ECOPHYSIOLOGY

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Mechanisms of competition: thermal inhibition of tree seedling growth by grass

Abstract The relative importance of thermal interference and competition for below-ground resources in the inhibition of tree seedling growth by grass was determined under field conditions. Snow gum (*Eucalyptus pauciflora*) seedlings were grown in bare soil or soil covered with either live grass or straw. Covering soil with straw produced thermal conditions in soil and air that were indistinguishable from those associated with live grass. In contrast, seedlings grown in bare soil experienced more rapid increase in soil temperatures during late winter and spring, less frequent and less severe frosts, and temperature maxima that more closely followed those of the atmosphere than seedlings growing in live grass or straw. After 1 year, seedlings in bare soil had four times the biomass of those grown in grass or straw. Inhibition of seedling growth by grass was attributed to alteration of the thermal environment which caused (1) seedlings to have a short growing season largely restricted to summer, (2) temporal separation in competition for resources with consumption of below-ground resources by grass in spring reducing availability of resources to support tree seedling growth in early summer, and (3) seedlings to be more subject to stress from temperature extremes. These results show that thermal interference plays a major role in interactions between plants.

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Introduction

Forest clearing can lead to difficulties in establishment of eucalypt seedlings in frost-prone areas (Stoneman 1994). Seedlings that have either grown from seed or been planted from nursery stock grow well for the first 2 to 3 years following forest clearing (Ellis and Lockett 1991). However, the tree seedlings can enter a phase known as growth-check once a grassy ground cover establishes (Ellis and Lockett 1991). Growth-check has been attributed to ineffective competition with grass for nutrients and water (Ellis et al. 1985; Nambiar 1990). However, grass could also adversely affect growth of tree seedlings through alteration of microclimate.

A grassy ground cover causes profiles in soil and air temperatures to be very different from those associated with a bare soil surface (Rosenberg et al. 1983; Oke 1987). Heat conduction through grass is poor, causing soil temperatures in temperate climates to undergo less diurnal fluctuation (Balisky and Burton 1995) and to change more slowly with the progress of seasons than where soil is bare. For example, Oke and Hannell (1966) showed that covering a soil surface with straw mulch retarded the loss of summer heat storage during autumn and slowed the penetration of warmth into the soil in spring. Such differences in soil temperatures between bare and mulch-covered ground surfaces are well known to affect the timing and rate of growth in agricultural systems (Rosenberg et al. 1983; Oke 1987), and could profoundly affect the growth of temperate tree seedlings following forest clearing or fragmentation.

Tree seedlings that are emergent from a grassy ground cover would also be more subject to greater extremes in both minimum and maximum air temperatures than seedlings growing in bare soil (Oke 1987). The most important mechanism for nocturnal cooling is the net loss in long wave thermal radiation from a surface exposed to

the night sky. Application of a straw or hay mulch to a soil surface moves the active cooling surface (and therefore the site of maximum frost occurrence) from the soil to the top of the mulch (Oke 1987). The net loss of energy by radiative means from this grassy surface at night is balanced by the flow of heat from the overlying air and the underlying soil. However, a grassy sward (and the layer of still air that it contains) acts as a good thermal insulator, impeding the flow of heat from soil to the overlying air. This causes the temperature of a grassy surface to be lower than a bare soil surface, and air temperatures immediately above grass to be lower than above bare soil (Leuning 1988, 1989). Indeed, recent studies have reported that, relative to bare soil, a grassy surface reduced minimum air temperature by an average of 2°C, with leaf temperatures of eucalypt seedlings emergent above grass being another 1–3°C lower than air temperature (Leuning and Cremer 1988; Ball et al. 1997). Thus, seedlings above a grass canopy are subject to lower minimum temperatures and can experience more frequent and more severe frosts than their counterparts surrounded by bare soil (Ball et al. 1997).

A grassy surface can also subject emergent seedlings to scalding temperatures during summer periods of high insolation and low wind speed (Oke 1987). The principles underlying this effect are beautifully illustrated in a classic study of energy balance and variation in temperature profiles caused by application of a 60-mm-thick layer of hay to a fine sandy loam in summer (Waggoner et al. 1960). In their study, surface temperatures of bare soil and hay were approximately 38°C and 50°C, respectively, despite albedo being similar for both surfaces. Two factors contributed to the higher temperature of the hay surface. Firstly, conduction of heat through hay is poor, and so there was relatively little transmission of heat into the soil. Secondly, the hay layer impeded the movement of water vapour from the soil to the overlying air, thereby reducing latent heat loss by approximately 50%. As these two heat sinks were small in hay relative to bare soil, there was a much greater increase in sensible heat associated with the hay than with the bare soil. Consequently, air temperatures above the hay layer were as much as 10°C greater than those above a bare soil surface even at a height of 20 cm above the surface (Waggoner et al. 1960). Thus, tree seedlings emergent above a grassy canopy, particularly where that ground cover dries and browns during summer, could be subject to greater heat and drought stress than seedlings growing in bare soil.

The snow gum (*Eucalyptus pauciflora* Sieb. ex Spreng.) is one of the most widely distributed eucalypt species. It dominates forest canopies in subalpine areas as well as at lower elevations around the floor of valleys receiving cold air drainage, and occurs over an enormous climatic range from the subalpine tree line to the southern coast of Australia (Austin et al. 1990). Temperature-dependent changes in photosynthetic capacity (Slatyer and Morrow 1977) and shoot growth (Green 1969) occur seasonally. Like many tree species, growth of snow gum seedlings is strongly suppressed by grass, a phenomenon that is usually attributed to competition for resources (Noble 1980; Egerton and Wilson 1993). However, as discussed above, grass cover also alters soil and air temperatures. Such changes in the thermal environment can have detrimental effects on both photosynthesis and growth, leading to reduction in competitive ability and ultimately a lower chance of survival (Ball et al. 1997). Clearly there is a need to separate effects of resource competition from those due to alteration of microclimate if we are to understand dynamic interactions between grass and trees.

Inhibition of the growth of one individual or species by another can occur directly through competition for resources required for growth and reproduction, or indirectly by interference with the ability of a competitor to acquire or utilise these resources. Thermal interference has been implicated as a major component of the competitive inhibition of tree seedling growth by grass during spring (Ball et al. 1997). This suggestion was based on observations that small-scale differences in minimum air temperatures above grass (i.e. 2°C or less) adversely affected photosynthesis and growth of seedling snow gum (*Eucalyptus pauciflora*). In their study, the tree seedlings were grown in grass or in patches of bare soil of 30, 60 or 120 cm in diameter, and light interception by seedlings was not impeded by the shorter grass canopy. The treatments had no significant effects on maximum air temperatures at canopy height, but minimum air temperatures increased with increase in patch size and differences in photosynthesis, bud break, frost damage and stem elongation were correlated with differences in minimum air temperature. Had there been significant effects of competition for below-ground resources on photosynthesis and growth, then relationships between these processes and temperature should have varied with patch size. However, there was no evidence of any systematic effect of patch size on seedling performance other than those due to minimum temperature. Thus, the authors concluded that cumulative effects of temperature-dependent phenomena could account for most of the competitive suppression of tree seedling growth by grass during spring (Ball et al. 1997). Nevertheless, effects of competition with grass for below-ground resources were not controlled and could not be dismissed. The purpose of the present study was to determine the relative contributions of thermal interference and competition for below-ground resources on the inhibition of tree seedling growth by grass.

Materials and methods

Plant material

Seeds of *Eucalyptus pauciflora* Sieb. ex Spreng. were collected from trees growing along the floor of the Orroral Valley at an elevation of 850 m in New South Wales, Australia. Seeds were cold-stratified under moist conditions at 3°C for 6 weeks before germinating on sand flats in a mist house. Seedlings of similar size were transferred to individual containers and grown out of doors for 4 months before the start of the experiment.

Experimental design

Determination of the relative contributions of thermal interference and competition for below-ground resources on the inhibition of tree seedling growth by grass depended on a treatment that would have a similar microclimate to grass but offer no competition for below-ground resources. Killing grass was not desirable because decaying grass could become a source of nutrients. Straw was found to produce temperatures above and below ground that were similar to those associated with a grassy ground cover. Also soil disturbance from removal of grass to create a straw treatment was the same as for a bare soil treatment, and straw in poor contact with the ground was unlikely to contribute substantially to the supply of soil nutrients. Thus, seedling growth was studied in relation to differences in microclimate associated with three treatments: live grass, straw and bare soil. Seedling growth in live grass and straw were compared to determine effects due to competition for below-ground resources under a common temperature regime; seedling growth in straw and bare soil were compared to determine effects due to thermal interference in the absence of below-ground competition.

The experiment was conducted in a flat, fully exposed pasture (elevation 700 m) near Bungendore, New South Wales, Australia (lat. 35°15′E, long. 149°27′E). The site was fenced to exclude mammalian herbivores, and seedlings were sprayed regularly with insecticide. The pasture was mown as needed to produce a short, dense cover of grass over the ground surface. The site was divided into five blocks, each with eight plots that were further subdivided into four 2×2 m planting squares. Harvests were allocated randomly to the plots and treatments were allocated randomly to planting squares in each plot. There were three treatments and a blank that consisted of pasture. Seedlings were planted in the centre of circular patches (120 cm diameter) within each treatment planting square. In one treatment, the patch supported a sward of live pasture grasses and herbs. In two treatments, the pasture plants were removed, and the soil was shaken from their roots and returned to the patch. Then the patch was either left bare or covered with straw to a depth of approximately 5 cm. These three treatments are hereafter referred to as live grass, straw or bare soil.

One-hundred-and-twenty-five seedlings of similar height and leaf area were selected for the experiment and randomly allocated to treatments and harvests. One group of five seedlings was harvested at the start of the experiment and the remaining 120 seedlings were planted into the treatments. There were five replicates of each treatment × harvest combination. Seedlings were planted in mid-autumn to allow sufficient time for acclimation to low temperatures under field conditions before the onset of winter. At the time of planting, seedlings had similar leaf area and leaf orientations, and averaged 20.1±3.3 cm in height. The shorter grass canopy did not interfere with light interception by the taller seedling canopy, and grass was mown as needed to prevent it from shading seedling canopies.

Growth studies

Harvests occurred at 6-week intervals after planting in mid-autumn. At each harvest, a pasture sample (20×20×25 cm soil volume) was collected from the centre of blanks (i.e. pasture without tree seedlings), and seedlings were harvested from the treatments. Most of the grass roots were densely clustered in the top 10 cm of the soil, but collection of seedling roots was more problematic. The shoots were severed, and roots were sampled from a volume of soil (20×20×25 cm) centred at the stem base. Soil was washed from roots of all plant samples. Samples of pasture vegetation were left intact whereas tree seedlings were divided into roots, stems and leaves. The pasture sample and seedling parts were then dried at 80°C before weighing.

Non-destructive measurements of grass height and total stem length of seedlings were made weekly from the start of spring on plants allocated to the final harvest. Measurements of grass height were made at the centre of treatment blanks. A square foam panel was placed on the pasture sward and the height was recorded as the average of the distance from the centre of the top edge of each side of the panel to the ground.

Soil moisture

Soil volumetric moisture contents averaged over soil depths from 0 to 28 cm were determined regularly from late winter using a TRASE 6050XI time domain reflectometry system (SOILMOISTURE Equipment, Calif., USA) to interrogate probes permanently established adjacent to plants assigned to the final harvest. Measurements were made on five replicates of each of the three treatments at each sampling date.

Micrometeorological studies

Effects of treatments on air and soil temperatures were measured in a site adjacent to the eastern side of the planting site. Three blocks were established adjacent to planting blocks 1, 3 and 5 to span the length of the study site. Each block was divided into three 2×2 m squares and treatments were allocated randomly to the squares in each block. The three treatments (live grass, straw and bare soil) were the same as in the growth studies except that seedlings were not planted. Instead a vertical array of thermocouples was established in the centre of each treatment to measure air and soil temperatures at heights of 50, 20 and 5 cm above ground and at depths of 0.5, 5, 15 and 25 cm below ground. Temperatures were measured with copper-constantan thermocouples (64 μm diameter) referenced against PT-100 platinum resistance thermometers. Thermocouples were arrayed without shielding because the latter would cause more interference to accurate measurement of small scale variation in temperature than would radiation errors recorded by minute thermocouple junctions. Thermocouples were scanned every 10 s and a 30 min average was recorded on a DT 100F datalogger (Data Electronics, Victoria, Australia). Thus temperatures from seven positions in a vertical profile were recorded at 30-min intervals for three replicates of each of three treatments for a year. Reference measurements were made in a weather screen (1.2 m above ground) located near the centre of the eastern side of the study site (block 3). Statistical analyses revealed no significant differences between temperatures measured by fully exposed thermocouples at a height of 50 cm above ground and corresponding temperatures measured by the thermocouple shielded in the weather screen, consistent with minimal radiation errors recorded by exposed thermocouples. Precipitation was recorded from weekly readings of a rain gauge near the weather screen.

Statistical analyses

The experiment was organised in a split-plot design where, within each of five blocks, harvests were randomly assigned to eight plots and treatments were randomly assigned to four squares within plots. This design satisfied assumptions for data analysis by ANOVA, using Genstat 5, version 4.1. Results were considered significant if $P<0.05$.

Results

Reference weather conditions

Average weather conditions occurred throughout the study year (Fig. 1). As is typical of the area, frequent frosts were followed by warm sunny days during most of the year and there was no marked seasonality in rainfall.
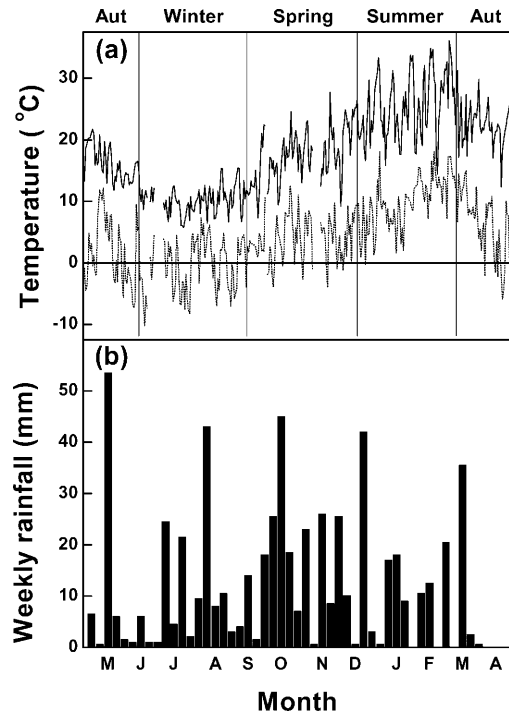
Fig. 1 Daily maximum and minimum air temperature (**a**) and weekly rainfall (**b**) recorded from mid-April 1996 to mid-April 1997. Temperatures were measured in a weather screen (height 1.2 m) adjacent to the study site

Fig. 2 Effects of different soil surface characteristics on the annual variation in daily average air temperature (**a**) and in daily average soil temperature with variation in depth below ground (**b–e**). Symbols indicate measurements made either above (*hollow*) or below (*solid*) a ground surface of bare soil (*circles*) or soil covered with either live grass (*squares*) or straw (*triangles*). All values are averages of measurements made daily for 6-week periods beginning in late autumn (i.e. from 15 April through 31 May), with *E* and *L* indicating, respectively, early and late season time periods. *Bars* indicate least significant difference (LSD) between means for values determined above (**a**) and below (**b–e**) ground

Thermal environment of seedlings

Daily average temperature was calculated as the average of temperatures measured at 30-min intervals for a 24-h period beginning at midnight. Daily average temperature significantly ($P<0.001$) changed during the course of the year from minimal values in late winter to maximal values in late summer (Fig. 2). Above ground, daily average air temperature was unaffected by soil surface treatments, but significantly ($P<0.03$) decreased with increasing height from 5 to 50 cm above ground (Fig. 2a). In contrast, daily average soil temperature at and below the ground surface was significantly ($P<0.001$) affected by interactions between soil surface treatments and depth during spring and summer (Fig. 2b–e). During this period, daily average soil temperatures were significantly ($P<0.001$) higher beneath bare soil surfaces than beneath soil covered with either straw or live grass, with differences in temperature between bare and covered soil surfaces diminishing with depth. Also, daily average soil temperatures were highest near the soil surface and declined significantly ($P=0.001$) with depth. Thus, there were no differences in daily average air and soil temperatures between patches covered with either straw or live grass, but daily average soil temperatures were significantly ($P=0.001$) higher beneath a bare soil surface during spring and summer.

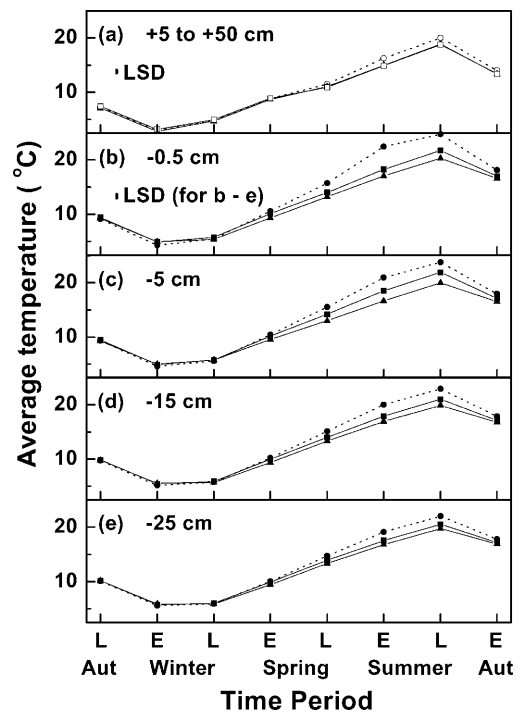The rate of increase in daily average temperature was calculated by linear regression of values measured from 1 August through 1 November for each thermocouple. There were no effects of different soil surface treatments on rates of increase in daily average temperature above ground, with the rates decreasing significantly ($P<0.001$), albeit only slightly, with increase in height from 5 to 50 cm above ground (Fig. 3a). However, below ground, rates of increase in daily average temperature were significantly ($P<0.001$) affected by interaction between soil surface treatment and depth. Rates of warming decreased with depth and were always significantly greater beneath bare soil than below soil surfaces covered with either live grass or straw (Fig. 3b). These patterns are consistent with greater solar heating and a greater air-soil heat transfer coefficient (i.e. no insulating layer) over bare soil than over grass or straw. A full analysis of this and other thermal processes will be submitted separately.

One difficulty in using average values is that they can mask effects of exposure to temperature extremes. Effects of the three treatments on the occurrence of daily minimum temperatures are shown in Fig. 4. Frosts occurred all year except during late summer. It is apparent that seedlings growing in live grass or straw were subject to lower minimum temperatures than their counterparts
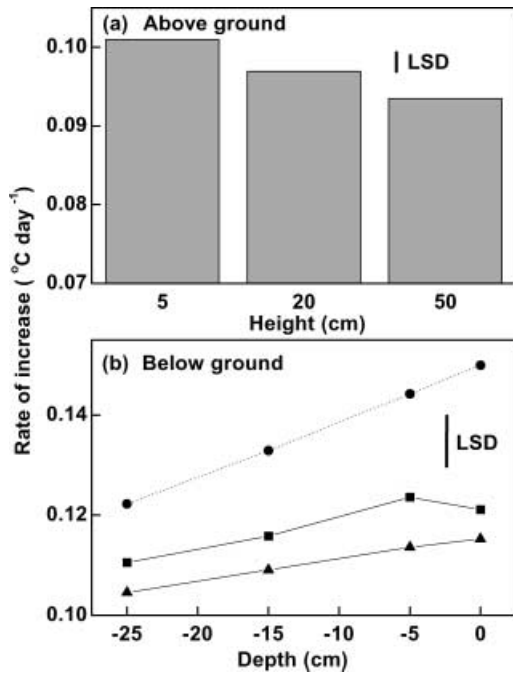
Fig. 3 Effects of different surface characteristics on the rate of increase in daily average air (**a**) and soil (**b**) temperatures from 1 August to 1 November. Values for air temperatures at different heights above ground are averaged over all soil surface treatments. Values for soil temperatures are averages at different depths beneath patches of bare soil (*circles*) or soil covered with either live grass (*squares*) or straw (*triangles*). *Bars* indicate least significant difference (LSD) between means
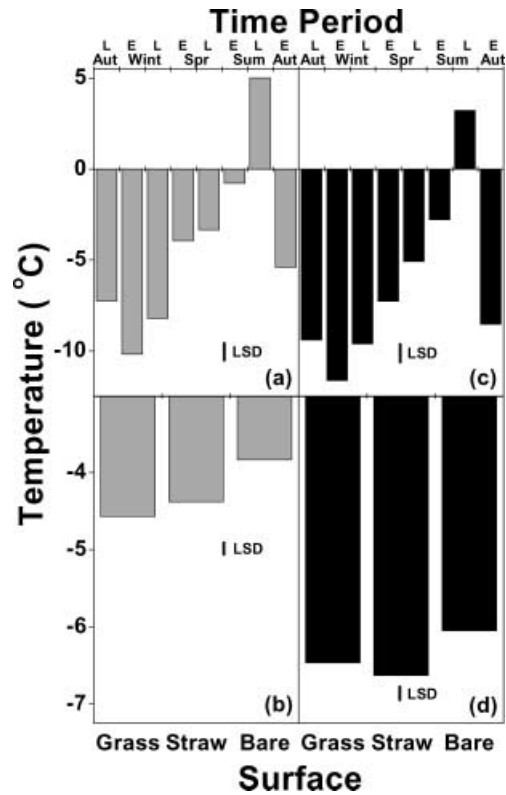

Fig. 5 Effects of season and soil surface treatments on the 10th percentile daily minimum temperature (**a**, **b**), and on the lowest minimum temperature recorded during each time period (**c**, **d**). Averages were calculated from data shown in Fig. 4. Early and late season time periods are indicated by *E* and *L*, respectively. *Bars* indicate LSD between means
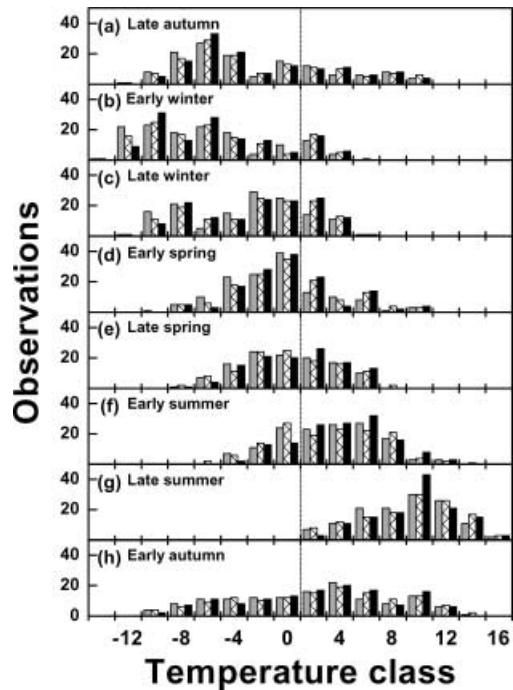

Fig. 4 Seasonal variation in the occurrence of daily minimum temperatures at 5 cm above bare soil (*black*) or soil covered with either live grass (*grey*) or straw (*hatched*). Values are the total number of observations recorded at three replicate sites for each of the three soil surface treatments during a 6 week period

growing in bare soil patches. These data were analysed by ordering from lowest to highest the daily minimum air temperatures recorded at each of three replicate sites for each treatment during each of the eight time periods. The 10th percentile temperature, i.e. the temperature at which 10% of all temperatures were lower, was then recorded for each combination of site × treatment × time period, and evaluated by analysis of variance. Averaged over the whole year, the 10th percentile daily minimum temperatures varied significantly with time period ($P<0.001$; Fig.5a) and with treatment ($P<0.003$; Fig. 5b), but there were no significant interactions between time period and treatment; the treatments affected daily minimum temperatures in the same way throughout the year. Averaged over the whole year, there were no significant differences in the 10th percentile daily minimum temperature between live grass and straw treatments, but the 10th percentile daily minimum temperatures were significantly ($P<0.003$) lower in these two treatments than in the bare soil treatment. Similarly, the lowest minimum temperature recorded during any of the eight time periods varied significantly with time ($P<0.001$; Fig. 5c) and with treatment ($P<0.003$; Fig. 5d), but there were no significant interactions between time period and treatment. Averaged over the whole year, there were no significant
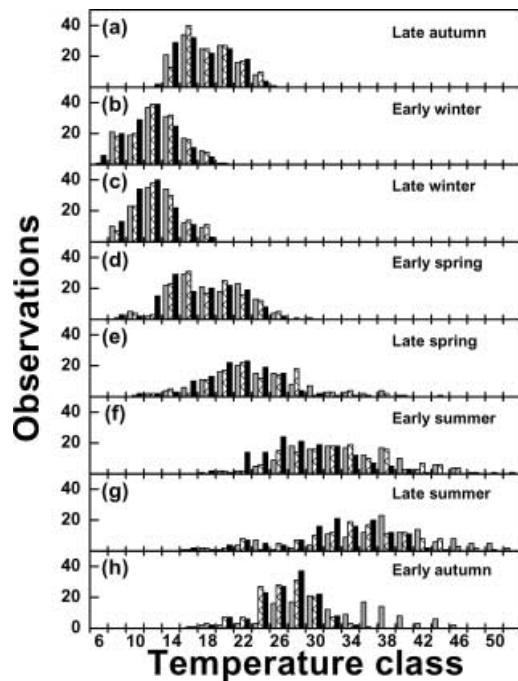
Fig. 6 Seasonal variation in the occurrence of daily maximum temperatures at 5 cm above bare soil (*black*) or soil covered with either live grass (*grey*) or straw (*hatched*). Values are the total number of observations recorded at three replicate sites for each of the three soil surface treatments during a 6-week period

Fig. 7 Effects of season and soil surface treatments on the 90th percentile daily maximum temperature (**a**, **b**), and on the highest maximum temperature recorded during each time period (**c**, **d**). Averages were calculated from data shown in Fig. 6. Early and late season time periods are indicated by *E* and *L*, respectively. *Bars* indicate LSD between means

differences in the lowest minimum temperatures per time period between live grass and straw treatments, but minimum temperatures were significantly ($P<0.003$) lower in these treatments than in the bare soil treatment.

Effects of the three treatments on the occurrence of daily maximum air temperatures at 5 cm above ground are shown in Fig. 6. It is apparent that seedlings growing in live grass or straw were subject to higher maximum temperatures than their counterparts growing in bare soil patches. Effects of treatments on temperature maxima were analysed by ordering from highest to lowest the daily maximum temperatures recorded at each of three replicate sites for each treatment during each of the eight time periods. The 90th percentile temperature, i.e. the temperature at which 10% of all temperatures were higher, was then recorded for each combination of site × treatment × time period, and evaluated by analysis of variance. Averaged over the whole year, the 90th percentile daily maximum temperatures varied significantly with time period ($P<0.001$; Fig. 7a) and with treatment ($P<0.003$; Fig. 7b), but there were no significant interactions between time period and treatment. Averaged over the whole year, there were no significant differences in the 90th percentile daily maximum temperature between live grass and straw treatments, but these values were significantly ($P<0.003$) higher than in the bare soil treatment. Similarly, the highest maximum temperature recorded during any of the eight time periods varied significantly with time ($P<0.001$; Fig. 7c) and with treatment ($P<0.003$; Fig. 7d) but there were no significant interac-
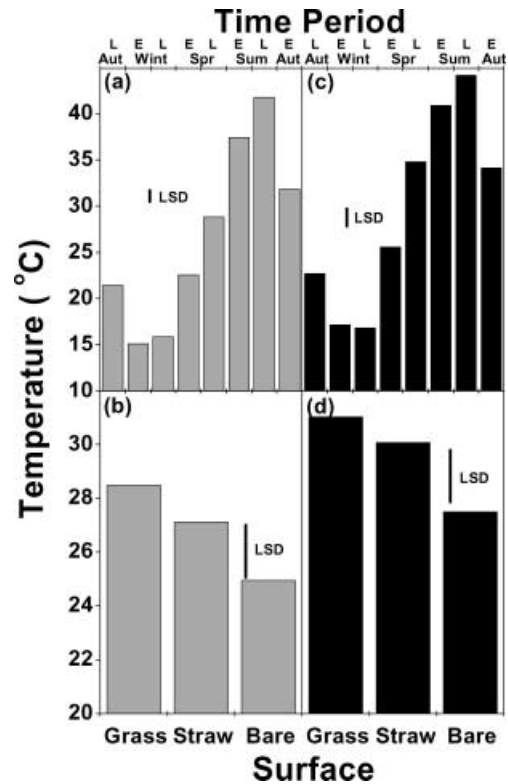
tions between time period and treatment. Averaged over the whole year, there were no significant differences in the maximum temperatures per time period between live grass and straw treatments, but maximum temperatures were significantly ($P<0.003$) higher in these treatments than in the bare soil treatment. Thus, seedlings growing in either the bare soil or the grass and straw treatments were subject to different diurnal ranges in air temperature even though there were no significant differences between treatments in average daily air temperatures (Fig. 2a).

Annual profiles in daily maximum and minimum temperatures collected at two adjacent sites, one where the soil was covered with live grass and the other where the soil surface was bare, are shown in Fig. 8. These data are shown to summarise and place into context several features of the thermal environments of the live grass and bare soil treatments. Temperatures measured at 50 cm above ground (Fig. 8a, h) were similar to those measured in the weather screen at 1.2 m above ground (Fig. 1). Apical meristems of grass shoots occur near the base of the plant where they would be strongly influenced by soil temperatures near the ground surface; minimum temperatures near the growing regions in grass plants (Fig. 8d) generally remained above 0°C when shoot growth was most vigorous from early September through
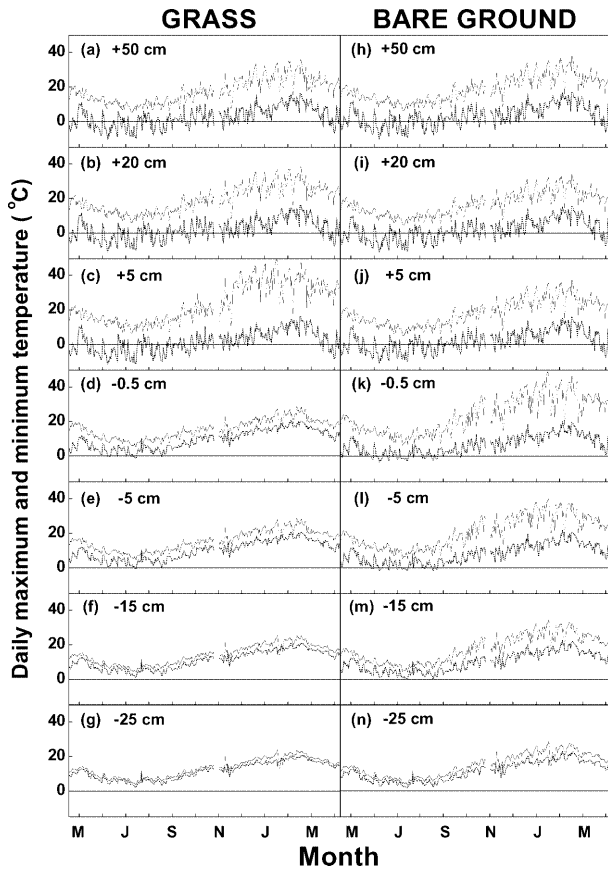
Fig. 8 Annual variation in daily maximum and minimum air and soil temperatures from 50 cm above ground to 25 cm below ground in two adjacent patches, one covered with live grass (**a–g**) and the other with a bare soil surface (**h–n**). Temperatures were recorded from mid-April 1996 to mid-April 1997
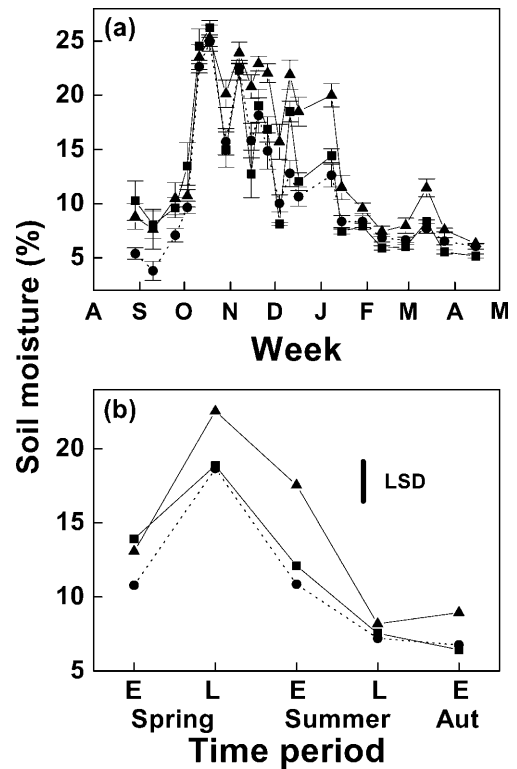

Fig. 9 Chronological change in soil moisture (**a**) and average soil moisture for different time periods (**b**) for *Eucalyptus pauciflora* seedlings grown in bare soil (*circles*) or in soil covered with either live grass (*squares*) or straw (*triangles*). Values in **a** are means±SE, n=5 for repeated measures made at 2-week intervals at the same sites. Values in **b** are corresponding treatment means for measurements averaged over 6-week time periods from early spring through early autumn where E and L indicate, respectively, early and late season time periods; *bar* indicates LSD between means

November. In contrast, minimum temperatures near the growing regions of seedling leaves and stems above a grass canopy were subject to frequent frosts (Fig. 8b, c). Shoots of seedlings growing in bare soil patches were also subject to frosts (Fig. 8i, j), but with less severity than seedlings emergent above a grassy surface. While the growing regions of grass plants rarely experienced freezing temperatures, the longest frost-free period for seedling shoots was 6 weeks in late summer. Note that maximum air temperatures at 5 and 20 cm above ground in grass and bare soil treatments were similar from late autumn through spring. In summer, however, seedlings growing in grass were subject to much higher maximum air temperatures than those growing in bare soil. Finally, soil temperatures below a grassy surface showed less diurnal amplitude, and increased more slowly in spring and summer (Fig. 8d–g) than those below a bare soil surface (Fig. 8k–n).

Soil moisture

Average soil moisture from the surface to a depth of 28 cm was measured by TDR every 2 weeks from late

winter until the end of the experiment in early autumn. The average moisture levels were low at the start of spring (Fig. 9) following a relatively dry period (Fig. 1b), but increased with increasing rainfall in late spring and then gradually declined with decreasing rainfall and higher temperatures (Fig. 1) as the season progressed through summer (Fig. 9). Soil moisture was similar in bare soil and live grass treatments throughout the study, whereas soil moisture was significantly higher in the straw treatment during most of the late spring and early summer periods (Fig. 9b).

Plant growth

Measurements of grass biomass (gram dry weight per 20×20×25 cm volume of soil) showed no significant differences during the year due to high variability between samples collected from an extant pasture (Fig. 10a, e). Nevertheless, there was a tendency for biomass to be maximal in late spring, decline during summer, and increase again in early autumn (Fig. 10a). The lower values in summer reflected combined effects of mowing and seasonal die-back of the grass. These trends in grass
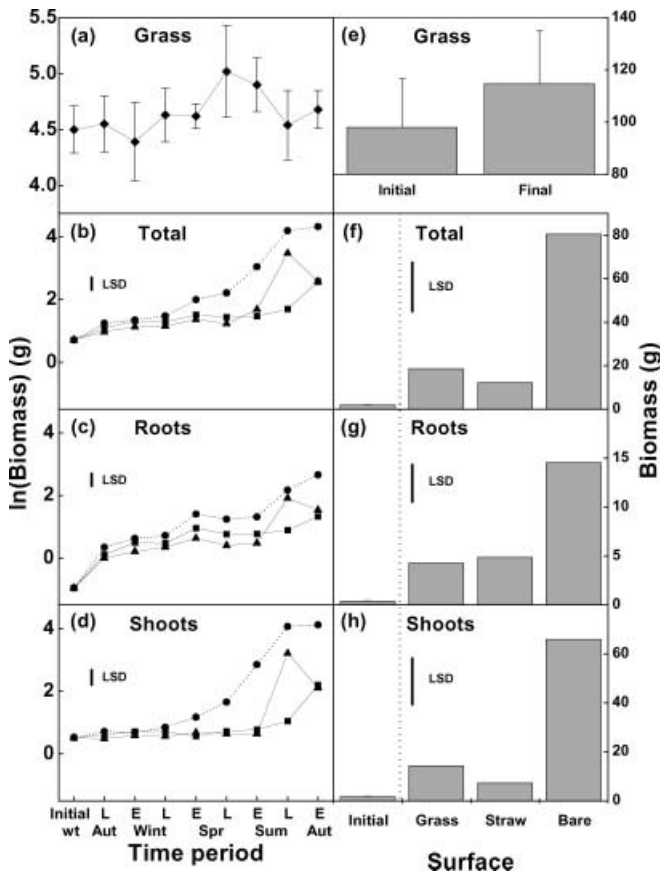
Fig. 10 Change in average biomass of grass (**a**) and *E. pauciflora* seedlings (**b–d**) as a function of time. *E* and *L* indicate, respectively, early and late season time periods. Average biomass of grass (**e**) and *E. pauciflora* seedlings (**f–h**) at the start and conclusion of the study. Tree seedlings were grown in bare soil (*circles*) or in soil covered with either live grass (*squares*) or straw (*triangles*). Values are treatment means, *n*=5; *bar* indicates LSD between means

Fig. 11 Time-dependent change in average height of grass (**a**) and total stem length of *E. pauciflora* seedlings (**b**). Values are mean±SE, *n*=5 for repeated measures made on the same plants assigned to the final harvest. Symbols indicate tree seedlings grown in bare soil (*circles*) or in soil covered with either live grass (*squares*) or straw (*triangles*)

growth were consistent with changes in average grass height, which increased rapidly during spring, and more slowly following mowing as the season progressed into summer (Fig. 11a).

Tree seedlings grew throughout the study (Fig. 10b). Biomass of seedlings growing in bare soil patches was significantly (*P*<0.001) greater than those growing in grass or straw treatments from early spring through the end of the study. There was no significant difference between biomass of seedlings grown in the grass and straw treatments except in late summer when two large individuals caused a relatively high average biomass of seedlings grown in straw. These more vigorous seedlings had escaped much of the frost damage to shoots suffered by other seedlings growing in the same treatments. By the final harvest, the average biomass of seedlings grown in bare soil patches was four times greater (*P*<0.01) than that of seedlings grown in grass or straw (Fig. 10f).

The increase in total seedling biomass during late autumn and winter was due mainly to root growth (Fig. 10c). For the three harvests from late autumn
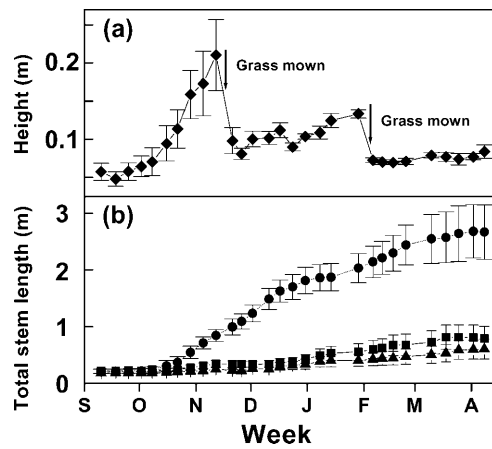
through late winter, the roots were contained within the 20×20×25 cm volume of soil samples. Thereafter, the patterns of root growth differed between treatments. Seedlings growing in bare soil patches showed vigorous root growth in late winter when a profusion of roots explored the shallow soil layer. By early spring, it was no longer possible to extract the whole root system from seedlings growing in bare soil as roots extended well beyond the sampling volume both laterally and to much deeper soil layers. It is unlikely that root growth ceased during late spring and early summer in these seedlings as growth probably continued in areas beyond the sampling volume. The marked increase in root biomass during late summer and early autumn was due to growth of lignotubers and substantial thickening of tap roots and major lateral roots, all of which exceeded 1 cm in diameter. Thus, root biomass was under-estimated for seedlings growing in bare soil from early spring through early autumn.

In contrast, seedlings growing in grass and straw treatments failed to initiate root growth in late winter and showed significantly (*P*<0.02) less root growth in spring than seedlings growing in bare soil patches. The root systems of seedlings growing in grass formed a net-like layer at a depth of about 10 cm along the base of a dense grassy root mat. The root systems of seedlings growing in straw explored shallow depths near the soil surface, with local profusion of root growth occurring where roots encountered rotting organic material. In both treatments, root growth was largely confined to lateral exploration of shallow soil during early spring with little penetration to depths greater than the sampling volume until late spring. By the final harvest (*P*<0.002), root biomass extracted from the sampling volume was similar in seedlings grown in grass and straw, but averaged only one-third of the biomass of seedlings grown in bare soil (Fig. 10g).

Shoot biomass ($P<0.001$) began to increase in early spring in seedlings growing in bare soil patches and in late summer in seedlings growing in live grass and straw treatments (Fig. 10d). These differences in growth were reflected in differences in non-destructive measurements of total stem length (Fig. 11b). In general, stem elongation began near the ground, with subsequent bud break occurring at increasingly greater heights above ground as the season progressed. Seedlings growing in bare soil patches began growth in mid-spring with measurable differences in stem lengths occurring by 9 October, approximately 3 weeks after the onset of increase in grass height (Fig. 11a). Stem elongation in seedlings growing in live grass and straw treatments began approximately 3 weeks later than in those growing in bare soil. However, stem growth of these seedlings was repeatedly stymied by frost damage with substantial increases in stem length not occurring until mid-summer (January). By the end of the experiment in mid-autumn, total stem length averaged 2.67 ± 0.48 m in seedlings growing in bare soil and 0.79 ± 0.22 m and 0.60 ± 0.18 m in seedlings growing in grass and straw, respectively (Fig. 11b), commensurate with shoot biomass being approximately 4–5 times greater ($P<0.001$) in seedlings grown in bare soil patches than in those grown in grass or straw (Fig. 10h). Similarly, height at the final harvest averaged 0.66 ± 0.09 m in seedlings grown in bare soil and 0.36 ± 0.09 m and 0.41 ± 0.08 m in seedlings grown in grass and straw, respectively.

Discussion

Recent reviews of mechanisms of negative interactions between plants (Aarssen and Epp 1990) or, more specifically, between grass and trees (Scholes and Archer 1997), emphasise resource depletion as the cause of competitive inhibition of plant growth. However, the results of the present study show that alteration of the thermal environment by a grassy surface inhibits growth of snow gum seedlings (*Eucalyptus pauciflora*). Covering the soil with straw produced thermal conditions statistically indistinguishable from those of live grass. This gives us confidence that differences between growth of seedlings surrounded by live grass or straw would relate to differences in competition for below-ground resources under common microclimatic conditions. The results showed no measurable differences between growth of seedlings in these two treatments (Figs. 10, 11), and hence no evidence of competitive inhibition of growth. In contrast, there were marked differences between thermal environments of bare soil patches and those in which the soil was covered with either live grass or straw. Seedlings growing in bare soil patches experienced more rapid increase in soil temperatures during late winter and spring (Figs. 2, 3), less frequent and less severe frosts (Figs. 4, 5), and temperature maxima that were better coupled with those of the bulk air mass than seedlings growing in the live grass and straw treatments

(Figs. 6, 7). These differences in temperature may account for greater growth rates of seedlings in bare soil. Clearly, thermal interference is of mechanistic importance in competitive interactions between plants.

Direct competition for below-ground resources between grass and tree seedlings

The grasses and herbs making up the pasture in the present study mainly have shallow root systems, with the bulk of the root mat occurring in the top 10 cm of soil, while eucalypts also possess very deep root systems. During early phases of establishment and growth, a tree seedling would depend on water and nutrients in shallow soil layers near the ground surface. Even at later stages in growth when roots may have tapped into deeper, more persistent supplies of water, a juvenile tree would still obtain nutrients primarily from soil near the surface, and the availability of those nutrients would depend on soil moisture and temperature. All of these factors are influenced by a grassy community.

In the present study, measurements of soil moisture from the surface to a depth of 28 cm indeed showed significantly lower water content beneath live grass than straw (Fig. 9) when rainfall was relatively abundant (Fig. 1), temperatures were mild (Fig. 1), and grass growth was most vigorous (Figs. 10a, 11a). While the depletion in soil moisture was undoubtedly due to transpiration by the grass sward, there was no evidence that this reduction in soil moisture adversely affected growth of tree seedlings under common microclimatic conditions. Seedlings surrounded by straw grew just as poorly as those surrounded by live grass (Figs. 10, 11) despite greater soil moisture beneath straw (Fig. 9). Indeed, soil moisture beneath straw approached field capacity (i.e. 24%) during early spring. Thus, inhibition of tree seedling growth, at least during spring, cannot be attributed directly to competitive reduction in below-ground resources by grass. However, thermal interference by grass would inhibit access of seedlings to soil resources, thereby causing temporal separation in resource use, and hence competition, as will be discussed later.

Thermal interference and the inhibition of tree seedling growth by grass

Effects of grass or straw on seedling growth may be partly attributable to effects on soil temperatures. In a recent review, Körner (1998) noted the importance to tree growth of a critical soil temperature under conditions otherwise close to optimum for photosynthesis during the day. For temperate, upper montane tree species, this critical temperature appears to range from 5.5°C to 7.5°C, although data are scant (Körner 1998). In the present study, there was little root growth during winter (Fig. 10c) when soil temperatures averaged 5°C (Fig. 2). A layer of grass or straw insulates the soil against heat

loss at night and heat gain during the day. Indeed, insulation of the soil by a grassy or straw covering greatly reduced both the diurnal amplitude (Fig. 8) and the rate of increase in average soil temperature as radiation loads increased in late winter and spring (Fig. 3), consistent with previous studies (Balisky and Burton 1995). As low soil temperatures can delay dehardening in frost-resistant *Eucalyptus* species (Paton et al. 1979), lower soil temperatures beneath grass and straw during late winter and early spring could delay the onset of seedling growth with major consequences for growth later in the year. Indeed, seedlings exposed to the higher soil temperatures in bare soil patches grew more roots from late winter to early spring (Fig. 10c) and initiated shoot growth three weeks earlier in spring than seedlings subject to lower soil temperatures in live grass and straw treatments. Root growth during late winter when soil moisture levels are relatively high may poise seedlings for rapid exploitation of water and nutrients near the soil surface when growing conditions become more favourable in early spring. Strong root growth during early spring may be critical for gaining access to deeper, more persistent water supplies, enabling seedlings to continue growing strongly (Fig. 11) as shallow soil water becomes depleted except when replenished by intermittent rainfall in early summer. Thus enhancement of root growth by warm soil temperatures in late winter and early spring may be particularly important for plant growth and survival later in the year.

Other effects of grass or straw on seedling growth may be partly attributable to effects on air temperatures. The insulating properties of grass or straw surfaces impede the flow of heat from the underlying soil to the overlying air at night, leading to lower air temperatures than above a surface of bare, moist soil (Leuning 1988, 1989). In the present study, minimum air temperatures were as much as 2°C lower above live grass and straw than above bare soil (Fig. 4), consistent with previous studies in both temperate eucalypt systems (Leuning and Cremer 1988; Ball et al. 1997) and boreal forests (Blennow 1997). Such a decrease in minimum temperatures would lead to a slower recovery of photosynthetic activity, a greater delay in bud break, greater frost damage to elongating stems and developing leaves, and lower rates of stem elongation for seedlings in grass and straw compared to those in bare soil (Ball et al. 1997).

The insulating properties of grass or straw can also lead to higher maximum temperatures in the overlying air than above bare soil (Oke 1987). During winter, when low solar angle limits the heat load, and during spring, when soil moisture levels were relatively high, there were no significant differences between daily maximum air temperatures above grass, straw or bare soil, consistent with a previous study (Ball et al. 1997). However, by early summer, when soil moisture was depleted and the grass shoots began to dry and brown, daily maximum air temperatures on sunny days with very low wind speeds were as much as 10°C greater at 5 cm above a ground surface covered with either live grass or straw than above bare soil (Figs. 6, 8), consistent with previous studies (Waggoner et al. 1960). Apparently, impedance of heat transmission into the soil coupled with little evaporative cooling led to greater increase in sensible heat above the insulated surfaces than above bare soil. Elevated air temperatures occurred at heights as much as 20 cm above live grass or straw (Fig. 8), causing shoots of seedlings in these treatments to grow under warmer conditions than those growing in bare soil. With air temperatures near the base of seedling canopies being as much as 10°C above ambient air temperatures, leaves of seedlings in grass or straw treatments would have been subject to much greater evaporative demand and to more frequent and more severe excursions in tissue temperature to deleterious levels than their counterparts at an equivalent height above bare soil. Such drought and heat stress might explain why seedlings in straw failed to grow better than seedlings in live grass during early summer despite the presence of greater soil moisture beneath straw.

Thus, there were no differences between the thermal environments of seedlings growing in live grass or straw, but there were three significant differences between these environments and those of seedlings growing in bare soil. Firstly, soil temperatures increased more slowly in late winter and early spring when the soil surface was covered with either live grass or straw than when the surface was bare. Secondly, seedlings growing in live grass and straw were subject to more frequent and more severe frosts and lower minimum temperatures than seedlings growing in bare soil. Finally, seedlings growing in live grass or straw were subject to greater heat (and hence also drought) stress in summer than seedlings growing in bare soil. These three features of the thermal environment could profoundly affect seedling growth, and account for the differences in growth between treatments.

The role of microclimate in grass/tree interactions

In grazing lands around Canberra, including the present study site at Bungendore, grass begins to grow in late winter as days become longer and ambient air temperatures rise (Fitzpatrick and Nix 1970). Grass growth becomes increasingly vigorous with progress into spring (Figs. 10, 11), reaching a maximum in mid to late spring when ambient temperatures are still mild (Fitzpatrick and Nix 1970). Growth early in spring would enable grass to exploit resources at a time when microclimatic conditions are conducive to its growth and below-ground resources such as water are relatively abundant.

In contrast, growth of tree seedlings (Figs. 10, 11) during this same period is inhibited by the presence of a grassy groundcover which causes shoots to experience continued frosts and roots to remain too cold to initiate growth. The seedlings begin to grow in summer as the

incidence of frost diminishes and soil temperatures rise. By this time, however, grass would have depleted the upper soil layers of moisture and nutrients, leaving the tree seedlings with relatively few resources to support growth. Thus, as a result of thermal interference from grass, seedlings would fail to take advantage of the spring growth period when resources are abundant, and would begin growth as the season progresses into summer when high temperatures and drought limit growth of both grass and tree seedlings. Under these conditions, seedlings may fail to gain sufficient height to lift canopies above the influence of a grassy surface before frosts return in early autumn. In this way, the microclimatic conditions induced by a grassy surface could contribute to a prolonged period of growth check.

Thus, alteration of the thermal environment by grass has several effects on tree seedling growth. Firstly, lower minimum temperatures cause tree seedlings to have a short growing season largely restricted to summer. Secondly, lower minimum temperatures cause temporal separation in competition for resources, with consumption of below-ground resources by grass in spring reducing availability of those resources to support tree seedling growth in early summer. Finally, seedlings surrounded by grass are more vulnerable to stress induced by both low and high temperature extremes.

Conclusion

The present study shows that temperature plays a major role in competitive interactions between grasses and tree seedlings. Small scale variation in above and below-ground temperatures induced by a grassy surface produces major differences in the timing, rate and extent of tree seedling growth and indeed accounts for most of the inhibition of tree seedling growth by grass. Replacement of forest with grassland can produce microclimatic conditions that favour the resistance of the grassland to invasion by trees in the absence of disturbances, such as fire, that create bare patches conducive to tree seedling growth. These results may help to explain the phenomenon of growth check induced by grassy ground cover and contribute to a solution for one of Australia's most pressing environmental problems, namely the re-establishment of native trees on deforested land.

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