Shade tolerance of pasture species in relation to deciduous tree, temperate silvopastoral systems

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Abstract

Ten hill pasture selections, with an emphasis on cocksfoot (*Dactylis glomerata* L.) and perennial ryegrass (*Lolium perenne* L.), were evaluated for their potential to tolerate the shade conditions found in silvopastoral systems based on deciduous trees. The three experiments were on plants grown in pots in a glasshouse under varying levels of photosynthetic photon flux density (PPFD, 81 – 720 µmoles photons/m^2/s) and red:far red ratio (R:FR, 0.57 – 1.34). The most productive selections in low PPFD had a high specific leaf area and tiller production that was relatively insensitive to the level of PPFD, and responded to decreased PPFD by increasing specific leaf area and the proportion of biomass allocated to leaf. The morphological responses of the pasture species to a decrease in R:FR ratio were small in comparison to the responses to low PPFD. The most shade tolerant selection in heavy shade (i.e., <25 % of ambient PPFD or approximately 200 µmoles photons/m^2/s) was cocksfoot cv. Grasslands Wana due to its greater leaf area as a consequence of its high specific leaf area and the insensitivity of its tillering to low light.

Additional key words: *red:far red, cocksfoot, perennial ryegrass, PPFD, specific leaf area, tillering.*

Introduction

Broad-leaved deciduous trees, particularly poplars and willows, are widely used in silvopastoral systems in New Zealand hill country. The principal role of the trees is erosion control. However, the trees decrease pasture production by shading and also probably by decreasing soil moisture and temperature (Guevara-Escobar *et al.*, 1997). The impact of shading by broad-leaved deciduous trees on the productivity and persistence of hill pasture species has received little research attention (Guevara-Escobar *et al.*, 1997; Wall *et al.*, 1997). In *Pinus radiata* L. based agroforestry, where the light intensity is lower than under deciduous trees, cocksfoot, Yorkshire fog and lotus have been found to be the most persistent of common hill pasture species (Hawke and Knowles, 1997; Pollock *et al.*, 1997).

Tree shade affects both the quantity and quality of light available to the understorey pasture (Hawke and Knowles, 1997; Wall *et al.*, 1997). To maximise light interception in low light shaded plants usually respond by increasing both biomass allocation to leaves and specific leaf area resulting in an increased proportion of shoot mass in leaf area (Kephart *et al.*, 1992; Wilson, 1997). Shade tolerant species also have an inherently high specific leaf area (Sanderson *et al.*, 1997). The decreased red:far red ratio (R:FR) in the light under tree canopies triggers many morphological responses in plants, including increased plant height and decreased initiation of axillary buds resulting in fewer tillers and stems (Assmann, 1992; Maliakal *et al.*, 1999; Wilson, 1997). Poor tillering in understorey pastures will decrease both the productivity and persistence of the perennial grasses (Brock *et al.*, 1996).

This paper presents part of a research programme (Devkota, 2000) which had the aims of determining how to select shade tolerant pasture species, and how to manage understorey pasture species in deciduous tree based silvopastoral systems (Devkota *et al.*, 1997, 1998; Devkota, 2000). The effect of light intensity and quality on the shoot growth, leaf:stem ratio, specific leaf area, leaf area and tiller number of a range of pasture species found in hill pastures was measured in three experiments. The general objectives were to examine the shade tolerance of some perennial hill pasture species, and to use a comparison of shade tolerant and intolerant species to determine the key morphological attributes and responses that conferred shade tolerance. In Experiment

1 the effects of low light intensities and a low R:FR ratio on the shoot growth and leaf:stem ratio of nine pasture selections were measured. In Experiment 2 the effects of low light intensities and a low R:FR ratio on the tiller number per plant of a shade tolerant (cocksfoot) and intolerant (perennial ryegrass) species under regular defoliation were measured. In Experiment 3 the variation in shade tolerance of ten cocksfoot selections was compared with perennial ryegrass by measuring shoot growth, number of tillers, specific leaf area and leaf area at two low light intensities.

Materials and Methods

All experiments are fully described in Devkota (2000).

Light measurements

Photosynthetic photon flux density (PPFD) was measured daily with a LI-COR portable quantum sensor (Model LI-185) and R:FR ratio was measured, on clear sky days only, with a Skye sensor. Both PPFD and R:FR were measured between 1200 and 1300 hours in all experiments and the means for the duration of each experiment calculated. The ambient PPFD and R:FR ratio were measured immediately outside the glasshouse; the treatment PPFD and R:FR were measured immediately above the plants.

Experiment 1

Plants (6/pot) were grown from seed in a glasshouse in PB $6^1/_2$ (3.9 litre) black polypots filled with fertilised potting mix from 10 June to 9 October, 1997. Plants were watered daily. The glasshouse temperature was 25 °C until all seeds emerged, and thereafter the day/night temperatures were 15-17 °C/8-10 °C. Plants were grown under full light until 10 August 1997 when the treatments were implemented. All fully expanded laminae were clipped before implementing the treatments to avoid any confounding effects resulting from some leaves developing in full light and others in the shade. Clipped laminae, and the plant shoots at the end of the experiment, after separation into laminae and stem or pseudostem, were oven dried at 70 °C for 24 hours. Leaves were not clipped once the treatments were implemented.

A split-plot design with four blocks was used. The main plots were two percentages (28 and 12 %) of the ambient PPFD (675 µmoles photons/m^2/s) measured outside the glasshouse, and two R:FR ratios (0.57 and 1.34). Subplots were pasture species. PPFD levels with ambient (1.34) R:FR ratio were imposed by using different densities of neutral shade cloth (Sarlon) with a layer of clear plastic filter (Effects filter 30 clear, Chris James & Co, London) underneath, while the low (0.57) R:FR ratio was created with the use of shade cloth and steel blue filters (Effects filter 117 steel blue). Pasture species used were white clover cv. Grasslands Tahora; lotus cv. Grasslands Maku; cocksfoot cv. Grasslands Wana, PG 74, and PG 321; perennial ryegrass cv. Grasslands Nui; Yorkshire fog cv. Massey Basyn; browntop cv. Grasslands Muster and *Poa trivialis* cv. Sabre.

The PROC GLM programme of SAS version 6.12 (SAS 1997) was used for the analysis of variance in all three experiments. For all tables SEM denotes standard error of the mean, NS non-significant at P<0.05 and d.f. degrees of freedom.

Experiment 2

Plants (6/pot) were grown from seed in a glasshouse (day/night temperatures: 15-17 °C/8-10 °C) in PB $6^1/_2$ (3.9 litre) black polypots filled with fertilised potting mix from 15 April to 10 August 1998.

Experiment 2 was a split-split plot design with three replicate blocks. The main plots were three shade treatments; the sub-plots were two grass species, cocksfoot cv. Grasslands Wana and perennial ryegrass cv. Grasslands Nui; and the sub-subplots were defoliation either weekly or three weekly at 50 mm above pot media level. The shade treatments were 25 and 71 % of the ambient PPFD (623 µmoles photons/m^2/s) outside the glasshouse. There were two R:FR ratios (0.68 and 1.34) at 25 % of ambient PPFD, and one (1.34) at 71 % of ambient PPFD. The 71 % of the ambient PPFD plus 1.34 R:FR ratio treatment was not covered by shade cloth as these were the prevailing light conditions inside the glasshouse; the other two treatments were implemented as in Experiment 1. Defoliation started on 8 June, 55 days after sowing, and three cycles of three weekly defoliation were completed by 10 August. All tillers in each pot were counted weekly.

Experiment 3

Plants (4/pot) were grown from seed in a glasshouse (day/night temperatures: 18-25 °C/8-10 °C) in PB $6^1/_2$

(3.9 litre) black polypots filled with fertilised potting mix in a glasshouse from 18 December 1996 to 4 May 1997. A split-plot design with four blocks was used: the main plots were two shade treatments (73 and 24 % of the ambient PPFD which was 989 μmoles photons/m^2/s) and the subplots were ten cocksfoot selections (Grasslands Apanui, Kara, Wana and Tekapo; PG 74, 301, 306 and 321; Saborto and Dora) and perennial ryegrass cv. Grasslands Nui. Neutral shade cloth was used for the 24 %, but not the 73 %, of the ambient PPFD treatment as in Experiment 2, but no plastic filters were used in Experiment 3. R:FR ratio was not measured during this experiment, but was approximately 1.34.

Plants were harvested on 22 February, 9 March, 23 March, 6 April, 20 April, and 4 May 1997. Only results for the final harvest are presented. At each harvest, all the plants were clipped to 50mm above the media surface. Shoots above 50 mm were oven dried at 70 ^{0} C for 24 hours, weighed, and added to the above ground shoot mass at the final harvest. At each harvest, the number of tillers per pot was counted. At the final harvest one plant was randomly selected in each pot and all the laminae and pseudostems were separated. Leaf area was measured, then laminae and pseudostems dried at 70 ^{0} C for 24 hours.

Results

The highest cumulative shoot dry weight was always produced at the highest level of PPFD. However, pasture species responded differently over the range of PPFD levels. In Experiment 1, at 28 % of ambient PPFD, perennial ryegrass and Yorkshire fog were the selections with the greatest shoot dry weight, but at 12 % of ambient PPFD cocksfoot cv. G. Wana, ryegrass and Yorkshire fog were similar (Table 1). The shoot dry weight of cocksfoot cv. G. Wana had the smallest decrease at 12 % of ambient PPFD relative to its shoot dry weight at 28 % of ambient PPFD of all the pasture selections (Table 1). There was no effect of R:FR ratio on shoot dry weight (Table 1).

Table 1. The effect of 28 % and 12 % of the ambient photosynthetic photon flux density (PPFD) of 675 μmoles photons/m^2/s, averaged over an ambient (1.34) and a low (0.57) ratio of red to far red light (R:FR), on the shoot dry weight (g/plant) of pasture species in a glasshouse (Experiment 1).

Species	% ambient PPFD transmitted 28 %	12 %
White clover	1.2	0.4
Lotus	1.1	0.4
Cocksfoot (Wana)	1.9	1.1
Cocksfoot (PG 74)	1.4	0.7
Cocksfoot (PG 321)	1.8	0.7
P. ryegrass (Nui)	2.8	1.2
Yorkshire fog	2.8	1.1
Browntop	1.9	0.7
Poa trivialis	1.8	1.0
Analysis of variance	**Probability**	**SEM**
PPFD (d.f.. = 1)	P<0.001	0.03
R:FR (d.f.=1)	NS	0.03
R:FR x PPFD (d.f. = 1)	NS	0.04
Spp. (d.f. = 8)	P<0.001	0.06
Species x PPFD (d.f. = 8)	P<0.001	0.09
Species x R:FR (d.f. = 8)	NS	0.09
Species x R:FR x PPFD (d.f.=8)	NS	0.12

Table 2. The effect of 28 % and 12 % of the ambient photosynthetic photon flux density (PPFD) of 675 μmoles photons/m^2/s, averaged over an ambient (1.34) and a low (0.57) ratio of red to far red light (R:FR), on the leaf:stem ratio of pasture species in a glasshouse (Experiment 1).

Species	% ambient PPFD transmitted 28 %	12 %
White clover	0.6	1.3
Lotus	0.8	0.7
Cocksfoot (Wana)	1.6	2.4
Cocksfoot (PG 74)	1.8	1.9
Cocksfoot (PG 321)	1.5	2.4
P. ryegrass (Nui)	1.9	2.6
Yorkshire fog	1.8	2.3
Browntop	1.1	1.7
Poa trivialis	1.1	1.9
Analysis of variance	**Probability**	**SEM**
PPFD (d.f.. = 1)	P<0.01	0.07
R:FR (d.f.=1)	NS	0.07
R:FR x PPFD (d.f. = 1)	NS	0.08
Spp. (d.f. = 8)	P<0.001	0.12
Species x PPFD (d.f. = 8)	P<0.01	0.17
Species x R:FR (d.f. = 8)	NS	0.17
Species x R:FR x PPFD (d.f. =8)	NS	0.25

The leaf:stem ratio of most pasture selections increased at 12 % of ambient PPFD compared with 28 % of ambient PPFD (Table 2). The greatest increases in leaf:stem ratio were for white clover, *Poa trivialis*, cocksfoot cv. PG 321 and Wana, and Yorkshire fog (Table 2). The pasture selections with the highest leaf:stem ratios were perennial ryegrass, the cocksfoot selections and Yorkshire fog (Table 2). There was no effect of R:FR on leaf:stem ratio, and no interactions between R:FR and the other treatments (Table 2).

There was an interaction effect on the number of tillers per plant between species and light treatment and species and defoliation frequency, but no interaction between light treatment and defoliation frequency in Experiment 2 (Table 3). The number of tillers per plant was decreased by both low PPFD and low R:FR, with the decrease greater for perennial ryegrass than cocksfoot (Table 3). The number of tillers per plant was fewer with a weekly than three weekly defoliation frequency for ryegrass, but cocksfoot tiller numbers were unaffected by defoliation frequency (Table 3).

At 73 % of ambient PPFD in Experiment 3, the shoot dry weight and the number of tillers per plant of ryegrass were greater than, or similar to, the shoot dry weight and number of tillers per plant of the ten cocksfoot selections (Table 4). In contrast, at 24 % of ambient PPFD the shoot dry weight and the number of tillers per plant of ryegrass were equivalent only to the minimum values for the cocksfoot selections (Table 4). The specific leaf area and leaf area of ryegrass were lower than the minimum values for any of the cocksfoot selections (Table 4). The mean specific leaf area for the cocksfoot selections was 18.6 mm^2/mg compared with 6.2 mm^2/mg for ryegrass (Table 4). The leaf dry weight (leaf area/SLA) of ryegrass was within the range for the cocksfoot selections at both PPFD levels (Table 4 and Devkota, 2000).

Discussion

The comparative effects of shade on the growth and development of the pasture selections depended more on the percentage of the ambient PPFD transmitted to the

Table 3. Effect of defoliation frequency, percentage of ambient photosynthetic photon flux density (PPFD, 623 µmoles photons/m^2/s) and red:far red light ratio (R:FR) on the number of tillers per plant. Cocksfoot ai perennial ryegrass were defoliated weekly or three weekly (Experiment 2).

	No. tillers/plant		
	Light treatments		
Species	71 % PPFD + 1.34 R:FR	25 % PPFD + 1.34 R:FR	25 % PPFD + 0.68 R:FR
Perennial ryegrass	41	13	9
Cocksfoot	40	31	23
	Defoliation frequency		
	One week	Three weeks	
Perennial ryegrass	15	26	
Cocksfoot	31	31	
Analysis of variance	Probability	SEM	
Species	P<0.001	1.0	
PPFD/R:FR	P<0.001	1.3	
Defoliation	P<0.001	0.7	
Species x PPFD/R:FR	P<0.01	1.0	
Species x defoliation	P<0.01	1.0	
PPFD/R:FR x defoliation	NS	1.0	
Species x PPFD/R:FR x defoliation	NS	1.7	

plants than on the level of R:FR. The levels of PPFD and R:FR ratios used were within the range observed under alder at mid-day (166 - 759 μmoles photons/m^2/s, 0.96 – 1.24) (Devkota, 2000), and the daily mean under mature poplar (88 μmoles photons/m^2/s) (Guevara-Escobar, 1999) in silvopastoral systems. Therefore, an alternative to sowing pastures based on shade tolerant species such as cocksfoot under deciduous trees would be to manage the tree canopy through pruning so that the light intensity is adequate for the growth and development of common pasture species. In Experiment 2 the number of tillers per plant was similar for cocksfoot and perennial ryegrass at 441 μmoles photons/m^2/s, but was lower in ryegrass at 153 μmoles photons/m^2/s, demonstrating the change in comparative shade tolerance of pasture selections as PPFD decreased. Devkota (2000) suggested that the threshold PPFD intensity if species such as ryegrass and browntop are to produce two-thirds of their production in full PPFD was 400 μmoles photons/m^2/s or approximately 35 % of full PPFD in Manawatu, New Zealand.

Morphological responses of plants growing under shade include: increased leaf area ratio, increased shoot to root ratio, increased specific leaf area, increased plant height, and reduction in vegetative shoots (Kephart *et al.*, 1992; Sanderson *et al.*, 1997; Wilson, 1997). Similarly, across Experiments 1, 2 and 3 increased specific leaf area, preferential allocation of biomass to leaves, and decreased tillers per plant were the main morphological responses to shade in the pasture selections examined.

Although the specific leaf area of cocksfoot and ryegrass increased in response to low PPFD the specific leaf area of cocksfoot was always greater than that of ryegrass. The increased specific leaf area in response to low PPFD was less important than the inherent specific leaf area of cocksfoot in determining its leaf area. High specific leaf area is an adaptation to shade in that for each unit weight of leaf dry matter a greater area of leaf is able to intercept the available light (Sanderson *et al.*, 1997). The greater tolerance of heavy shade (81 – 232 μmoles photons/m^2/s) by the shoot growth of cocksfoot

Table 4. Effects of two percentages of ambient photosynthetic photon flux density (PPFD, 989 μmoles photons/m^2/s) on leaf area, specific leaf area, tiller number/plant and cumulative shoot dry weight of ten cocksfoot selections and perennial ryegrass under glasshouse conditions (Experiment 3).

Treatments	Leaf area (mm^2×100/plant)	SLA (mm^2/mg)	No. tillers/plant	Shoot dry weight (g/plant)
73% PPFD; 720 μmoles photons/m^2/s				
Cocksfoot selections				
minimum	93	12.9	25	3.0
maximum	173	20.0	38	4.5
mean	119	15.9	32	3.8
Perennial ryegrass cv. G. Nui	33	4.7	37	4.9
24% PPFD; 232 μmoles photons/m^2/s				
Cocksfoot selections				
minimum	49	17.8	18	1.4
maximum	92	28.9	28	2.2
mean	66	21.3	26	1.9
Perennial ryegrass cv. G. Nui	22	7.6	18	1.2
Analysis of variance				
PPFD (A)	P<0.001	P<0.05	P<0.0001	P<0.05
SEM for PPFD (d.f.=2)	5.06	0.82	0.59	0.28
Selections (B)	P<0.0001	P<0.0001	P<0.0001	P<0.0001
SEM for selections (d.f.=10)	6.15	1.00	0.84	0.11
Interaction (A x B)	NS	NS	P<0.01	P<0.001
SEM for A x B (d.f.=20)	10.66	1.74	1.46	0.20

compared with ryegrass appeared to result from its greater leaf area, and consequent greater light interception. This advantage of cocksfoot over ryegrass was due to the greater specific leaf area of cocksfoot, and to the lesser sensitivity of the leaf appearance and tillering rates of cocksfoot to low PPFD (Devkota, 2000).

It is suggested that the differences between cocksfoot and ryegrass in specific leaf area and the sensitivity of tillering to low PPFD, attributes that determine their performance in heavy shade, were largely due to genetic differences rather than differences in their morphological responses to low PPFD or low R:FR ratio. The morphological responses of the pasture species to a decrease in R:FR ratio were small in comparison to the responses to low PPFD. Nevertheless, responses such as reduced tillering or branching were triggered by low PPFD as well as low R:FR ratio (Assmann, 1992, Maliakal *et al.*, 1999).

Photosynthetic rate was not measured in these experiments, but the shoot dry weight of ryegrass relative to its leaf area suggested that its photosynthetic rate per unit area was higher than that for cocksfoot. However, the photosynthetic rate per unit leaf mass of the two species would have probably been similar as their leaf masses were similar (see Table 4 and Devkota, 2000). Therefore, it was concluded that a key advantage of cocksfoot in heavy shade was its greater light interception. This is supported by the observation that the cocksfoot selection with the lowest specific leaf area and leaf area had the lowest shoot dry weight (Devkota, 2000).

The shade tolerance of the cocksfoot selections varied, due to variation in specific leaf area and tillering, which suggested that a more shade tolerant cocksfoot could be found. The most shade tolerant of the cocksfoot selections evaluated in these experiments and other experiments by Devkota (2000) were cv. Grasslands Wana. Cocksfoot was regarded as the most shade tolerant temperate grass species under radiata pine trees (Pollock *et al.*, 1997).

The variation in shade tolerance within other temperate pasture species was not examined, but the main criteria to use in evaluating shade tolerance would be production, specific leaf area and tillering in low light intensities, and defoliation tolerance. Although there was no interaction between defoliation frequency and the shade treatments, defoliation tolerance is essential in a perennial pasture species.

Conclusion

Cocksfoot was the most shade tolerant selection in terms of production in heavy shade (i.e., <25 % of ambient PPFD or approximately 200 μmoles photons/m^2/s) due to its greater leaf area as a consequence of its high specific leaf area and the insensitivity of its tillering to low light.

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