Performance of perennial ryegrass and cocksfoot cultivars under tree shade

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Abstract

The shade from trees in silvopastoral systems potentially decreases the persistence and production of pasture species by reducing tillering and shoot dry weight accumulation. However data from a glasshouse trial indicated that cocksfoot (*Dactylis glomerata* L.) had better tolerance to shade than other pasture species at the lowest photosynthetically active radiation. To verify the results obtained in the glasshouse, and also to evaluate whether any differences exist among cocksfoot cultivars in terms of shade tolerance attributes, seven cultivars of cocksfoot along with perennial ryegrass (*Lolium perenne* L.) cv. Grasslands Nui were field tested under 11-year old alder trees at the Horticultural Research Centre, Aokautere. A split-plot design with four replicate blocks was employed for the experiment. The main plot treatments were three levels of photosynthetic photon flux density (PPFD) (77%, 27%, and 17% of full sunlight) created by pruning trees to different heights. The sub-plot treatments were pasture species and cultivars grown at first in a glasshouse and then transferred in pots to the field. Five plants per pot were maintained and plants were watered daily. Water and fertilizer were non-limiting. The experiment ran from 3 February to 30 April, 1997. Tillers per plant and shoot dry weight were assessed 5 times at 15 day intervals and leaf area, leaf dry weight, specific leaf area, and root dry weight per plant were determined at the final harvest. Shade affected ryegrass more than all the cocksfoot cultivars, especially at the low PPFD. Eighteen tillers were produced in ryegrass compared with twenty nine ($p<0.001$) for cocksfoot cv. Grasslands Wana at the final harvest. Ryegrass leaf area per plant was also significantly ($p<0.001$) lower (1559 mm^2) than cocksfoot cv. Grasslands Wana (8163 mm^2), and similarly for relative specific leaf area, and leaf dry weight at the low PPFD. Cocksfoot cultivars were better able to tolerate low PPFD than perennial ryegrass, and cv. Grasslands Wana was a particularly shade tolerant cultivar.

Additional key words: *PPFD, shade, pasture species, leaf area, specific leaf area, leaf dry weight, tiller, Grasslands Nui, Grasslands Tekapo, Grasslands Kara, PG 321, PG 306, PG 74, PG 301, Grasslands Wana, alder*

Introduction

Planting of conservation trees (Miller *et al.*, 1996) has become a common land use practice in recent years as a means of income diversification and/or erosion control (Pollock *et al.*, 1994). Trees may be planted at both high or low densities to allow grazing of the pasture until tree canopy closure (Pollock *et al.*, 1994).

The shade from trees in silvopastoral systems potentially decreases the persistence and production of pasture species. Leaf area development, growth rate, and yield of pastures vary directly with the amount of sunlight available under the canopy (Sanderson *et al.*, 1997). Low levels of irradiance reduce growth (Shelton *et al.*, 1987) and affect morphological attributes of pasture species through altered partitioning of photosynthate (Kephart and Buxton, 1993). Shade intolerant species have a high light compensation point (20-30 μmol photons/m^2/s) for photosynthesis (Boardman, 1977; Herrera *et al.*, 1991) compared with 0.5-10 for shade tolerant species (Boardman, 1977). Saturating intensities of 400-600 μmol photons/m^2/s for shade intolerant plants (Boardman, 1977), and 60-300 μmol photons/m^2/s for shade plants performing C_3 photosynthesis (Ball *et al.*, 1991, Boardman, 1977) have also been reported.

The general responses to low-light stress include increases in plant leaf area to maximize light interception and changes in physiological processes to enhance the efficiency of carbon utilization (Sanderson *et al.*, 1997). Other responses include higher leaf area ratios and reduced specific leaf weight. Therefore, the ability of plants to generate leaf area and tillers in low light are critical factors that determine pasture production in shade conditions (Chen, 1993).

As well as decreasing the quantity of light, the tree canopy absorbs more red (R) wavelengths (approximately 660nm) than far-red (FR) wavelengths (approximately 730nm) such that R:FR ratio of light decreases towards the base of the canopy (Sanderson *et al.*, 1997). The ratio of the photon irradiance in the R, to that in the FR, is a parameter of the light environment which is directly related to the spectral properties of phytochrome (Smith, 1994). Owing to the presence of phytochrome pigment system, plants are sensitive to the ratio of the red and far-red quanta that influence plant development (Lee *et al.*, 1994; Smith, 1994). Generally,branching is more affected by shade due to low photosynthetically-active radiation and low R:FR (Thomson, 1993; Teuber and Laidlaw, 1996; Sanderson *et al.*, 1997; Wan and Sosebee, 1998).

Devkota *et al.* (1997) in a glasshouse study found that the tillering of cocksfoot in heavy shade (14% of full sunlight) was superior to that of perennial ryegrass in both absolute and relative terms. When unshaded (73% of full sunlight), cocksfoot and perennial ryegrass developed 18 and 24 tillers per plant, respectively. At 14% of full sunlight cocksfoot developed 4 tillers per plant which was 19% of the tillers at 73% of full sunlight. In contrast perennial ryegrass developed only 4% of the tillers at 14% of full sunlight that it had at 73% of full sunlight.

This study aimed to verify the results from the glasshouse in 1996 (Devkota *et al.*, 1997), and to evaluate variation among cocksfoot cultivars in terms of shade tolerance attributes. This research was part of a program to determine suitable pasture species for silvopastoral systems based on deciduous trees. Accordingly, seven cultivars of cocksfoot and one cultivar of perennial ryegrass were field tested for their morphological characteristics and responses to shade under eleven-year old alder trees.

Materials and Methods

The experiment was conducted from 18 December, 1996 to 30 April, 1997 (134 days). Plants were at first grown in pots in a glasshouse under full available sunlight (Plant Growth Unit, Massey University), then transferred to the field in the pots on 3 February, 1997. The field site was at the Horticultural Research Centre, Aokautere, under 11-year old alder trees. Pots in the field were arranged in a split plot design with four replicate blocks. The main plots were shade treatments created by pruning trees to different heights from ground level, and subplots were cocksfoot cultivars and perennial ryegrass. Pruning heights were to 2.5 m, 5.0 m and 7.0 m from the ground, which resulted in three levels of transmitted photosynthetic photon flux density (PPFD) (17%, 27% and 77% of full sunlight, hereafter called heavy, medium, and light shade respectively) as determined by measuring on three occasions (7 February, 19 March, and 14 April, 1997) on clear sky days between 1200 to 1300h using a Licor Quantum Sensor. The R:FR ratio of the light was also measured on the three occasions with a Skye Sensor at just above the swards under the trees. Mean R:FR ratio of the three measurements was 0.96, 1.17, and 1.24 for heavy, medium and light shade respectively.

Details of the pasture species and cultivars used are given in Table 1. Seeds of the pasture species were sown on 28 December, 1996 in PB 6½ (3.9 litre) black polypots filled with potting mix (80% tree bark + 20% pumice). Dolomite 300 g, agricultural lime 300 g, iron sulphate 50 g, and Osmocote plus (16N-3.5P-10.8K) 400 g per 100 litre were blended with the potting mix, which was rated for medium to long term (< 9 months) greenhouse crops. Five plants were maintained per pot. Pots in the field were buried in the soil with approximately the top 30 mm above soil level. Plants were watered daily when there was no rain.

Plants were first harvested on 5 March, 1997 (77 days after sowing). Subsequent harvests were on 19 March (91 days after sowing), 2 April (105 days after sowing), 16 April (126 days after sowing), and 30 April (133 days after sowing) 1997. At each harvest, all the plants were clipped to 50 mm above the media surface. Shoots above 50 mm in length were dried at 70°C for 24 hours,

Table 1. Cocksfoot (*Dactylis glomerata* L.) and Perennial ryegrass (*Lolium perenne* L.) cultivars used.

Pasture species and cultivar
Cocksfoot cv. Grasslands Tekapo (tetraploid)
Cocksfoot cv. Grasslands Kara (tetraploid)
Cocksfoot, PG 321, subsp. *izcoi* (tetraploid)
Cocksfoot, PG 306, subsp. *marina* (tetraploid)
Cocksfoot, PG 301, subsp. *marina* (tetraploid)
Cocksfoot, PG 74, subsp. *izcoi* (diploid)
Cocksfoot cv. Grasslands Wana (tetraploid)
Perennial ryegrass cv. Grasslands Nui

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 leaves and stems were separated. Leaf area was measured, then leaves and stems dried at 70°C for 24 hours. Roots of all the plants in each pot were washed then oven dried at 70°C for 24 hours to calculate root dry weight per plant. Tiller numbers at the final harvest only are reported in this paper. Statistical analysis was by analysis of variance using the GLM model of the SAS package (SAS Institute Inc. 1989).

Results

Shoot dry weight

The cumulative shoot dry weights (g/plant) of the grasses at different shade levels are presented in Table 2. All the grasses produced their highest yield under light shade and lowest under heavy shade, indicating the significant ($P<0.001$) effects of shade. There were also significant differences among the cocksfoot cultivars at each of the shade levels (Table 2).

Under light shade, perennial ryegrass had the greatest shoot dry weight (Table 2). The shoot dry weight of cv. Grasslands Wana was significantly greater than all the other cocksfoot cultivars except for PG 306. Under medium shade perennial ryegrass still had a significantly greater shoot dry weight than all the cocksfoot cultivars.

Table 2. Effects of shade on cumulative shoot dry weight (g/plant) of seven cocksfoot cultivars and perennial ryegrass under alder trees.

	Shade level (S)		
Cultivar (C)	Light	Medium	Heavy
Tekapo	3.53	3.16	1.89
Kara	4.08	2.71	2.22
Wana	5.01	3.54	2.34
PG 321	3.77	2.95	1.76
PG 306	4.30	2.87	1.67
PG 74	3.75	2.95	2.28
PG 301	3.76	3.03	1.93
Perennial ryegrass	5.90	3.97	1.93

Analysis of variance

	d.f.	P	SEM	$LSD_{0.05}$
Shade (S)	2	<0.0001	0.10	.38
Cultivar (C)	7	<0.0001	0.15	.44
Interaction (C*S)	14	<0.01	0.27	

Within the cocksfoot cultivars cv. Grasslands Wana, which had the highest shoot dry weight, was significantly greater only than cv. Grasslands Kara. There were no significant differences ($P>0.05$) between perennial ryegrass and any of the cocksfoot cultivars under heavy shade. Perennial ryegrass shoot dry weight under heavy shade was 33% of that at light shade, whereas shoot dry weight of cocksfoot cv. Grasslands Wana was 47% of that under light shade (Table 2).

Tillers per plant

The main effects of shade and cultivars were significant for tillers per plant at the final harvest in absolute ($p<0.001$), and in relative ($p<0.01$) terms (Table 3), but the interaction of cultivar × shade was not significant. The highest number of tillers was produced by cv. Grasslands Wana under light shade followed by PG 321 and perennial ryegrass (Table 3). The number of tillers per plant for PG 74 and PG 301 were similar and lowest among the cocksfoot cultivars. At medium shade, PG 74 had the lowest number of tillers per plant but was only significantly different ($P<0.05$) from PG 306 and cv. Grasslands Wana which had the greatest number of tillers per plant. All the other cocksfoot cultivars and perennial ryegrass had a similar number of tillers per plant. Cv. Grasslands Wana had the highest number of tillers per plant under heavy shade, which was significantly ($P<0.05$) more than for cv. Grasslands Kara and PG 306, among the cocksfoot cultivars, and for perennial ryegrass (Table 3). Perennial ryegrass produced fewer tillers than all the cocksfoot cultivars studied, but this was not significantly different ($P>0.05$) from cv. Grasslands Kara, PG 306, and PG 301.

The response of relative number of tillers per plant to shade was different from absolute tillers (Table 3). Relative to light shade, cv. Grasslands Kara produced more tillers under medium shade than the other cocksfoot cultivars, but this was only significantly different ($P<0.05$) from cv. Grasslands Wana and perennial ryegrass. Under heavy shade, cv. Grasslands Tekapo had the highest relative tillering but was only significantly greater than perennial ryegrass.

Specific Leaf Area (SLA)

The main effects of shade, and the interaction between shade and cultivars for specific leaf area (SLA) were not significant. However, the SLAs among the cultivars were significantly different (Table 4). Cv. Grasslands Kara had highest SLA at light shade which was significantly different to the rest of the cultivars except PG 321. SLA of the other PG lines was similar. Perennial ryegrass had the lowest SLA and was significantly different to the cocksfoot cultivars. Under medium shade, PG 74 had the highest SLA, but this was not significantly greater than the SLA of cv. Grasslands Wana, cv. Grasslands Kara, and the other PG lines except PG 306. SLA of perennial ryegrass was significantly lower than that of the cocksfoot cultivars. Under heavy shade, all the cocksfoot cultivars, except cv. Grasslands Tekapo, had similar SLA, but SLA of cv. Grasslands Tekapo was similar to that of cv. Grasslands Wana. SLA of the perennial ryegrass at each PPFD level was approximately half that of the cocksfoot cultivars (Table 4).

Table 3. Effects of shade on tillers per plant of seven cocksfoot cultivars and perennial ryegrass after 134 days grown under alder trees.

Shade (S) and Cultivar (C)	Tillers per plant	Relative tillers per plant
Light shade (trees pruned to 7 m height)		
Tekapo	32	100
Kara	29	100
Wana	41	100
PG 321	38	100
PG 306	36	100
PG 74	31	100
PG 301	32	100
Nui	37	100
Medium shade (trees pruned to 5 m height)		
Tekapo	30	94
Kara	28	97
Wana	33	80
PG 321	30	81
PG 306	34	94
PG 74	25	81
PG 301	28	89
Nui	29	78
Heavy shade (trees pruned to 2.5 m height)		
Tekapo	25	79
Kara	22	77
Wana	29	71
PG 321	24	65
PG 306	23	64
PG 74	24	77
PG 301	23	73
Nui	18	47
Analysis of variance		
Shade (S)	P<0.0001	P<0.01
Cultivar (C)	P <0.001	P <0.005
Interaction (S*C)	NS	NS
SEM (S) (d.f.=2)	0.68	2.48
SEM (C) (d.f.=7)	1.25	4.15
SEM (S*C) (d.f.=14)	2.17	5.87
$LSD_{(0.05)}$ for S	2.38	11.17
$LSD_{(0.05)}$ for C	3.55	11.85

Leaf area per plant

Shade and cultivars affected leaf area per plant (Table 4). The highest leaf area was produced by PG 321 (17821 mm^2) under light shade but this was not significantly different from cv. Grasslands Wana, cv. Grasslands Kara, PG 306, and PG 301. Ryegrass produced the lowest leaf area (10707 mm^2) under light shade. Under medium shade leaf area of PG 301 was the highest, followed by PG 321 and cv. Grasslands Wana. However, leaf areas of cv. Grasslands Wana, all the PG lines, and cv. Grasslands Tekapo were not significantly different. Ryegrass always had the lowest leaf area (5476 mm^2) per plant and was significantly different from all cocksfoot cultivars except cv. Grasslands Kara (Table 4). Under heavy shade, leaf areas of the cocksfoot cultivars did not differ but all were, however, significantly greater than perennial ryegrass. The leaf area of perennial ryegrass was only 19% of that of cv. Grasslands Wana under heavy shade whereas it was 65% of that of cv. Grasslands Wana under light shade. In contrast, Cv. Grasslands Tekapo, the cocksfoot cultivar with the smallest leaf area, had 69% of the leaf area of cv. Grasslands Wana under heavy shade and 74% of cv. Grasslands Wana under light shade.

Leaf dry weight per plant

Similarly to leaf area, the highest leaf dry weight per plant was under light shade, and the lowest under heavy shade for all species. Under light shade, perennial ryegrass had the highest leaf dry weight but this was only significantly different from cv. Grasslands Kara and PG 74. Cv. Grasslands Kara had the lowest leaf dry weight and was similar to PG 74 (Table 4). This was repeated under medium shade where all the cultivars had similar leaf dry weight, and were not significantly different, except for cv. Grasslands Kara and PG 74. However, leaf dry weight of ryegrass was 86% of PG 301 (highest producer) compared with 57% for cv. Grasslands Kara (lowest producer). Under heavy shade, leaf dry weight did not significantly differ among the cocksfoot cultivars, but that of cv. Grasslands Wana was greater than that for perennial ryegrass. Leaf dry weight of perennial ryegrass, which was the lowest under heavy

Table 4. Effects of shade on leaf area per plant, leaf dry weight, specific leaf area, and root dry weight of seven cocksfoot cultivars and perennial ryegrass after 134 days, grown under alder trees.

Shade (S) and Cultivar (C)	Leaf area (mm^2)	Leaf dry weight (mg/plant)	Specific leaf area (mm^2/mg)	Root dry weight (mg/plant)
Light shade (trees pruned to 7 m height)				
Tekapo	12655	660	1965	540
Kara	14305	550	2597	480
Wana	17027	740	2273	560
PG 321	17821	750	2341	470
PG 306	15789	720	2186	530
PG 74	12419	560	2217	410
PG 301	15419	760	1971	530
Nui	10707	810	1284	780
Medium shade (trees pruned to 5 m height)				
Tekapo	10006	530	1902	380
Kara	7316	330	2203	300
Wana	11338	490	2312	440
PG 321	12233	540	2245	360
PG 306	10214	480	2086	380
PG 74	9404	380	2458	320
PG 301	12870	580	2182	290
Nui	5476	500	1105	470
Heavy shade (trees pruned to 2.5 m height)				
Tekapo	5669	270	1950	170
Kara	6425	250	2520	230
Wana	8163	360	2235	210
PG 321	8053	330	2395	130
PG 306	6025	250	2381	160
PG 74	5839	230	2502	220
PG 301	8152	330	2452	180
Nui	1559	140	1106	210
Analysis of variance				
Shade (S)	$P < 0.01$	$P < 0.001$	NS	$P < 0.0001$
Cultivar (C)	$P < 0.0001$	$P < 0.01$	$P < 0.0001$	$P < 0.001$
Interaction (S*C)	NS	NS	NS	$P < 0.05$
SEM (S) (d.f.=2)	976	40	64.5	7
SEM (C) (d.f.=7)	829	30	67.7	20
SEM (S*C) (d.f.=14)	1435	60	117.3	40
$LSD_{(0.05)}$ for S	2343	90	191.4	70
$LSD_{(0.05)}$ for C	3390	150	223.3	20

shade, was 39% of cv. Grasslands Wana compared to 64% of PG 74 (Table 4).

Root dry weight per plant

In general, root dry weight per plant decreased in all species from light to the heavy shade. Highest root weight per plant was for ryegrass (780 mg) at light shade followed by cv. Grasslands Wana. Root weight of PG 74 was the lowest and significantly different to some of the other cultivars (Table 4). Under medium shade, ryegrass had a larger root weight (470 mg) than the cocksfoot cultivars, but was significantly different only from cv. Grasslands Kara, PG 74 and PG 301. Among the cocksfoot cultivars cv. Grasslands Wana had the highest root weight and PG 301 the lowest. Under heavy shade, however, root dry weight per plant of all the cultivars was similar (Table 4).

Discussion

The ability of species to maintain production under shade indicates shade *tolerance*, and a sharp decrease in production due to shade, *intolerance* (Toledo *et al.*, 1989). A shade tolerant pasture species needs to have good annual and seasonal dry matter production under defoliation, and to be able to regenerate (Devkota *et al.*, 1997). Leaf area development, growth rate and yield of forage vary directly with the amount of sunlight available to the canopy (Sanderson *et al.*, 1997). However, tillering ability and biomass production are the cumulative expression of plant processes affected by shade.

Cocksfoot cultivars maintained a comparatively higher relative shoot mass than perennial ryegrass especially in heavy shade, due to higher leaf area, higher absolute and relative tiller numbers, as well as a higher specific leaf area. Accordingly, cocksfoot cv. Grasslands Wana produced about half of the shoot dry weight under heavy shade of that of light shade while perennial ryegrass produced only about one third. Cocksfoot cultivars were more able to produce more tillers than ryegrass in heavy shade. At a medium level of shade, however, the performance of perennial ryegrass was similar to that of cv. Grasslands Wana cocksfoot in terms of shoot yield and leaf dry weight, but not in terms of tillering. These results were in line with an earlier screening experiment with grasses and legumes in pots under glasshouse conditions (Devkota *et al.*, 1997).

In this study ryegrass was affected more by shade than cocksfoot. Low ryegrass production under heavy shade has also been indicated by Percival *et al.* (1984) and Hunt and Easton (1989). Pollock *et al.* (1997) reported that cocksfoot/clover production under radiata pine at Lincoln, was better than either ryegrass/clover or ryegrass.

Shoot yield of ryegrass was comparatively low under the heavy shade due to the low absolute as well as relative tillering, and low leaf area per plant. One possible reason for fewer tillers in ryegrass could be a high level of sensitivity towards the changes in light quality (lower R:FR ratio) in the lower levels of the canopies (Deregibus *et al.*, 1983). Average R: FR ratio in the heavy shade in this experiment was 0.96. Exact effects of a lower R:FR ratio on the tillering of plants is debatable; however, R:FR ratio could serve as a signal to indicate canopy cover which is thought to interact with other stimuli related to the availability of water, assimilates, and nutrients to determine the rate of tiller formation (Everson *et al.*, 1988). Such an effect may be greater for perennial ryegrass. Nonetheless, an important result in this experiment was that the performance of ryegrass in the medium level of shade was similar to cv. Grasslands Wana. However, ryegrass did not tolerate the heavy shade.

The comparatively greater shoot dry weight of cocksfoot cv. Grasslands Wana in heavy shade could be associated with its ability to continue to produce to tillers. Cv. Grasslands Wana also had both greater leaf area and leaf dry weight in heavy shade conditions than the other cultivars. Cv. Grasslands Wana may be more shade tolerant than some of the other cocksfoot cultivars used in the experiment.

PG 74, a diploid cocksfoot cultivar, was next best to cv. Grasslands Wana in terms of shoot dry weight production in heavy shade, but not in terms of absolute or relative tillers per plant. One reason for the fewer tillers in PG 74 compared with cv. Grasslands Wana could be that diploid cocksfoots are mainly confined to forest floors (Bretagnolle and Thompson, 1996), and perhaps adapt under the heavy shade by allocating more resources to leaves rather than to develop new tillers, although this remains to be determined.

Morphological changes of plants under shade, such as reduction in root mass, high shoot/root ratio, and increased leaf: stem ratio, although perhaps of value ecologically (Wilson, 1997), may not be directly relevant attributes for the production of pasture under shade. Absolute and relative tillers per plant and the shoot dry weight along with leaf area and SLA are important attributes that determine not only shade tolerance (Devkota *et al.*, 1997), but also the productivity and persistence of pasture species under shade. The cocksfoot cultivars, particularly cv. Grasslands Wana, were often superior to perennial ryegrass in heavy shade for these attributes, which are also important for defoliation tolerance.

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