2	8	00.4
Cocksfoot	4	19	03.8
Yorkshire fog	4	9	08.0
Tall fescue	0	0	00.9
Plantain	0	0	05.0
Perennial ryegrass	1	4	01.9
Poa trivialis	3	9	00.7
Analysis of variance			
Shade p (A)	<0.0001	<0.0001	<0.0001
Species p (B)	<0.0001	<0.0001	<0.0001
Interact'n p (A*B)	<0.0001	<0.0001	<0.0001
$LSD_{(0.05)}$ for shade	0.81	4.15	2.90
$LSD_{(0.05)}$ for spec.	0.68	3.31	1.94
SEM for shade	0.26	$1.29_{(df=3)}$	0.94
SEM for species	0.24	$1.18_{(df=9)}$	0.69
SEM for A*B	0.54	$2.36_{(df=27)}$	1.55

Among legumes, lotus always produced a higher number of branches per plant than white clover and subterranean clover in 73% (27% shade) to 18% (86% shade) ambient PAR. However, at 14% ambient PAR, only lotus produced branches (Table 2).

The response of relative tiller or branch numbers to PAR was different from absolute tiller or branch numbers. Relative to 73% ambient PAR, browntop (99%) followed by lotus (85%), subterranean clover (78%) cocksfoot (76%), and white clover (76%)

produced more tillers or branches at 43% ambient PAR. All other species produced about 60-70% of the tillers or branches at 43% ambient PAR relative to 73% ambient PAR. At 27, 18 and 14% ambient PAR, cocksfoot produced relatively more tillers than the other species (Table 2). The relative tillering of Yorkshire fog and Poa was similar at the three lower levels of PAR, intermediate between that of cocksfoot and tall fescue and ryegrass (Table 2). Among the legumes, relative branching was decreased by low PAR in a similar fashion to the better performed grasses, the exception being at 14% ambient PAR where lotus was the least affected species after cocksfoot, but white and subterranean clovers produced no branches (Table 2).

Ranking pasture species for shade tolerance

Ranking of pasture species for shade tolerance on the basis of relative tillers or branches per plant and leaf area per plant in light shade (43% ambient PAR) and in dense shade (14% ambient PAR) indicated that Yorkshire fog and cocksfoot among the grasses and lotus of the legumes were the most shade tolerant. Browntop was shade tolerant in light shade, but tall fescue was the least shade tolerant species at 14% ambient PAR (Table 3). Plantain was intermediate in its ranking for shade tolerance.

Table 3. Rank of pasture species for their shade tolerance on the basis of relative tillers/branches per plant (to that of 73% ambient PAR), and leaf area at 43% and 14% ambient PAR at final harvest under glasshouse conditions.

	43% ambient PAR		14% ambient PAR	
Pasture species	Relative tillers or branches	Leaf area ($m^2 \times 10^4$) per plant	Relative tillers or branches	Leaf area ($m^2 \times 10^4$) per plant
Browntop	1	5	5	10
Lotus	2	9	2	2
Sub. clover	3	8	7	5
Cocksfoot	4	3	1	4
W. clover	4	10	7	6
Tall fescue	6	7	7	8
York. fog	7	1	3	1
Poa trivialis	8	6	3	9
P. ryegrass	9	4	6	7
Plantain	10	2	7	3

Discussion

A shade tolerant pasture species needs to have good annual and seasonal dry matter production under defoliation, and to be able to regenerate. In this screening experiment the most shade tolerant species were those that maintained a comparatively high absol ute and relative shoot yield in low PAR, due to maintaining a higher leaf area and higher relative number of tillers or branches. On these criteria Yorkshire fog and cocksfoot were the most shade tolerant grasses, and lotus the most shade tolerant legume. Among the grasses tall fescue, perennial ryegrass and *Poa trivialis* exhibited poor shade tolerance. Browntop was one of the worst ranked grass species in heavy shade, but was more tolerant of light shade, in terms of tillering, but not in terms of shoot yield. Lotus was the most shade tolerant legume at higher shade levels, but its shoot yield was less than that of white clover and subterranean clover, possibly because lotus takes longer to establish than other legumes, so the shoot yield of lotus in the long term may not differ. Plantain ranked in the middle of the species screened for shade tolerance.

Seo *et al.* (1989) found that under pine trees, cocksfoot was the most shade tolerant species and that it persisted well. West *et al.* (1991) found that initial stands of pure Maku lotus changed to a progressive mixture of Yorkshire fog, and reported Yorkshire fog as a shade tolerant grass. Gadgil *et al.* (1986), West *et al.* (1988), and West *et al.* (1991) all indicated that lotus is one of the most successful legumes under shade, and can be readily established on a range of sites. This experiment also showed that lotus was the best legume to grow under heavy shade.

Ryegrass and white clover were more affected by shade than cocksfoot, Yorkshire fog and lotus. Percival *et al.*, (1984) in their study on pasture yield under radiata pine also reported that the yields of ryegrass and white clover declined with increasing tree density (higher level of shade) and these species were mainly replaced by annual grasses and Yorkshire fog. Likewise, browntop has been found to be intolerant of shade, as Brauen *et al.*, (1993) reported that browntop grows well only in full sun or moderate shade. *Poa trivialis* has been reported to have good tolerance of cool shade (Hurley *et al.*, 1990; Bar and Schulz, 1995), but this was not shown in this experiment. Similarly, subterranean clover has been reported by Lodge (1996) as being shade tolerant at seedling emergence, and as mature plants, and Pardini *et al.* (1995) found that subterranean clover under forest cover in productive and non-productive Mediterranean sites was shade tolerant. However, results from this experiment showed that subterranean clover may only be tolerant in moderate shade. Additionally, it was observed that subterranean clover etiolated faster in the shade in comparison to lotus, which would make it susceptible to having its growing points grazed.

The comparatively greater shoot dry weights of Yorkshire fog and cocksfoot in heavy shade could be associated with their ability to produce more tillers in absolute as well as in relative terms (Table 2). Yorkshire fog and cocksfoot also had a greater leaf area in heavy shade conditions than the other grasses. Cocksfoot specific leaf area was less responsive to low light than the other grasses, suggesting it has a different adaptive mechanism to low light. Possibly, the shade tolerance of lotus was related to its upright growing habit, which would facilitate greater interception of PAR in comparison to other legumes. Lotus can form new plants from rhizomes (West *et al.*, 1991) which could also be an added advantage for better persistence under shade.

The relatively poor shade tolerance of white clover and perennial ryegrass appeared to result from the sensitivity of the stolons and tillers respectively, to low light. The shoot yield of these species was comparatively low at 14% ambient PAR, due to the low number of leaves per plant resulting from the suppression of tillers and stolons.

Absolute and relative number of tillers or branches per plant could be important characters that determine the shade tolerance of pasture species. In general, all components of growth are depressed by a low energy input, but tillering ability of plants is particularly dependent on carbohydrate supply (Cooper and Tainton, 1968). Persistence of pasture species under shade could be evaluated on their ability to produce tillers or branches which will contribute to the accumulation of shoot weight. If a particular species is able to produce more tillers, it may also withstand defoliation better than those plants with less tillers/branches. A shade tolerant pasture species needs defoliation tolerance as well as shade tolerance.

The levels of ambient PAR in this experiment may not exactly represent the situation under conservation trees. Both light quantity and light quality signals could be important in the reactions of plants to shade. R:FR values for deciduous woodlands ranged from 0.36 to 0.97 (Smith, 1982) in comparison to about 1.2 in open areas. Smith (1982) further pointed out that morphogenetic reactions occur in response to reductions in the total fluence rate. Developmental response to low R:FR is often a marked and sometimes spectacular increase in stem elongation rate. Therefore, to validate the results of this glasshouse experiment, a field experiment with ten year old Alder trees has been established with different levels of shade and combinations of pasture species.

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