The response of *Panicum maximum* to a simulated subcanopy environment. 2. Soil × shade × water interaction

P.A. DURR AND J. RANGEL[1]
James Cook University, Townsville, Queensland, Australia
[1]*Current address: Embrapa Tabuleiros Costeiros, Aracaju, Sergipe, Brasil*

Abstract

Continuing on from previous work examining the mechanisms by which increases in the biomass of *Panicum maximum* might occur when growing under the canopy of mature *Samanea saman* trees (Durr and Rangel 2000), a further pot trial was undertaken. This applied a similar methodology of using soil collected from under and away from the canopy of trees and imposing variable light levels by shade cloths. A third variable was introduced, that of water stress, through varying the period of re-watering: every day, every 5 days and every 10 days. The major effect of water stress was to reduce the biomass. However, the degree of reduction was dependent upon the soil and the shade level, as there was relative compensation in grasses grown in the subcanopy-collected soil at intermediate shade levels due to an increase in the water use efficiency. This finding suggests that one of the major benefits of nutrient enrichment by trees in these environments acts via improved water utilisation and suggests a generalised explanation of why relative increases of grass biomass under the canopy of trees might occur in subhumid environments.

Introduction

The "over-yielding" phenomena can be defined as relative increases in crop and herbage yields under the canopy of trees as compared with nearby open areas (Anderson and Sinclair 1993). Although documented to occur in open woodlands and plantations (Kennard and Walker 1973; Wilson *et al.* 1990), most attention has focused upon cases involving individual trees in tropical pastures and rangelands (Christie 1975; Lowry *et al.* 1988; Belsky *et al.* 1989; Weltzin and Coughenour 1990; Durr and Rangel 2002). For this over-yielding under individual trees, it is possible to identify 3 key features: (1) a strong association with the immediate canopy such that there is often a sharp transition in productivity at its edge; (2) the involvement of a range of tree species, both leguminous and non-leguminous; and (3) a species shift, with the subcanopy species being generally more mesic in their growth requirements.

To date, most explanations of over-yielding in tropical grasslands have focused on the importance of shade and soil nutrients (Belsky 1994; Wilson 1996). By contrast, the role of subcanopy water relations has received less attention, despite many of the documented examples occurring in subhumid and arid environments. Furthermore, some of the beneficial effects of shade and soil nutrients might themselves be expected to be mediated through enhanced subcanopy water relations (Wilson 1996).

One factor that may affect the growth response of species under the canopy of trees is the water use efficiency (WUE), the ratio of dry matter produced for a given unit of transpired water. WUE has been scarcely investigated in tropical grasses, but has been demonstrated to be highly variable, both between (Pressland 1982) and within (Pieterse *et al.* 1997) species. The WUE is also known to be affected by the rate of applied nitrogen (Pieterse *et al.* 1997). As a consistent effect of the tree canopy is to augment the soil N (Rhoades 1997), consequent changes in the WUE might be expected.

In a previous paper, we used a simulated subcanopy environment to investigate the relative roles of soil nutrients and shade to explain

Correspondence: P.A. Durr, Department of Epidemiology, VLA (Weybridge), New Haw, Addlestone, England. email: p.durr@vla.defra.gsi.gov.uk

increases in biomass of guinea grass, *Panicum maximum*, growing beneath the canopy of *Samanea saman* (Durr and Rangel 2000). That experiment clearly showed that increased relative yields could occur under shade as a direct result of the compensatory effect of the higher sub-canopy soil nutrient levels. Here, we describe an extension of this methodological approach to investigate the 3-way interaction between shade, soil fertility and water stress. Specifically, we wished to test the hypothesis that, in situations of limiting water, biomass response to the sub-canopy habitat would remain augmented due to changes in the WUE.

Materials and methods

In August 1994, 4 *S. saman* trees at the study site were selected at random and topsoil (0–20 cm) was collected, as for the first experiment, from under the canopy and in the open grassland. The soil from each location was dried, sifted and homogenised. Plastic pots of 19.5 cm diameter were then filled with 3450 g of the soil. Soil was not collected from near the canopy as the first experiment showed only a minor difference in growth response compared with the open grassland.

Seeds of *P. maximum* cv. Riversdale were germinated in seedling trays in early September 1994 and allowed to develop for 14 days. They were then transplanted, one per pot, and 5 days later were allocated at random to the 4 shade treatments as described in Durr and Rangel (2000). Briefly, these consisted of 3 different thicknesses of commercial shade cloths stretched over a longitudinal trellis, with a fourth area of equal size to the shaded treatments left as a control. The photosynthetic flux density (PFD) levels under these treatments were determined on 5 separate occasions, at approximately 10-day intervals, using 4 standardised quantum sensors. Data collection and processing were essentially similar to that for the first experiment.

In contrast to the first experiment, water relations were more strictly controlled. Evaporative losses of applied water to each pot were minimised by placing polyethylene beads on the soil surface, and water draining from the pots was retained in trays so that it could subsequently be absorbed by the plants. Prior to transplanting, the field capacity (FC) of the homogenised soil was determined by wetting 4 pots of each soil type to saturation and allowing drainage for 3 days. During the experiment, all pots were taken to this FC and then the water treatments were imposed. These consisted of: daily watering to the predetermined FC; a drying cycle of 5 days followed by re-wetting to FC; and a drying cycle of 10 days followed by re-wetting to FC. For the fourth of the 10-day drying cycles, pots were weighed daily and the gravimetric moisture content (θ_g) determined. During this drying cycle, the grasses were observed for signs of water stress, and the days noted when either leaf rolling (mild stress) or wilting (severe stress) was occurring. Relative potential evaporation was estimated during this period by the measurement of water loss from small plastic containers (diameter 17 cm) placed in the middle of each shade treatment 10 cm above the ground.

The experiment continued until mid-November 1994. All plants were harvested 50 days after commencement of the shade and water treatments (= 69 days post germination). The shoots were separated into leaves and stems and then dried at 65°C for 2–3 days. The root weight was determined by hosing under moderate pressure to remove soil, and then drying the roots at 65°C. Shoot material was subsequently partitioned into green and senesced (yellow plus dead) fractions.

The experimental design was a split-split plot with 3 replicates, 4 light treatments (the main plot), 2 soil treatments (the first subplot), and 3 water stress treatments (the second subplot). The total dry weights (TDW) and the shoot:root (S:R) ratios were analysed by a mixed model ANOVA using SPSS for Windows 6.1 (SPSS Inc., Chicago, Illinois). Both analyses required a logarithmic transformation to satisfy the assumptions of the linear model. Significant treatments were partitioned by single degree of freedom contrasts and significant interactions were analysed first for each water treatment and then by specific contrasts. The data for the 10-day drying cycle were analysed as a repeat measures design using a univariate mixed model as replication was inadequate for a multivariate profile analysis. The data for wilting were analysed by a mixed model ANOVA.

Results

Shade and soil nutrient levels

All-day measurements during the experiment established that the PFD levels (mean ± s.e.) were 42.3 (±4.8) mol/m^2/d for the unshaded treatment and 21.7 (±2.1) mol/m^2/d, 16.1 (±1.2) mol/m^2/d, and 6.4 (±0.9) mol/m^2/d for the shaded treatments. The proportional PFDs relative to the non-shaded treatment were therefore 51, 38 and 15%. The corresponding relative evapotranspiration rates, as compared with full sunlight, were 70.6 (± 3.3)% for the 51% relative PFD; 64.1 (± 3.3)% for the 38% relative PFD; and 53.4 (± 2.5)% for the 15% relative PFD. Relative shade and relative evapotranspiration were linearly related (r^2 = 0.99). The soil nutrient levels were comparable with those in the first experiment (Table 1), with markedly higher N and P levels in the subcanopy compared with the open grassland soil.

Non-water stress treatments

There was a marked soil effect, and the average biomass of the grass grown in the soil collected from under the canopy was *c.* 3 times that of grass grown in soil collected from the open grassland (Figure 1). This increment was consistent across the treatments and there was no soil × shade interaction (P = 0.893).

The shade treatments gave different results from those in the first simulation experiment, with a significant difference between the full sunlight treatment and the first shaded treatment (the 51% relative PFD). Although there was no statistically significant difference between the 3 shaded treatments, this was in part due to a high variation in the 38% relative PFD, and a clear trend for diminished biomass was evident, particularly for the under canopy soil treatment. Shoot:root (S:R) partitioning differed from that of the first experiment with a significant soil

Table 1. Nutrient levels for the soil (0–20 cm layer) collected from different locations relative to *Samanea saman* trees.

Parameter	Location	
	Under canopy	Open grassland
Kjeldahl N (%)	0.29	0.10
Available P (ppm)	66.7	22.2
Exchangeable K (meq/100g)	1.54	1.48
Exchangeable Ca (meq/100g)	7.10	2.57
Exchangeable Mg (meq/100g)	2.63	1.68

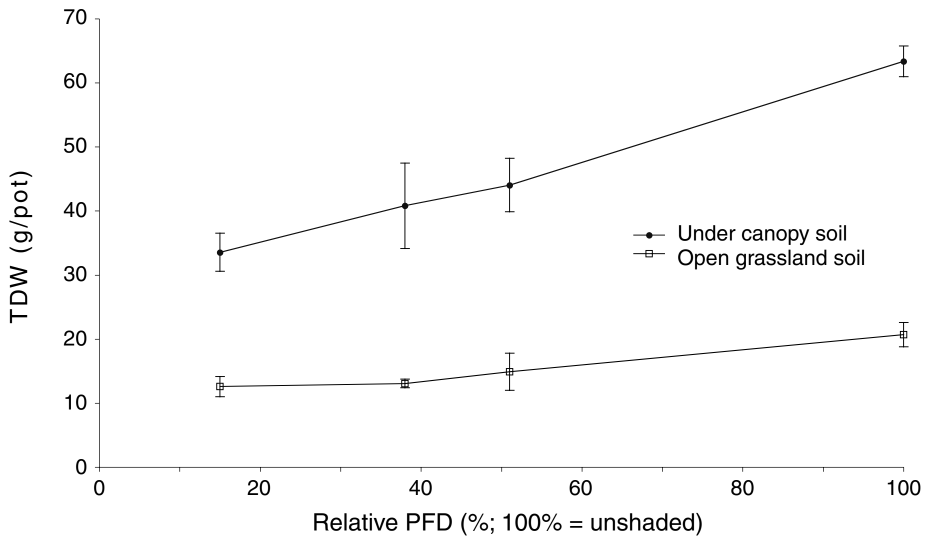

Figure 1. Total dry weight (TDW) of *P. maximum* (n = 3) grown in soil collected from under the canopy of *Samanea saman* and from open grassland at 4 levels of shading with daily watering to field capacity. Vertical bars indicate s.e. of the mean.

treatment effect, the average S:R ratio for the under canopy soil being significantly higher ($P = 0.002$) than for the open grassland soil (2.3 *vs* 1.6). There was no soil × shade interaction ($P = 0.938$).

Soil moisture response

The gravimetric FC for the under canopy soil was determined to be 45.1% and for the open grassland soil 41.6% (Figure 2). After 10 days of drying, the θ_g had declined to an overall average of 6.3% for the under canopy soil and 5.4% for the open grassland soil, these values being significantly different ($P < 0.001$).

There were significant differences in the drying curves, these differences being conditional on both the shade levels and the soil type (soil × shade interaction, $P = 0.034$). For the under canopy soil, moisture levels were significantly higher at the deepest shade, than at the 2 intermediate shade levels, which in turn had significantly higher moisture levels than the full sunlight treatment (Figure 2a). For the open grassland soil, the deep shade also had significantly higher overall moisture levels (Figure 2b). There was no significant difference in the drying curves between the intermediate shade levels and the full sunlight treatment.

There was a significant soil × shade × time interaction ($P < 0.001$). The higher soil moisture with deep shade as compared with the other shade treatments was most marked between Days 3 and 6. In this period, soil moisture levels for both soils were 140% of the average for the other shade treatments. In contrast, between Day 6 and Day 10, the increase in soil moisture was 20% for the under canopy soil and 25% for the open grassland soil.

Leaf rolling and mild wilting occurred at an average θ_g of 9.4% (±0.3) for the under canopy soil and 8.1% (±0.3) for the open grassland soil. Severe wilting occurred at 7.3% (±0.2) for the under canopy soil and 5.8% (±0.15) for the open grassland soil. These soil differences were statistically significant ($P<0.01$). There was, however, no significant difference between the shade treatments for the θ_g at which either mild or pronounced wilting occurred.

Water stress treatments

There were highly significant decreases in biomass in response to water stress, the average TDW for the 5-day watering being 21.4 g/pot, and for the 10-day watering 9.3 g/pot (Table 2). This compares with the average for the non-limiting water treatment of 30.4 g/pot. For the 5-day watering, there was an overall soil response, with the under canopy soil producing an average of 27.6 g *vs* 15.1 g for the open grassland soil. The shade response was, however, conditional upon the soil. For the under canopy soil, the intermediate shade treatments yielded significantly higher than both the full sunlight and the high shade (15% relative PFD) treatments. In contrast, for the open grassland soil, no significant differences were induced by the shade although biomass tended to increase with higher relative PFD.

When watering was reduced to every 10 days, the biomass difference between soils was still significant ($P <0.001$). However, these differences became less marked, with the average for the open grassland being 7.5 g as against 11.1 g for the soil from under the canopy. As for the 5-day watering, there was a positive response to intermediate shade, with the average for the 38% and 51% relative PFD (11.7 g/pot) being significantly higher than that for the grass grown in full sunlight (7.0 g) and at high shade (7.8 g). This benefit of intermediate shade was consistent between the two soil types (soil × shade interaction, $P = 0.075$).

Water stress increased the proportion of dead and senescent shoot material ($P < 0.001$). The percentage for the non-water stress plants was 11.4%, increasing to 22.8% for the 5-day watering and 62.3% for the 10-day treatments. All plants grown in the open grassland soil in full sunlight died during the final drying cycle, as well as one replicate grown in the subcanopy soil in full sunlight. Water stress significantly increased the S:R ratios from an overall average of 2.0 for the non-water stress to 2.5 for the 5-day watering treatment and 2.7 for the 10-day treatment. There was a significant soil effect for both water stress treatments, the averages being 3.1 for the under canopy soil and 2.2 for the open grassland soil. For the 5-day watering, there was no significant increase in the ratio from full sunlight to the intermediate shade, the overall average being 2.3; however, there was a signifi-

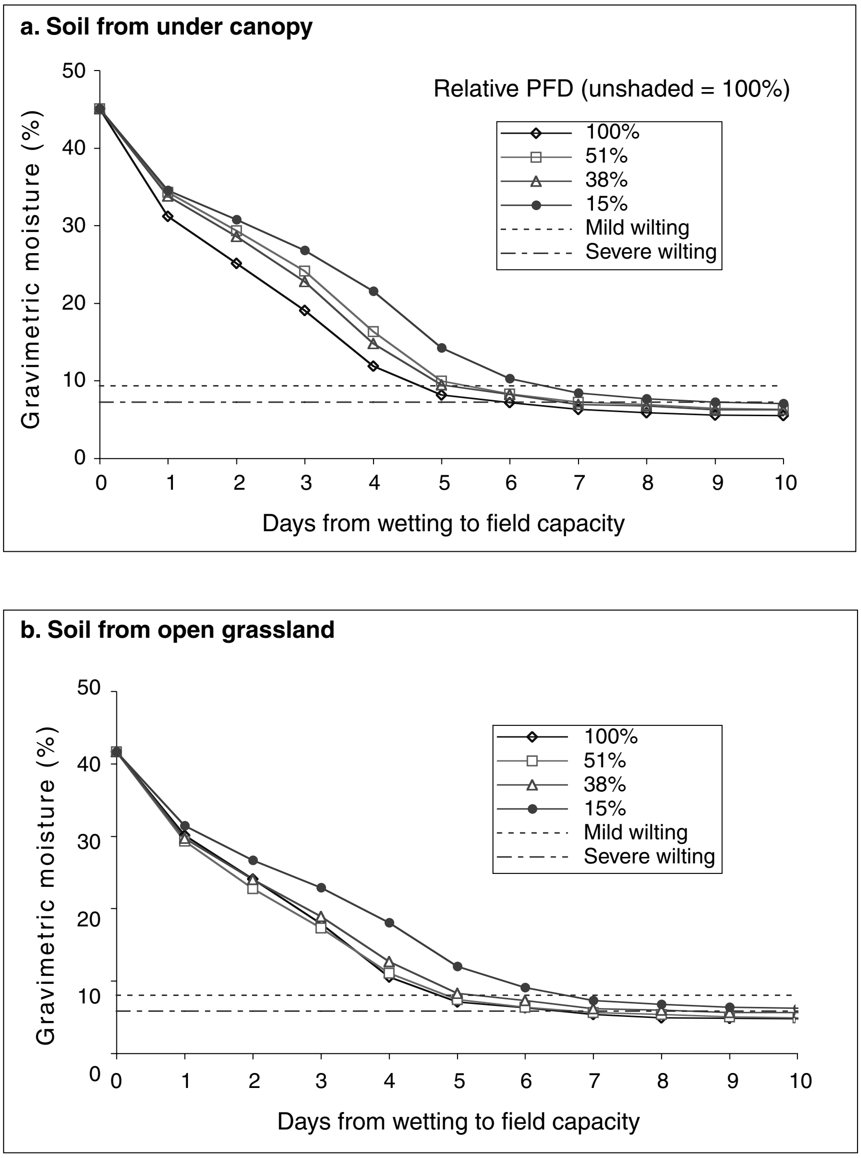

Figure 2. Drying curves for soil for the 4th 10-day drying cycle under 4 different shade treatments for: a) soil collected from under the canopy of *S. saman*; and b) soil collected from the open grassland. The gravimetric soil moisture (θ_g) at which mild and severe wilting occurred is indicated by the dotted lines.

cant increase at the highest level of shade to an average of 3.4. For the 10-day watering treatment, there was no significant shade effect (P = 0.732).

For both water stress treatments, the assumption was made that all added water was lost via transpiration, and the WUE was calculated as the ratio of dry matter (mg) per gram of added water. The WUE for the moderate water stress treatment was significantly higher than the average for the severe water stress treatment (1.9 mgDM/gH_2O *vs* 1.4 mgDM/gH_2O; $P < 0.001$) (Table 3). For the moderate water stress treatment there was a significant difference between the 2 soils, the average efficiency of grass grown in the under canopy soil being higher than that of grass grown in the open grassland soil (2.5 *vs* 1.5 mg DM/gH_2O; $P < 0.001$). For the under canopy soil,

Table 2. Total dry weight (TDW; g/pot) of *P. maximum* (± s.e.; n = 3) with a 5-day and a 10-day drying cycle grown in soil collected at different locations relative to *S. saman* trees at 4 levels of shading. Full sunlight was 100% PFD.

	Relative PFD (%)	Location	
		Under canopy	Open grassland
Watering every 5 days	100	24.98 (± 1.22)	17.84 (± 0.49)
	51	31.67 (± 0.81)	16.20 (± 1.06)
	38	31.33 (± 0.22)	13.43 (± 1.19)
	15	19.26 (± 0.53)	13.03 (± 0.71)
Watering every 10 days	100	8.97 (± 0.63)	5.09 (± 0.30)
	51	13.19 (± 0.44)	8.45 (± 0.40)
	38	13.73 (± 0.13)	9.32 (± 0.21)
	15	9.15 (± 0.88)	7.27 (± 0.32)

Table 3. Water use efficiencies (WUE; mg DM/g H_20) of *P. maximum* (± s.e.; n = 3) with a 5-day and a 10-day drying cycle grown in soil collected at different locations relative to *S. saman* trees at 4 levels of shading. Full sunlight was 100% PFD.

	Relative PFD (%)	Location	
		Under canopy	Open grassland
Watering every 5 days	100	2.11 (± 0.08)	1.56 (± 0.04)
	51	2.74 (± 0.04)	1.55 (± 0.07)
	38	2.79 (± 0.02)	1.37 (± 0.10)
	15	1.95 (± 0.03)	1.45 (± 0.06)
Watering every 10 days	100	1.38 (± 0.08)	0.84 (± 0.05)
	51	2.05 (± 0.06)	1.46 (± 0.08)
	38	2.15 (± 0.02)	1.58 (± 0.03)
	15	1.51 (± 0.14)	1.29 (± 0.04)

the WUE for the moderate shading was significantly higher than for either full sunlight ($P = 0.005$) or high shade treatment ($P = 0.002$). In contrast, there was no shade effect for the open grassland soil ($P = 0.246$).

For the severe water stress treatment, the difference in WUE for the two soils was significant (1.8 *vs* 1.3 mg DM/gH_2O; $P = 0.001$), though less marked than for the moderate water stress. As for the moderate water stress treatment, WUE was highest for the intermediate shade, this increment being consistent for both the under canopy soil and the open grassland soil.

The measured TDW was regressed on H_2O consumption, the slope corresponding to the WUE (Figure 3). This regression was highly significant for each of the two soil treatments, with a co-efficient of determination (r^2) of 0.74 for the under canopy soil and 0.56 for the open grassland soil.

Discussion

The non-water stress treatments

The non-water stress treatment responded to soil type in a manner similar to that in the previous experiment (Durr and Rangel 2000), with the average yield of the subcanopy soil being approximately 3 times that of the open grassland in both experiments. This result was to be expected considering that the relative soil nutrient levels were comparable in both experiments. In contrast, the shade response was dissimilar with an increase in biomass when the PFD increased from moderate shade to full sunlight. The growth response to the higher PFD was probably due to the improved water relations in the current experiment. When the plants were subjected to the moderate water stress of watering every 5 days, biomass accumulation plateaued as was observed in the first experiment.

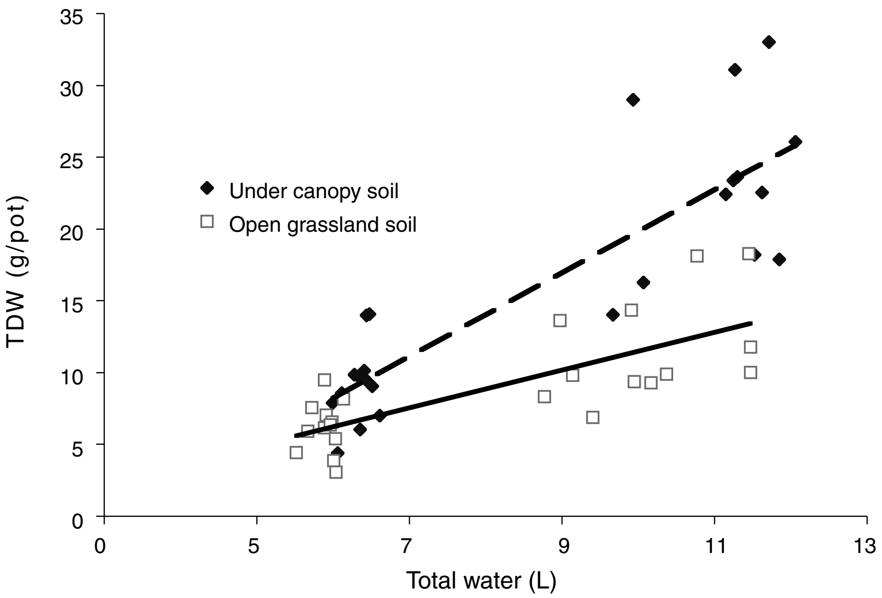

Figure 3. Regression of total dry weight (TDW) on the total water administered for soil collected from under the canopy of *Samanea saman* and from open grassland, with the slope representing the WUE. For under canopy soil, $r^2 = 0.74$; for open grassland soil, $r^2 = 0.56$.

Another difference between the two experiments in their response to the shade treatments was the absence of a large decline in biomass at the deepest shade for grass grown in the under canopy soil. This was surprising as the relative PFDs at this shade level were comparable (15% *vs* 12%). However, a closer analysis showed that there was a higher absolute PFD in the current experiment because it was conducted under relatively cloudless conditions compared with the more overcast conditions during the first experiment. Average PFD values for the non-shaded treatments were 42.3 mol/m^2/d and 36.6 mol/m^2/d, respectively. The first simulation showed that *P. maximum* was very sensitive to changes in PFD in the range 4.4–6.4 mol/m^2/d. We therefore suggest that the latter is the threshold below which its physiological and morphological shade adaptations become increasingly ineffective.

A further result in which the current experiment differed from the first was the significantly higher S:R ratio for grass grown in the subcanopy soil as compared with that from the open grassland. This was probably a response to the improved water relations, which removed the confounding effect of water stress. This allowed full expression of the positive effect of nutrients in allowing a high shoot weight to be supported by a given root mass.

The water stress treatments

The reduction in biomass under water stress is explained at the physiological level as being due to stomatal closure reducing CO_2 uptake and limiting carbon fixation (Ludlow and Ng 1976). Consequently, the water-stressed grasses were unable to utilise the high PFD levels for net photosynthesis. Moreover, as the duration of water stress was increased to 10 days, the plants were unable to utilise the high nutrient levels in the subcanopy soil. One of the major effects of water stress was therefore to reduce the role of shade and nutrients as determinants of biomass production.

The increases in the S:R ratios with water stress was surprising as previous experimental work with *P. maximum* (var. *trichloglume*) subjected to drying cycles showed a decrease in this ratio (Ng *et al.* 1975). This apparent contradiction is probably a function of the large amount of senescent material in the water-stressed plants. When the dead and senescent material is discarded, the ratio decreases from an average of 1.93 for the 5-day watering treatment to 1.03 for the 10-day watering. This modified result did not alter the conclusion that for both water stress treatments, there was a consistently higher ratio for the under canopy soil as well as an increase in the ratio for the high shade treatments.

The increase in senescent material with water stress is an important adaptive mechanism used by plants to conserve water by limiting transpiration losses (Turner and Begg 1978). This effect was observed by Ng *et al.* (1975) in an experiment on the effects of water stress on *P. maximum* (var. *trichloglume*). The larger amount of senescent material in the subcanopy soil as compared with the open grassland soil was related to the more rapid growth of the grasses during the days following re-wetting. Consequently, a large leaf area was rapidly accumulated, a high proportion of which was wasted during the subsequent period of water deficit when it underwent senescence.

Water use efficiency

The marked effect of the under canopy soil in raising the WUE, irrespective of shading or the water stress treatment, is consistent with experiments showing the positive response of added nutrients (Pressland 1982; Pieterse *et al.* 1997). It is not clear, however, from the current experiment how the higher nutrient levels of the under canopy soil augmented the WUE. It might be surmised that the higher nutrient levels, especially N, removed a rate-limiting step for leaf photosynthesis which thus allowed it to proceed at an optimal rate, at least compared with the open grassland soil (Wilson and Wild 1991). Further detailed physiological research is required to answer these questions.

Even if the exact mechanism remains unclear, the finding of a higher WUE in the simulated subcanopy environment has relevance in explaining the effect of the canopy on rain use efficiency (RUE), the above-ground biomass per unit of rainfall (Amundson *et al.* 1995). Field measurements showing an increase in RUE under the canopy of trees may reflect a true increase in WUE, but equally could result from increased water utilisation due to improved soil water extraction and/or reduced soil evaporation (Fischer and Turner 1978). Our results clearly show that the former may occur, while not discounting that improved water utilisation may be an important component of over-yielding in the field situation.

Soil water-plant interactions

The drying curves can be taken as a rough approximation of the soil moisture characteristic (SMC) in that the first day of the drying cycle corresponds with the FC and the final day is close to the permanent wilting point. The curves show that the open grassland soil behaved in a similar manner to the under canopy soil except that its values were consistently lower. Additionally, the available water was similar in both soils, although an average 2.5% higher for the under canopy soil. These results are comparable with laboratory estimation of the SMC of the undisturbed soil cores, except that the FC is considerably higher for the soil in the pots than in the field cores (Durr 1997). This discrepancy is a function of the difference in bulk density between the undisturbed cores and the sifted soil. Sifted soil would have a lower bulk density, especially as the FC was determined soon after the pots were filled and before there was sufficient time for the soil to settle fully.

An important result was the demonstration that the occurrence of wilting was determined solely by the percentage moisture in the soil and was not directly affected by presence of shade. However, shading had a significant effect on the time to onset of wilting. For the unshaded grasses grown in both the open grassland and subcanopy soils, the onset of mild wilting occurred on Days 4 and 5. In contrast, at the high shade level, wilting did not commence in either soil until Days 6 and 7. This delay in wilting had important consequences for plant survival and leaf shedding. The amount of dead material at the final harvest for the grass grown in the subcanopy soil increased from an average of 38% under high shade to 82% when grown in full sunlight. For the open grassland soil, the effect was even more extreme and all non-shaded replicates died during the last drying cycle.

One explanation for the slower decline in soil moisture in the shaded pots is that it was related to the lower growth rate imposed by the reduced PFD, an effect demonstrated by Ludlow *et al.* (1974). In the non-shaded situation, growth was rapid following watering, so soil water depletion occurred quickly. Under shade, growth was slowed and soil water levels were maintained for longer periods. This was beneficial for the grass as it reduced the period during which severe water stress was experienced.

Applications to the field

In seeking to understand the over-yielding phenomena, there has been an ongoing debate over the relative importance of soil nutrient increases and the changes in the subcanopy microclimate due to the shade (Wilson 1989; Cruz *et al.* 1995; Amundson *et al.* 1995). To date, experimental and field results have been inconsistent as these effects are confounded in the subcanopy environment (Belsky 1994; Wilson 1996).

Although considerable care is necessary in extrapolating our experimental results to the field situation, they do suggest a plausible mechanism to explain the over-yielding phenomena in terms of all 3 growth factors. The primary mechanism is the increase in soil nutrient levels under the canopy, which corrects any nutrient deficiency present in the open grassland areas. In situations of water stress, an increase in WUE under shade will permit relative increases in biomass as compared with the open areas. However, this is itself conditional upon the presence of intermediate shade levels, and will not be expressed if the shading is too high. Therefore, over-yielding under the canopy is dependent upon the presence of all 3 factors, *i.e.* relative subcanopy soil nutrient increase *and* water limitations *and* moderate to light shade.

The drying curve observations provide an explanation of why a strong species shift might occur at the canopy edge in subhumid environments. Following a rainfall event, canopy shading will slow growth rates and therefore soil moisture extraction as compared with the open grassland. This means that the subcanopy species suffer a shorter period of wilting, and are less likely to die or undergo anthesis in response to water stress. This allows more mesic species to survive and out-compete those adapted to the harsher environment of the open, non-canopied areas. As this is primarily a shading effect, a sharp transition will occur at the canopy edge.

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