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Growth of *Festuca pallescens* in silvopastoral systems in Patagonia, Part 1: positive balance between competition and facilitation

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Abstract

Silvopastoral systems may overyield compared to monocultures as a result of higher resource capture and/or facilitation effects of the trees on the pastures. *Festuca pallescens* (St. Ives) Parodi, a forage species of Patagonia, is vulnerable to water deficit, suggesting that it may benefit from the facilitative effects of trees. Radiation (PPFD), temperature, relative humidity (RH) and soil water distribution during the growing season were measured under different tree cover levels in ponderosa pine-based silvopastoral systems. PPFD decreased with increasing tree cover, and the decrease was lower in the positions under than between tree crowns. No significant differences were observed for temperature, RH nor for soil water content between treatments. Pre-dawn water potential of grasses during the growing season showed similar high values in all treatments. However, cumulative water stress was slightly lower in high tree cover treatments than in open situations. Leaf water potential of the grasses during the day was always lower in open grassland than in forested plots. The growth of the grasses showed no significant differences between treatments, but mean growth tended to decrease in the more densely planted treatments. We concluded that *F. pallescens* is a species that is biologically sound for use in silvopastoral systems, because the balance between facilitation and competition can be positive under the semiarid conditions of Patagonia.

Introduction

Silvopastoral systems may overyield compared to monocultures as a result of higher resource capture and/or facilitation effects of the trees on the pastures growing beneath or between them (Huang and Xu 1999). Many studies have reported that, as trees grow, pasture production decreases (Kellas et al. 1995; Ong et al. 2000). However, other results showed that understorey productivity can increase under trees under certain circumstances (Belsky 1994; Holmgren et al. 1997). In turn, even when trees decrease crop production, the sum of tree and intercrop yields in agroforestry systems may be higher than if they were grown in monocultures (Huang and Xu 1999).

Trees may improve the water storage capacity of soils (Joffre and Rambal 1988) and nutrient availability (Belsky 1994). Also, by reducing radiation levels beneath them, trees decrease the evaporative demand for understorey species (Breshears et al. 1997; Holmgren et al. 1997). The net result of these effects over understorey productivity will depend on species characteristics (Belsky 1994), and the intensity of adverse environmental conditions (Callaway and Walker 1997).

In many temperate regions, radiation is the major limiting resource (Kho 2000). In these regions, opportunities for yield benefits by agroforestry technologies may exist if other factors, such as nutrient and water availability, are more limiting for understorey production than radiation (Kho 2000). In the same way, in a given environment, water may be a more limiting resource for one species than for another. Thus, species more vulnerable to soil water deficits might be more able to take advantage of improvement of water conditions under trees than drought tolerant species.

Traditionally, the most important economic activity in semi-arid Patagonia (South Argentina) has been sheep livestock. Presently the sustainability of these production systems is threatened by desertification, with its negative effect on pasture quality and quantity. During recent years, forest plantations based on fast growing species, have been promoted through a subsidy policy in the country. In Patagonia, the exotic *Pinus ponderosa* Doug. ex Laws is the species most commonly planted. Considering cultural, economic and environmental aspects, silvopastoral systems may be an interesting alternative for small-scale land-owners in semiarid Patagonia.

Many studies have related stem basal area, percentage of crown cover or a stand density index in ponderosa pine native forests to understorey productivity (Mitchell and Bartling 1991; Moore and Deiter 1992). In almost all cases, a negative non-linear model described the relation between cover provided by ponderosa pines and grass productivity. In Patagonia, the influence of the exotic ponderosa pine on production of a native grass species, *Stipa speciosa* Trin. et Rupr., was described for two experimental silvopastoral systems. The studies were carried out both at the stand level (Schlichter, unpublished data) and at the individual plant level (Fernández et al. 2002). The results at the individual plant level showed a linear relation between tree cover and grass growth. The decrease in growth occurred despite the observed facilitation effect on its water status (Gyenge et al. 2002).

Another native grass, *Festuca pallescens* (St. Ives) Parodi, is considered to be one of the best Patagonian forage species because of its palatability and preference by sheep and cattle (Defossé et al. 1990). In natural conditions, this species is associated with wetlands ('mallines') and graminoid foothills of the Andes mountains on the border between the forest and the steppe. On some occasions, *F. pallescens* may be also found in forest gaps (Nicora 1978), indicating that it may have some degree of shade tolerance. Considering the response to herbivory, it was stated that this species tolerates grazing well through mechanisms such as a decrease in leaf senescence rates in clipped plants (Bertiller and Defosse 1990). However, severe over-grazing leads to its decline in natural grasslands and its replacement by shrubs. This species has a higher vulnerability to water deficits than *S. speciosa*, particularly in relation to the effects of low plant water potentials on photosynthesis (Fernández et al., submitted). For these reasons, *F. pallescens* might be able to gain advantage from facilitation effects on its water status and so maintain high growth rates under trees. To test this hypothesis, growth and other physiological variables of *F. pallescens* were evaluated in relation to water and radiation distribution under differing canopy cover provided by ponderosa pine, in experimental silvopastoral systems of North-Western Patagonia.

Materials and methods

Study area and experimental design

The study was carried out in a silvopastoral trial located in Estancia Lemú Cuyén, (40.3°S, 71.1°W), in Lanín National Park, Patagonia, Argentina. The climate is Mediterranean with cold wet winters and hot and dry summers. Average annual rainfall (1978–1999) at the site is 684 (SD: 283.1) mm (with approx. 579 mm in autumn and winter and 105 mm in spring and summer). Maximum and minimum annual average temperatures are 17.1 ± 0.5 and 4 ± 2.1 °C, respectively.

The experiment included two densities of trees and an open grassland area (control). The original plantation density was 500 pines ha^{-1} (4×5 m spacing) with a pruning height of 1.5 m from the ground level. At the beginning of the growing season examined (2000–2001), mean tree height was 8.57 ± 1.21 m, and mean diameter at breast height was 22.02 ± 3.17 cm. Thinning and pruning treatments were applied to provide the final experimental treatments in 1999, when the trees were 15 years old: these provided five plots each

1600 m^2 in area, containing 350 pruned pines ha^{-1} (350 P), and five plots containing 500 pruned pines ha^{-1} (500 P). The pruning height was approximately 4.5 m. In the plots containing trees, tussocks of *Festuca pallescens* were measured in two locations, under (UC) and between the tree crowns (mid-way between adjacent tree trunks, BTC). Measured tussocks were grown in the different situations naturally (i.e. they were not transplanted), and were chosen based on uniformity of their size. In this sense, all plants were medium-sized, with a mean basal diameter of 20–25 cm. Tree canopy cover was measured over each grass tussock using a convex spherical densiometer (Robert Lemmon Forest Densiometers, USA, model A). Each cover value was the mean of four measurements made following the cardinal points (N–S–W–E).

The perimeter of the trial (2 ha) was surrounded with a wire fence to exclude the entry of medium to large herbivores.

Light and water distribution

An empirical model of photosynthetic photon flux density (PPFD) as a function of tree canopy cover was developed to provide estimates of PPFD level over each grass tussock. For this purpose, data recorded at hourly intervals throughout sunny days in November, December and January were used. Measurements of PPFD were carried out with a sunscanner (Delta T, UK) in the following situations within plots with 350 and 500 pruned pines ha^{-1} and 500 unpruned pines ha^{-1} (three replicates per treatment): under canopy (UC) north, UC south, EC west, UC east, between tree crowns (BTC) north/south, BTC west–east. Also, at the same time as measurements in the forested plots, PPFD levels were also recorded in a grassland plot with a similar sunscanner. In all measurement positions, tree canopy cover was measured with a spherical densiometer. Values of forested plots were related to radiation level in the open, and 'relative PPFD' values were related with each canopy cover for each day of measurement. Because no significant differences in curves of relative PPFD vs. canopy cover were detected between dates (*F* test, Neter and Wasserman 1974), values of November month were used for further analysis. Finally, regression models for the positions UC and BTC were developed for each hour of the day (between 8 am and 6 pm) (for more details about radiation models, see Fernández 2003). These simple models allowed to the light reaching the understorey grasses to be estimated at hourly intervals for different positions within a forested area. Then, a numerical integral of PPFD during a day was calculated for each treatment, in a similar way to that for leaf water potential (Myers 1988).

Volumetric soil water content (%Vol) was measured at 15 days intervals using a TDR equipment with Tecanat tubes (IMKO Gmbh, Germany) for the 0–20 cm and 20–40 cm soil horizons. The measurements were carried out in four locations within each forested plot: two tubes were installed under the tree canopy (one to the North and one to the South side, at 20 cm from the base of the stem) and two tubes between neighbouring tree crowns (1.5 m from the tree stems). This gives a total of 40 tubes installed in forested plots (four tubes per plot × five plots of each tree density × two densities). Ten tubes were installed in the open grassland area.

Relative humidity (RH) and air temperature (*T*) were measured for different days (one day in November, two days in December, one day in January) and different hours within a day (9, 10, 12 am, 3, 5 pm) for all treatments ($n = 5$). The measurements were made approximately 75 cm above the ground using a digital hygro-thermometer (Thies Clima, Germany). Vapour pressure deficit (VPD) was estimated assuming that leaf temperature was equal to air temperature.

Plant water status

Pre-dawn water potential was measured for three grass plants in each treatment at 15 days intervals during the growing season. Leaf water potential was also measured for three plants of the open grassland, 350 and 500 P treatments, at one or 2 h intervals during a sunny day in December. Regarding plants of forested plots, no distinction was made between the location 'under' or 'between tree crown'. Water potential was measured using a pressure chamber (PMS Instruments Co., Corvallis, USA). The integral of water potential was calculated following Myers (1988) for the whole growing season (using values of pre-dawn water potential), and for a whole day. These integral values were calculated as follows:

$$\int \Psi = \mathrm{abs}[\Sigma(\Psi_i - c)n]$$

where 'Ψ' is leaf water potential, 'abs' denotes the 'absolute value' (positive sign), 'Ψ_i' is the average of leaf water potential of two consecutive measurements, c is the higher value of Ψ of the whole measurement period, and n denotes the time period between two consecutives measurements (number of days in the case of the integral of water potential for the whole season, and minutes in the case of the integral of water potential for a single day).

To investigate the relationship between leaf water potential and transpiration rate, both variables were measured for plants in all treatments at different times of day on 2 days in November and December. Transpiration rate was measured with an infrared gas analyser system (Li-Cor 6200, Lincoln, Nebraska, USA).

Plant growth under different tree canopy cover

Several growth variables were measured at monthly intervals for three grass plants in each treatment. For plants growing under the tree canopy, these were located to the North of the trees. At the beginning of the season, 15 tillers were marked in each tussock. The appearance of new tillers was recorded for these plants (subsamples) counting monthly the number of tillers with at least one green leaf. The number of green leaves per tiller and length of the longest green leaf on each tiller (measured in mm) were also recorded for five marked tillers per plant. Data were expressed as relative ratios of the values for specific variables for each month over the first recorded value (November). Four relative ratios were obtained: net tillering ratio, tiller height ratio, number of green leaves per tiller ratio, and relative growth ratio. This last value was calculated as the product of the other three in each month. With this type of measurement, relative growth ratio can be similar in different treatments even when they are differences in biomass. This is because measured growth variables (number of tillers, number of leaves and leaf length) do not account for differences in specific leaf area (SLA, foliar area divided by its dry weight) of the plants. Therefore, relative growth ratio for each month was divided by SLA of plants grown in the different treatments. SLA was measured in November, January and May, and their values were reported in Fernández et al. (2004).

Statistical analysis

Analysis of variance (ANOVA) and Tukey tests were used to detect statistical differences ($p < 0.05$) between treatments in PPFD, relative humidity of the air, air temperature, pre-dawn water potential in each day of measurement, and the integral of water potential during a day. The significance of differences in soil water content between locations within each tree density was tested with paired *t*-tests (Zar 1996). The values for each plot were then pooled, irrespective of the positions under and between tree crowns, and ANOVA and Tukey-tests were used to test for differences between the open grassland, 350 and 500 P treatments. In cases in which variables were measured in several dates (pre-dawn water potential, soil water content), statistical analysis was applied for each day. Repeated measures ANOVA was also used to detect differences between treatments in pre-dawn water potential considering the whole growing season.

To detect differences in growth variables, two-way analysis of variance, with factors 'Tree Density' (350 and 500 P) and 'Location of the Plant' (under canopy and between the tree crowns) was applied to data for plants growing in the forested plots (three observations in each factor combination) in each month. A general comparison considering mean and confidence intervals was then made between the treatments containing trees and the control (open grassland), in which there was no true replications. The three plants measured in the open grassland were located in the same plot because it was not possible to find another open grassland area with similar soil and aspect characteristics than those of the forested areas.

Results

Light and soil water distribution

Table 1 shows values of the integral of PPFD during a day (total daily receipt) expressed as a fraction of the value for open grassland. Values of the table are the average (and SD) of the light received by the plants for which growth was measured ($n = 3$). As expected, PPFD decreased from the open grassland to the treatments with 350 and 500 pines ha^{-1}. However, in spite of the differences in canopy cover level of treatments 350 UC and BTC (Table 1), a similar amount of radiation reached the understorey in both situations. Significant differences ($p < 0.05$) were detected in daily total radiation between the open grassland and all other treatments. Within forested treatments, differences were observed between the 350 UC and 350 BTC treatments and 500 UC ($p < 0.05$), but no significant ($p > 0.05$) differences were observed between 500 BTC and the other three treatments (Table 1).

In general, soil water content in the 0–20 and 20–40 cm of soil horizons did not differ significantly between treatments (ANOVA, $p > 0.05$; Figure 1). A higher water content ($p < 0.05$) in the open grassland than in all other treatments was only recorded during the autumn (differences indicated with asterisks in Figure 1). A gradual decrease in soil water content was recorded through the growing season until early March. However, several increases in soil water content occurred during this period, being more marked in the upper 20 cm of soil than in the 20–40 cm horizon. The unusual occurrence of frequent small rains during the entire season (Bustos, INTA EEA Bariloche, unpublished data), may explain these patterns of relatively high soil water content in all treatments.

No significant differences in air temperature and relative humidity were found between the different treatments.

Plant water status

The seasonal trends for pre-dawn water potential (ψ_{pd}) in *F. pallescens* are shown in Figure 2. No clear trend or significant differences between treatments were found within each day, except for a significant higher water potential value in the treatment with higher tree canopy cover (500 UC) than in 350 UC (Tukey test, $p < 0.05$) in one date (November 11th). Values of pre-dawn water potential remained higher than -0.8 MPa during the entire growing season, even in the driest months (January and February). The integral of water stress integral decreased with increasing tree canopy cover (Table 2) indicating a positive effect of shade. However, repeated measures ANOVA indicated no statistical differences ($p > 0.05$) between treatments considering the entire season.

Daily courses of leaf water potential are shown in Figure 3. During three times of day (7 and 9 am and 2 pm), no significant differences were detected between treatments. At the other hours, grasses growing in the open grassland had a lower leaf water potential than those in any of the other treatments (see Figure 3 in which significant differences are indicated). The integral of water potential for the whole day (between 7 am and 5:30 pm) was significantly higher (indicating lower water potential values) for the plants in the grassland than for those in forested plots (1042 (SD: 93.7) MPa.minute for open grassland plants, 649 (SD: 73.5) and 543 (SD: 48.5) MPa.minute for plants in 350 and 500 P, respectively). No statistical differences were observed between

Table 1. Tree canopy cover and total daily receipt of PPFD expressed as the integral of PPFD during a sunny day in each treatment, as a proportion of the integral of PPFD in the open grassland.

	Open grassland	350 UC	350 BTC	500 UC	500 BTC
Tree canopy cover (%)	0	68.9 acd (11.5)	49.3 b (4.7)	86.4 c (6.7)	60.7 d (3.4)
Relative PPFD level	1 a	0.56 b (0.14)	0.56 b (0.04)	0.31 c (0.11)	0.45 bc (0.03)

Each value is the average (and standard deviation) of measured variables for the three individuals of *Festuca pallescens* evaluated for growth patterns in each treatment. Different letters in the same row indicate significant differences between treatments ($p < 0.05$). 350/500 = number of pines ha^{-1}; BTC = between tree crowns; UC = under tree crown. Ea. Lemú Cuyen, Neuquén Province, Argentina.

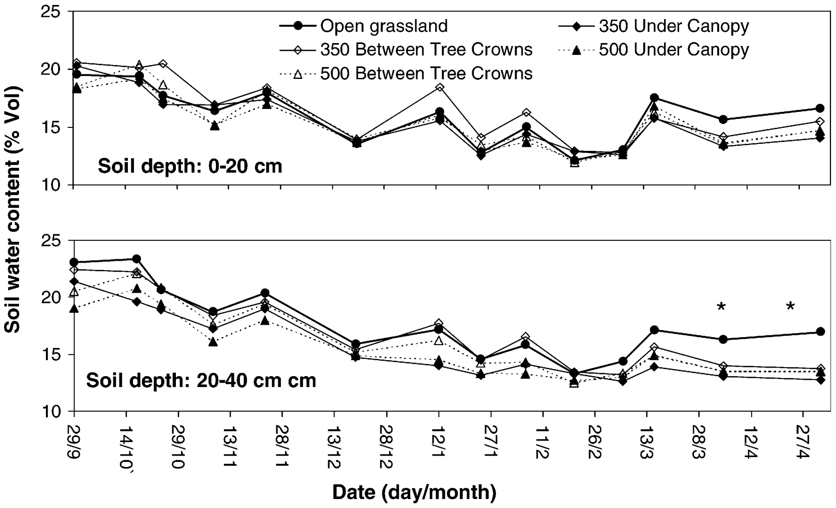

Figure 1. Soil water content in 0–20 cm (upper panel of the figure) and 20–40 cm (lower panel of the figure) soil horizons, between September 2000 and May 2001 in the different silvopastoral treatments and in the open grassland. Significant differences ($p < 0.05$) between the open grassland and all other treatments are indicated with asterisks. Ea. Lemú Cuyen, Neuquén Province, Argentina.

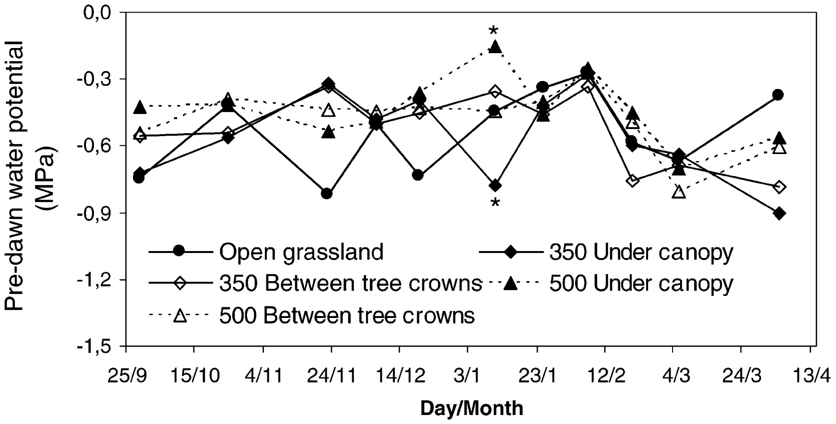

Figure 2. Pre-dawn leaf water potential (MPa) measured in leaves of *F. pallescens* growing in different silvopastoral treatments and in open grassland, during 2000–2001 season. Significant differences between two treatments in November 11st are indicated with asterisks. Ea. Lemú Cuyen, Neuquén Province, Argentina.

grasses of both forested treatments. Higher water potentials (less negative values) were consistently associated with shading by the trees. Leaf water potential (in absolute value) was positively correlated (Pearson correlation coefficient, $r^2 = 0.77$, $p < 0.05$) with the transpiration rate of the leaf (Figure 4). Thus, differences in leaf water potential between treatments as those measured during a day (Figure 3) may reflect differences in transpiration rates resulting from differences in evaporative demand.

Influence of tree cover on the growth of F. pallescens

Net tillering ratio showed no significant differences between the silvopastoral treatments at any stage of the observation period. An interaction between factors was detected ($p < 0.05$) in April, when mean tillering ratio increased under the tree canopy in the 350 P treatment but decreased in this position in 500 P treatment. However, no significant differences were detected for any combination of factors (Tukey tests, $p > 0.05$). At the end of the

Table 2. Integral of water stress (MPa.day) for two grass species during two growing seasons: September–April 1999–2000, measurements for *Stipa speciosa* (*data from Gyenge et al. 2002), and September–April 2000–2001, measurements for *Festuca pallescens.*

	F. pallescens (2000–2001) (MPa.day)	*S. speciosa* (1999–2000)* (MPa.day)
Open pasture	72.7	266.9
350 P, UC	73.7	288.4
350 P, BTC	67.7	279.4
500 P, UC	53.6	252.7
500 P, BTC	60.7	260.7

350/500 = number of pines ha^{-1}; P = pines; BTC = between tree crowns; UC = under tree crown. Ea. Lemú Cuyen, Neuquén Province, Argentina.

growing season, the mortality exceeded tiller production only in the more densely planted treatment (500 P, under canopy, ratio < 1). Tillering ratio in the grassland was greater, although not significantly, than in the silvopastoral treatments.

The relative number of leaves per tiller (green leaf ratio) was very similar between treatments, except under the highest tree canopy cover (500 P, under canopy), in which no leaf production was observed in the first 2 months of measurement. However, even during this period, no significant differences were observed between forested plots (two-way ANOVA, $p > 0.05$). A marked leaf mortality was observed in all treatments during the autumn.

Tiller height ratio was almost constant throughout the growing season in all treatments, but was slightly greater in the silvopastoral treatments with higher tree canopy cover. In the open grassland, the length of the new leaves was always less than the initial values. However, neither the absolute nor the relative length of the leaves differed significantly between treatments in any time.

A similar pattern characterized by no significant differences between treatments was also observed for the relative growth ratio (RGR). However, a trend towards higher average values (relative growth ratios around 3 at the end of the growing season) was observed in the treatments with tree canopy cover between 60 and 70% (350 P, under canopy, and 500 P, BTC, Table 1) compared to the other treatments. Mean RGR of grasses in the open grassland was 2.45 at the end of the growing season, a value very similar to that of grasses in 350 BTC (mean RGR = 2.40). The lowest growth rates were measured at the highest tree canopy cover (500 P, under canopy, RGR = 1.36), although even in this treatment the leaf number and length both increased compared to the initial values (ratio > 1).

Figure 5 shows values of RGR in each month divided by SLA (m^{-2} kg^{-1}) for each treatment.

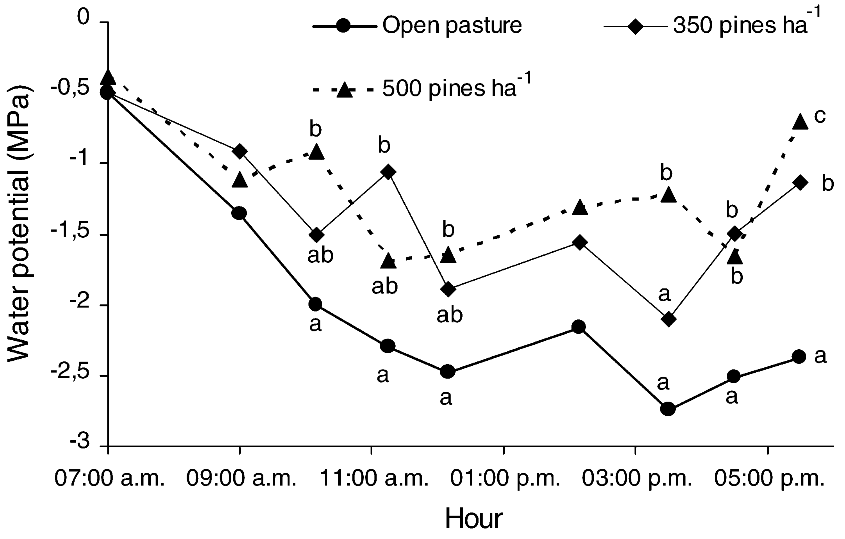

Figure 3. Leaf water potential of *F. pallescens* plants growing in different treatments, measured every one or 2 h intervals during a sunny day. Different letters within each time of day indicate significant differences between treatments (*t* test, $p < 0.05$). When no letters appear, no significant differences were observed between treatments. Ea. Lemú Cuyen, Neuquén Province, Argentina.

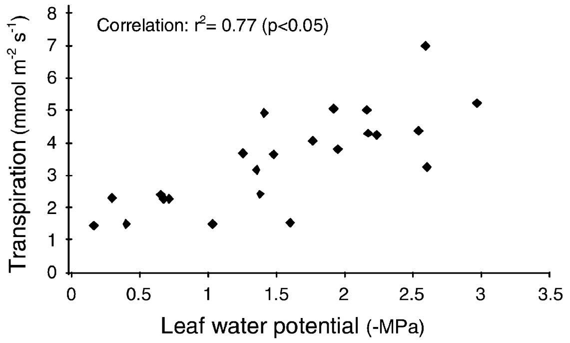

Figure 4. Leaf transpiration rate and leaf water potential of individuals of *Festuca pallescens* measured at different hours (during the morning, midday and afternoon), in two days during the growing season. Pearson correlation coefficient, $n = 23$. Ea. Lemú Cuyen, Neuquén Province, Argentina.

Despite the observed differences in the average values between treatments, these were not significant (two-way ANOVA, $p > 0.05$), reflecting the high dispersion of values, mainly in the treatments with high radiation levels (open grassland and 350 P).

Discussion

Regarding radiation level reaching the understorey, it is not the same a particular percentage of tree canopy cover in the situation 'under canopy' than 'between the tree crowns'. For instance, a larger amount of light reaches the understorey in a situation with 50% of tree cover measured under a pine crown (under canopy) than in a situation with 50% of tree cover measured between tree crowns. In this sense, Table 1 shows the similar amounts of radiation reaching both 350 UC and BTC treatments in spite of tree cover level being higher in the former situation. These differences may result from the movement of canopy shades at high latitudes, which are displaced with respect to the axis of the tree. At this latitude (40.5 S) and with pruning resulting in a large distance between the bottom of the crown and the ground, the shade lies almost always to the south of the tree. The same pattern, but with a displacement of shades to the north, was calculated by Kuuluvainen and Pukkala (1987) for high latitudes in the Northern Hemisphere.

Soil water content, in this particular season, did not present the typical pattern for semiarid environments, which is usually characterized by a long dry period. During the growing season, the upper soil layers, from which grasses extract water (Schulze et al. 1996), remained above permanent wilting point (10%Vol for the studied soils). The similarity of the values for soil water content of surface horizons between open grassland and the two silvopastoral treatments may have occurred because the lower evaporation rates in the latter compensated for the increased interception of rain by the tree crowns (Breshears et al. 1998),

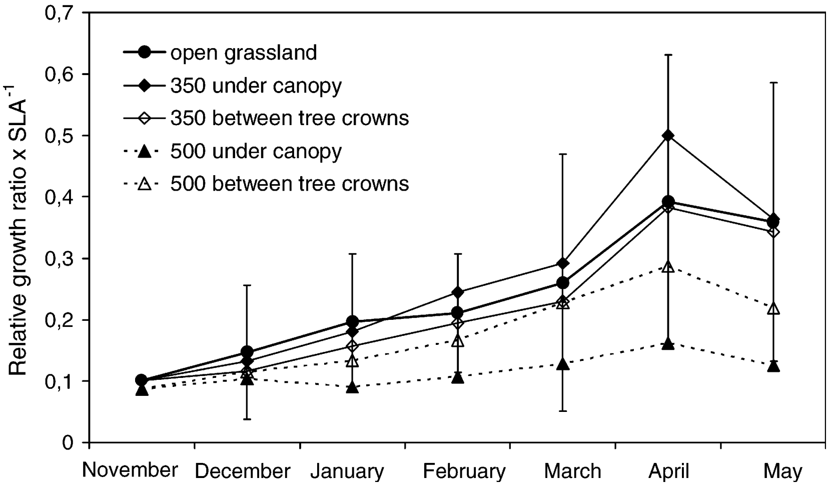

Figure 5. RGR divided by the SLA of individuals of *Festuca pallescens* (from Fernández et al. 2004) growing in different treatments, during 2000–2001 growing season. Error bars correspond to the standard deviation of values for the open grassland ($n = 3$). Ea. Lemú Cuyen, Neuquén Province, Argentina.

particularly at the higher tree densities. The similar pre-dawn leaf water potentials observed in all treatments reflect the similar values recorded for soil water content in all treatments throughout the growing season. However, grass growing under the higher tree density showed some decrease in cumulative water stress (as shown by the seasonal integral of water potential, Table 2). The same trend was found in the previous year for another grass species under drier conditions (Gyenge et al. 2002; Table 2). Despite the fact that in the 350 P treatment, radiation levels were very similar under and BTC (Table 1), cumulative water stress was higher under the tree canopies. This may have resulted from lower water availability due to greater rain interception or uptake by the trees (not detected with the TDR in the present study) under the trees. Notwithstanding these differences in cumulative water stress between plants of 350 UC and BTC, the measured values of pre-dawn water potential were much higher (less water stress) than those recorded for *Stipa speciosa* in the previous year, when pre-dawn water potentials decreased below −2.5 MPa in January (Gyenge et al. 2002). The better water status of grasses growing in forested plots during the abnormally humid season 2000–2001 suggests that the magnitude of facilitation effects may be even higher during drier summers, that is those without rains during one or 2 months (January and/or February).

A lower evaporative demand could be expected under trees in relation to open grassland conditions due to similar relative humidity and air temperature in both situations but lower amounts of radiation under shade (see Penman-Monteith equation for evapotranspiration in Monteith and Unsworth 1990). This lower evaporative demand resulted in higher leaf water potential during the day in grasses growing in the forested plots than in the open grassland. Measurements of the diurnal course of leaf water potential were carried out in a single sunny day. In spite that it is not possible to extrapolate those results to the entire season, considering that there was an unusual high soil water content during the whole measurement period (see Gyenge et al. 2002 and Fernández 2003 for soil water values in other seasons), it is possible to assume that similar daily patterns could be found in other sunny days during the same growing season. This is not expectable during periods with very low soil water contents as occurs in other growing seasons. On the other hand, leaf water potential was also correlated with transpiration rate, indicating that water consumption in plants growing in the open was greater than those under trees. Such differences in water potential and transpiration are not necessarily detrimental for plants if soil water availability is sufficiently high, as was the case during the growing season reported here. However, in years when the summer is dry, as is common in the region, this difference might be critical for grass growth and may explain, at least in part, the persistence of the species under trees despite the reduction in incident radiation cause by shading (Holmgren et al. 1997).

Grass growth was similar in all treatments (particularly until tree cover reached ca. 85%), even though the grass plants received only 50% of the radiation reaching the open grassland. The growing season was characterized by an abnormally high soil water availability. Even in this situation, and contrary to what may be expected in relation to negative balances in ecological interactions between plants during wet years (Callaway and Walker 1997), plants growing under low light conditions exhibited shoot values similar to those grown in the open grassland. Photosynthesis measurements showed that this species is very vulnerable to water deficits (Fernández et al., submitted). In this sense, stomatal conductance decreased abruptly when pre-dawn leaf water potential is lower than − 0.8 MPa, which has a linear effect on maximum photosynthesis rate (Fernández et al., submitted). In the present study, pre-dawn leaf water potential did not differ between treatments. However, considering that grasses of shaded treatments had lower root biomass than those grown in the grassland (Fernández et al. 2004) this may imply a facilitation effect due to the lower evaporative demand in forested plots. In addition, despite that differences were not statistical different, a trend of a better water status was detected for grasses in treatments with higher tree canopy cover. Furthermore, higher SLA values were found in the treatments providing lower radiation levels (Fernández et al. 2004). This type of response allows plants growing in shaded microenvironments to capture more light per unit of leaf mass. Plants growing under high tree cover may therefore increase carbon fixation producing an aboveground biomass similar to those in open canopy treatments despite receiving less radiation.

It is possible that the main process favouring grass growth under shade was the differential biomass allocation and SLA of plants growing in those situations compared to those in the grassland. But the lower evaporative demand under trees could allow grasses growing with trees to have similar water status than in the open even having less roots.

Growth did not show a bimodal pattern, as is common in *F. pallescens* (Defossé et al. 1990). High water availability and high predawn leaf water potential, even in the summer, may explain the uniformity of growth throughout the season. This lack of summer dormancy in *Festuca pallescens* allows it to use unpredictable short pulses of water, as happens also with other semiarid-species such as *Stipa tenacissima* (Pugnaire et al. 1996).

Conclusions

The results of this study suggest that *Festuca pallescens* may be grown successfully in silvopastoral systems with ponderosa pine, if plantations are pruned and tree densities are relatively low. This grass species can take advantage of the microenvironmental conditions produced by trees. As a consequence, the balance of facilitative and competitive interactions may be neutral or positive, until a threshold tree canopy level is reached, which is higher than for *S. speciosa* (Fernández et al. 2002). However, in order to recommend conclusively the use of this species in these systems, response of shade grown individuals to grazing must be studied.

The observed differential growth of *F. pallescens* and *S. speciosa* when grown under trees is in agreement with the initial hypothesis that species exhibiting differing vulnerability to water deficits may exploit the advantages of facilitation effects under trees in different ways in a same habitat, giving a different net balance in competition–facilitation interactions.

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