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Ecophysiology of Species with Distinct Leaf Morphologies: Effects of Plastic and Shadecloth Tree Guards

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Abstract

Ecological restoration using seedling tubestock is challenging under a Mediterranean-type climate of hot, dry summers. We investigated the ecophysiological effects of plastic tree guards and shadecloth tree guards during seedling establishment of four co-occurring tree species that differ in leaf morphology. Average temperature was 6.7°C higher in plastic guards than controls over a summer, with a maximum of 53.5°C compared to 47.9°C in controls. Light levels were 2-fold lower in both tree guard treatments relative to control. In spring, photosynthesis and specific leaf area were significantly elevated in shadecloth tree guards relative to other treatments. In summer, photosynthetic rate was significantly lower, and midday photochemical efficiency was significantly higher, in both tree guard treatments relative to controls. The effect of elevated temperature in plastic tree guards may partially explain our results of higher mortality of seedling in plastic tree guards. The relatively elevated spring photosynthesis of seedlings in shadecloth tree guards may partially explain the result of reduced mortality and increased growth in this treatment. We conclude that shadecloth tree guards create a microclimate more favorable for seedling establishment in a Mediterranean-type environment than plastic tree guards and control treatments. Our results may have wide applicability to the range of restoration settings where seedling tubestock is planted, except in environments where low temperature is limiting to plant growth.

Introduction

Seedling establishment is one of the most limiting processes in the perpetuation of plant populations, particularly in disturbed environments (Schemske et al. 1994; Hobbs & Yates 2003). Urban bushland remnants are often characterized by significant weed infestation, high browsing pressure, altered edaphic and hydrological regimes, and altered vegetation structure due to the increased frequency of fire. For these reasons, native vegetation in urban bushland remnants can fail to recruit and regenerate, necessitating ecological restoration. A favored method for restoration is the use of direct seeding following weed control and sometimes soil scarification (Turner et al. 2006). However, preference for use of local provenance seed to avoid genetic pollution of indigenous genotypes (Krauss et al. 2005) often results in limited seed resources, particularly when bushland is fragmented and where remnant populations are small and old and/or where stressed plants set limited seed numbers per plant. Thus, limited seed resources combined with the inherent variability of climate can preclude the practice of direct seeding and result in ecological restoration of urban bushland by planting nursery-raised seedlings.

In Mediterranean-type environments, different strategies for coping with low soil water and high atmospheric evaporative demand may contribute to differences in the competitive ability and the distribution of species (Damesin et al. 1998). Stomatal closure, which minimizes water loss through transpiration (Jones 1998), is a common plant strategy although different species may have different stomatal responses and the net effect of this on transpiration is affected by leaf morphology and leaf angle. Conversely, stomatal closure limits transpirational cooling and leads to carbon dioxide limitation to photosynthesis and thus reduced competitive ability. In order to maximize early growth, seedlings can have higher stomatal conductance and photosynthesis than mature plants during the wet season of a Mediterranean-type climate year (Kolb & Stone 2000).

Plant water availability can alter specific leaf area (SLA) that affects leaf transpiration and photosynthesis (Niinemets 2001). Within species, ecotypes have morphological and anatomical traits that result in leaves of relatively low leaf SLA where water availability is least (Gratani et al. 2003). Within ecotypes, significant plasticity in physiological traits (Valladares et al. 2000) enables plant success within spatially and/or temporally variable environments. Thus, plasticity in leaf morphological and physiological traits is a significant factor in the distribution of a given plant species (Ackerly et al. 2000).

In Mediterranean-type environments, seedlings must survive the inherently long, hot dry summers (Roche et al. 1998) with an immature root system that has limited access to soil water (Donovan & Ehlringer 1991; Cavender-Bares & Bazzaz 2000). Irrespective of climate, transplanted tree seedlings commonly suffer water stress that can limit early growth or cause mortality (Kozlowski & Davies 1975; Close et al. 2005*a*). The volume of soil occupied by a planted container-raised tree seedling is 10-fold less than that of a seedling of similar top growth that has established from in situ seed (Burdett 1990). The capacity for transplanted seedlings to maintain photosynthesis and growth is strongly influenced by the effects of nursery culture on characteristics such as stomatal response to high atmospheric evaporative demand and leaf SLA (Vilagrosa et al. 2003).

Close and Davidson (2003) found that many revegetation plantings in the Midlands of Tasmania, Australia, have low success due to the management of seedling establishment. Commercially available clear plastic tree guards have been widely used and recommended for improving the success of seedling establishment for ecological restoration plantings. Plastic tree guards have been shown to significantly improve restoration efforts due to protection of seedlings from vertebrate herbivores across a range of landscapes (Opperman & Merenlender 2000; Sweeney et al. 2002; Close et al. 2005*b*). Furthermore, tree guards improve restoration outcomes, speculated to be through improving the microclimate around seedlings, in temperate (Ward et al. 2000) and tropical (Lai & Wong 2005) environments. However, these effects may not be favorable for seedling establishment in hot, dry Mediterranean-type or arid climates. Although no research has been conducted on this question, observation indicates suboptimal outcomes in many community-based plantings in Mediterranean Australia. In addition to the possibility of creating an unfavorable temperature and light microclimate, plastic tree guards reduce wind speeds (Bergez & Dupraz 1997) that lead to depressed carbon dioxide (CO_2) levels and CO_2 limitation of photosynthesis (Dupraz & Bergez 1999). Increased leaf CO_2 availability, as a result of ventilation, significantly increased photosynthesis and growth (Bergez & Dupraz 2000).

The effect of shadecloth tree shelters on decreasing ambient light has been shown to increase eucalypt seedling survival by decreasing the damaging effects of high light in combination with low temperature (photodamage; Egerton et al. 2000; Close et al. 2002). In Mediterranean-type environments, shadecloth shelters have been shown to keep leaf temperature below air temperature and to increase photosynthesis 2.5-fold and increase stomatal conductance 1.5-fold of oak seedlings relative to controls during drought (Danner & Knapp 2003). Thus, the available evidence indicates that shadecloth tree guards could be an effective technique for seedling establishment in ecological restoration plantings.

The objective of this study was to investigate techniques that maximize seedling tubestock survival and establishment in an ecological restoration context. The central question was

- What effects do plastic and shadecloth tree guards have on tubestock seedling growth and survival and what ecophysiological mechanisms underpin these observations?

In 2003, restoration trials investigating the effects of plastic tree guards and shadecloth tree guards on air temperature, and of seedling survival and growth in plastic tree guards, were undertaken. In 2004, we conducted two restoration trials investigating the effects of shadecloth tree guards on seedling growth and survival. In 2005, we conducted an ecophysiology trial that compared seasonal trends in photosynthesis and transpiration, photochemical efficiency, and SLA. *Eucalyptus marginata*, *E. gomphocephala*, *E. rudis*, and *Banksia attenuata* seedlings under establishment treatments of control, plastic tree guard, and shadecloth tree guards were investigated.

Methods

Experimental Sites

Perth, in the southwest of Western Australia, has a warm Mediterranean-type climate of warm dry summers (average 30.7°C and 34.6 mm) and cool wet winters (average 18.3°C and 448.4 mm). Bold Park is a large (437 ha) coastal urban bushland remnant, located 8 km west of the Perth central business district. The tall woodland communities of Bold Park are prone to high levels of weed invasion, feral animal activity, recreational pursuits, and frequent fire events due to arson that transiently increase the available soil nutrients, thus favoring weed species. In the urban environment, the proximity of household gardens that are a source of weed seed and the introduction of weed seed through recreational use (walking and horse riding) have led to the replacement of native species with nonlocal species dominated by

Veldgrass (*Ehrharta calycina*), Rose pelargonium (*Pelargonium capitatum*), Geraldton carnation weed (*Euphorbia terracina*), and Bridle creeper (*Asparagus asparagoides*).

All trial sites were located within the tall woodland communities in the presence of canopy gaps that were created by mortality of mature woodland trees and had been converted to Veldgrass (*Eh. calycina*) "meadows." Gaps containing one trial plot were a minimum of approximately 0.5 ha. Seedlings were planted so that shade cast by surrounding adult trees did not produce an edge effect. Fusilade (4 L/ha) was broadcast applied for *Eh. calycina* control and Roundup (3 L/ha) spot applied for *P. capitatum* and *A. asparagoides* control at least 4 weeks prior to planting. The trials were established by experienced planters using "pottiputkis" at a density of approximately 2 plants/m^2, approximately half the density of seedlings observed soon after natural recruitment events (Ruthrof 2001; Ruthrof et al. 2003), to account for self-thinning. Plastic tree guards were 460 mm high with width of 260 × 260 × 260 mm (staked into a triangle). Shadecloth tree guards were of similar dimensions to plastic tree guards and were constructed of green, wavelength-neutral shadecloth that intercepts approximately 54% of incident photosynthetically active radiation (PAR) (Close et al. 2002).

Restoration Trials 2003: Plastic Tree Guards

In June 2003, a trial was established as described above at "Zamia Road" (lat 6465147N, long 0383970E). Three replicates of 40 plants of each species (*Eucalyptus gomphocephala* and *Banksia attenuata*) were planted and randomly evenly allocated to either plastic tree guard or control treatments. In April 2005, percentage of mortality and height growth (cm) of live seedlings were recorded.

In an additional adjacent plot (in a trial of the same layout but investigating different species that are not reported here), Tinytag Plus (−40 to +125°C; Hastings Data Loggers, Port Macquarie, NSW, Australia) thermoprobe and data logger units were allocated to each of control, plastic tree guard, and shadecloth tree guard treatments. The units were attached to a stake at 10–15 cm from the soil level and equidistant from the seedling stem and side of the tree guard or a similar distance from the seedling stem for the control treatment. The Tinytag Plus units recorded temperature from 27 October 2003 to 29 January 2004.

Restoration Trials 2004: Shadecloth Tree Guards

In June 2004, two trials were established as described above at “Corner Hovea/Zamia Road” (lat 6465040N, long 0383759E) and “Zamia East” (lat 6465023N, long 0383775E). Three replicates of 22 *E. gomphocephala* seedlings and 30 seedlings each of *B. attenuata* and *B. menziesii* at the Zamia East site, and three replicates of 22 *E. gomphocephala* seedlings only at the Corner Hovea/Zamia Road site, were established under randomly allocated treatments of control and shadecloth tree guards (given the adverse air temperature in plastic tree guards in the 2003 trial). In April 2005, percentage of mortality and height growth (cm) of live seedlings were recorded.

Ecophysiology Trial: Shadecloth and Plastic Tree Guards

In order to understand the mechanisms underpinning observed results in the restoration trials of 2003 and 2004, seedling ecophysiology was investigated under establishment techniques of control, plastic tree guards, and shadecloth tree guards. In May 2005, a trial was established approximately 50 m from the seasonally wet “Camel Lake” within Bold Park (lat

0384506N, long 6464676E). A scattered overstory of *E. rudis* occurred within and around the "Lake" (Camel Lake has not contained free-standing water for five to six decades), with *E. marginata*, *E. gomphocephala*, and *B. attenuata* woodland surrounding Camel Lake. Seedlings of the indigenous species have distinct leaf morphology: compared with *E. marginata* seedlings, that have few, relatively large and thick leaves held horizontal to the stem, *E. gomphocephala* has many, relatively small and thin leaves held at approximately 45°C from the stem; *E. rudis* has many relatively small leaves held vertically to the stem; and *B. attenuata* has narrow, highly sclerophyllous leaves held more or less horizontal to the stem (Boland et al. 1992). Four replicate plots of 60 seedlings for each of *E. rudis, E. marginata*, *E. gomphocephala*, and *B. attenuata* were established. Only three plots of replicate seedlings were measured as the fourth was considered atypical due to some canopy cover of adult trees. Seedlings were randomly allocated within plots, except for *E. rudis* that were preferentially planted at the downslope (toward Camel Lake) end of the plots (consistent with the natural distribution of adult trees). An equal number of seedlings (20) were randomly allocated to each of the three treatments: control, plastic tree guard, or shadecloth tree guard. In March 2006, mortality and height growth (cm) of live seedlings were recorded. To conduct the ecophysiology measurements, two seedlings of each species of each treatment were selected at random from each plot, one for gas exchange and one for chlorophyll fluorescence measurement.

Plant Material and Treatments

Local provenance seeds from within the Bold Park bushland were collected in the summer prior to each trial year. In early December of the respective year, treated seeds were sown into germination trays, covered with a fine layer of vermiculite, watered, and placed into a cool room set to 17°C (±2) for 4 weeks. Following germination, seedlings were "pricked" into forestry tubes (115 cm^3 volume, 120 mm depth) containing a potting mix of 2 parts composted *E. marginata* sawdust, 1 part sand, 1/2 part coarse river sand, 3 kg osmocote, 8–9 months low phosphorous, 1 kg dolomite, 1.2 kg lime, and 500 g ferrous sulfate (per m^3). Seedlings were watered with overhead irrigation as required from early January to May of the respective year.

Gas Exchange, Chlorophyll Fluorescence, and SLA

Gas exchange (photosynthesis, transpiration, and water use efficiency [WUE] calculated as photosynthesis/transpiration) and chlorophyll fluorescence (midday photochemical efficiency [F_v/F_m]) were assessed on clear-sky days prior to planting, first in the nursery (10 May 2005) and second in the field in winter (24 May 2005), in spring (20 October 2005), and at the end of summer (4 March 2006). Only the most recently fully expanded leaves located on the north side of the crown were measured, one leaf per seedling. Species and treatments were measured in a random order to avoid bias due to diurnal changes that occurred within the approximate 3-hour measurement period for gas exchange and subsequent approximate 40-minute measurement period for midday chlorophyll fluorescence.

Gas exchange was measured on intact leaves at preplanting and in winter and spring using a CIRAS-2 portable infrared gas analyzer (PP Systems, Amesbury, MA, U.S.A.) and using a leaf chamber with a 6 × 2–cm window. Leaf chamber carbon dioxide concentration was set to 380 μmol m^{-2} s^{-1} using a flow rate of 300 μmol/s. Summer gas exchange measurement was conducted with an ADC LCA4 portable open-flow infrared gas analyzer (Analytical

Development Corporation, Hoddesdon, Herts, U.K.) fitted with a Parkinson PLC-B leaf chamber of 6 cm^2 in which the quantum light sensor was not functioning.

Midday photochemical efficiency (F_v/F_m) was assessed with an ADC $F_{?m}$ 1,500 chlorophyll fluorometer (Analytical Development Corporation) following dark adaptation of leaves for 15 minutes with leaf clips.

The leaf assessed for gas exchange and chlorophyll fluorescence and a leaf from the leaf pair of the next node down were sampled and were measured within 24 hour for single-sided leaf area (Li-Cor Li-300 leaf area meter, John Morris Scientific Pty. Ltd., Willoughby, NSW, Australia, calibrated with plates of known area) for calculation of photosynthesis and transpiration rates (area of leaves measured for gas exchange only) and for calculation of SLA. Sampled leaves were oven dried at 45°C until constant weight before determination of leaf dried weight with a four decimal place scale.

Data Analysis

Given that one leaf per seedling was measured for gas exchange and chlorophyll fluorescence, individual leaves were the units of replication in the analyses of these data. SLA data were averaged per seedling, and this average was the unit of replication. Height data were averaged per species per plot, and mortality percent calculated per species per plot, and plot used as the unit of replication. One-way analyses of variance (ANOVAs) were applied to height and mortality data (mortality data were arc sine transformed). Two-way ANOVAs (variables of establishment technique and species) within season, given the focus on effects of establishment techniques, were conducted on gas exchange, chlorophyll fluorescence, and SLA datasets using StatView software. Results for *E. rudis*, except for SLA, were not included in the analyses for summer due to high mortality at this time. Pair-wise comparisons were made using Fisher's *t* test. Results were considered significantly different at the $p < 0.05$ level.

Results

Restoration Trial 2003: Plastic Tree Guards

During the 2003/2004 summer, average daily maximum and absolute maximum air temperatures were considerably higher (5–6°C) in plastic tree guards than in shadecloth tree guards and control (Table 1).

Neither *Eucalyptus gomphocephala* mortality ($F_{[1,4]}$= 3.156, p= 0.1503) and height growth ($F_{[1,4]}$= 0.399, p= 0.5619) nor *Banksia attenuata* mortality ($F_{[1,4]}$= 0.801, p= 0.4214) and height growth ($F_{[1,4]}$= 0.146, p= 0.3219) were significantly different between control and plastic tree guard treatments (Fig. 1a). The observed trend toward higher mortality of *E. gomphocephala* under the control compared to the plastic tree guard treatment was likely due to rabbit browsing, whereas the majority of mortality of seedlings in plastic tree guards was probably due to high-temperature damage as indicated by leaf desiccation and abscission (K. Ruthrof 2005, Botanic Gardens and Parks Authority, personal observation).

Restoration Trial 2004: Shadecloth Tree Guards

Percent mortality of *E. gomphocephala* was not significantly different between establishment technique treatments at the Corner Hovea/Zamia ($F_{[3,8]}$= 1.875, *p*= 0.2122) or at the East Zamia site ($F_{[3,8]}$= 0.671, *p*= 0.5933; Fig. 1b). Similarly, there were no significant effects of establishment techniques on percent mortality of *B. attenuata* ($F_{[3,8]}$= 2.664, *p*= 0.1191) or *B. menziesii* ($F_{[3,8]}$= 0.246, *p*= 0.8621). There was no effect of establishment techniques on height of *E. gomphocephala* at Corner Hovea/Zamia ($F_{[3,8]}$= 1.536, *p*= 0.2784) or East Zamia ($F_{[3,8]}$= 0.907, *p*= 0.4795; Fig. 1c). However, there were significant effects of establishment technique on height of *B. attenuata* ($F_{[3,8]}$= 8.36, *p*= 0.0076) with controls significantly lower than shadecloth (*p*= 0.002 and *p*= 0.006) treatments.

Ecophysiology Trial: Plastic and Shadecloth Tree Guards

Percent mortality was not significantly different between establishment treatments in any species due to the variability in the data. However, there was a consistent trend toward less mortality in shadecloth tree guard treatments than control or plastic guard treatments in *E. gomphocephala*, *B. attenuata*, and *E. marginata* (Table 2). Percent mortality was high in all treatments for *E. rudis*. Height growth was similar between control and plastic tree guards in all species but significantly higher in shadecloth tree guards than controls in *E. gomphocephala*, *B. attenuata*, and *E. marginata*.

PAR incident on seedling leaves was significantly higher in spring than winter ($F_{[1,63]}$= 5.915, *p*= 0.0179) and was significantly higher in the control than the tree guard treatments

($F_{[2,63]}$= 28.618, p < 0.0001; Table 1). Levels of PAR were not significantly different between the plastic and the shadecloth tree guard treatments.

In winter, there was no establishment technique effect on photosynthesis ($F_{[2,24]}$= 0.286, p= 0.7535; Fig. 2a). There was a significant species effect ($F_{[3,24]}$= 4.228, p= 0.0156) with photosynthetic rate of *E. gomphocephala* greater than *B. attenuata* (p= 0.03), and *E. marginata* (p= 0.0143) and *E. gomphocephala* (p= 0.0077) greater than *E. rudis*. Trends in establishment technique effects on transpiration mirrored those of photosynthesis in winter (Fig. 2b), and there was a significant effect of species on WUE ($F_{[3,24]}$= 11.158, p < 0.0001) with *E. marginata* greater than *E. gomphocephala* (p= 0.0141), *B. attenuata* (p= 0.0002), and *E. rudis* (p= 0.0005; Fig. 2c).

In spring, there was a significant effect of establishment technique on photosynthesis ($F_{[2,20]}$= 3.968, p= 0.0354; Fig. 2a). Seedlings in shadecloth guards had significantly higher photosynthesis than those in plastic guards (p= 0.0109). There were no species or interaction effects. Again, differences in photosynthesis were mirrored by trends in transpiration (Fig. 2b), and there were no effects on WUE (Fig. 2c).

In summer, there was a significant effect of establishment technique on photosynthesis ($F_{[2,13]}$= 8.93, p= 0.0036; Fig. 2a). Seedlings in the control treatment had higher rates than those in plastic tree guards (p= 0.0028) and those in shadecloth guards (p= 0.0036). There was no species effect ($F_{[2,13]}$= 1.048, p= 0.3786). There were no measurements of *E. rudis* due to almost complete mortality. Transpiration results mirrored those of photosynthesis (Fig. 2b), and there were no significant effects on WUE (Fig. 2c).

In summer, there was a significant establishment technique effect on midday F_v/F_m ($F_{[2,14]}$= 6.043, p= 0.0128; Fig. 3). Midday F_v/F_m was significantly higher in plastic tree guards (p= 0.0412) and shadecloth tree guards (p= 0.0053) than in control seedlings.

Leaf SLA was higher in shadecloth than control seedlings in spring (p= 0.0062) and in summer (p= 0.0257; Fig. 4). There were significant effects of species on leaf SLA at planting ($F_{[3,20]}$= 26.202, $p < 0.0001$) where leaf SLA of *B. attenuata* was less than *E. marginata* (p= 0.0002), and leaf SLA of *E. marginata* (p= 0.0004) and *E. gomphocephala* (p= 0.0101) was less than *E. rudis*. This trend similarly occurred in winter ($F_{[3,17]}$= 28.605, $p < 0.0001$), spring ($F_{[3,24]}$= 30.949, $p < 0.0001$), and summer ($F_{[2,25]}$= 5.782, p= 0.0086).

Discussion

Restoration Trials of Plastic and Shadecloth Tree Guards

The common and widely used establishment technique of plastic tree guards had a profound effect on the microclimate of seedlings. Maximum and average temperature differences of 5.6 and 6.7°C (between plastic tree guards and control treatments), respectively, over a typical summer are extremely significant in a Mediterranean-type environment, where summers are typically hot and dry. Most likely, seedlings in plastic tree guards were stressed by high midday temperatures that could not be ameliorated by leaf transpirational cooling due to water limitation. Although results from the 2003 restoration trial were confounded by rabbit browsing, significant numbers of *Eucalyptus gomphocephala* seedlings within plastic tree guards were observed to have desiccated and to have abscised leaves at the end of summer consistent with high temperature induced by a “glasshouse” effect in plastic tree guards. This led to the abandonment of the technique for seedling establishment in ecological restoration plantings.

The 2004 trials incorporated shadecloth tree guards in order to minimize temperature effects of the guard but retain the protection against browser damage. It should be noted that less mortality and height of *E. gomphocephala* in the 2004 trial controls than the 2003 trial controls are likely due to the former being 1 year younger than the latter at the time of assessment (April 2005). Shadecloth guards significantly decreased the mortality of *E. gomphocephala*, and *Banksia* species attained significantly greater height in shadecloth tree guards. Thus, detailed studies were conducted on the ecophysiological mechanisms underpinning the effects of plastic tree guards and shadecloth tree guards on seedling establishment.

Ecophysiological Effects of Shadecloth and Plastic Tree Guards

Similar to the 2004 restoration trial, percent mortality showed a trend toward being lower in shaded than control *E. gomphocephala* seedlings. Unlike the 2004 trial, this trend was also observed in *Banksia attenuata* in 2005, possibly due to the Camel Lake site having more available soil moisture, given that *B. attenuata* is phreatophytic (Zencich et al. 2002). Height growth was significantly greater in shaded than control in *E. gomphocephala*, *B. attenuata*, and *E. marginata*, consistent with the trends observed in the 2004 restoration trial. These overall similar outcomes over three successive field trial seasons give confidence to the generality of our ecophysiological results measured in 2005.

Our study of ecophysiology showed that the establishment techniques of plastic tree guards and shadecloth tree guards had significant effects on seedling leaf morphology, transpiration, and photosynthesis. The main effect of shadecloth tree guards was to significantly elevate levels of photosynthesis across all species in spring relative to photosynthesis in control and plastic tree guard treatments. The shadecloth treatment marginally decreased measured average summer air temperatures (by 1.4°C) but would have significantly reduced leaf temperature due to a reduction in radiant heat transfer. This would have reduced the effective vapor pressure deficit to the atmosphere and enabled more sustained photosynthesis over the diurnal cycle for a given level of water availability during a seasonal period when temperatures were mild and soil available water was high. The hypothesis that the microclimate created by shadecloth tree guards is significantly more favorable for seedling establishment in a Mediterranean-type environment was supported by a significant species effect of higher leaf SLA in the shadecloth tree guard than other treatments in spring and summer (when water limitation was greatest). It is likely that this morphology difference contributed to the lack of difference detected in WUE between shadecloth tree guards and other establishment technique treatments; leaves of higher SLA lose more water to the atmosphere per unit area (Niinemets 2001). The result of elevated spring photosynthesis in seedlings established in shadecloth guards is consistent with greater growth of seedlings established using this technique during the 2004 and 2005 trials. In contrast, midday photosynthesis was lower in both plastic and shadecloth tree guards than control treatments in summer. This is indicative of light limitation of photosynthesis, consistent with the approximately 2-fold lower light levels, and significantly elevated midday photochemical efficiency measured in plastic and shadecloth tree guard relative to control treatment seedlings in summer.

In contrast to the finding that plastic tree guards led to carbon dioxide limitation of photosynthesis (Dupraz & Bergez 1999), we found no significant difference in photosynthesis between seedlings in plastic tree guards and fully ventilated shadecloth tree guards in winter or summer. The tree guards used by Dupraz and Bergez (1999) were considerably taller and narrower and buried at the base (limiting ventilation) relative to the plastic guards of our study. Bergez and Dupraz (2000) demonstrated that ventilation with a gap at the base of their tall narrow tree guards overcame the problem of seedling carbon dioxide limitation of photosynthesis.

At the species level, *E. marginata* had generally higher WUE than all other species, particularly in winter. This higher photosynthesis per unit water lost may be a function of leaf thickness and stomatal control (Stape et al. 2001) and/or of stomata occurring exclusively on the leaf abaxial side. These characteristics may limit water loss in an environment where the horizontal leaf angle intercepts high radiation levels during the hotter midday period (King 1997). This strategy, relative to the vertical leaf angle of *E. rudis* and *E. gomphocephala*, is consistent with regeneration niche: *E. marginata* regenerates under existing canopies of mature *E. marginata*, where light could otherwise be limiting, and can remain suppressed for decades. In contrast, *E. gomphocephala* and *E. rudis* regenerate exclusively post severe disturbance of fire (or sometimes flood in the case of *E. rudis*) in environments of high light. *Eucalyptus nitens,* which similarly mass regenerates following wildfire, shows the capacity to rapidly adjust leaf angle in seedlings in response to excess light absorption (Close & Beadle 2006).

The widespread mortality of *E. rudis* seedlings in summer highlights the requirement of significant soil water availability for seedling regeneration, an environment that may be relatively common in the seasonally inundated sites that this species inhabits (Boland et al. 1992). Consistent with this, *E. rudis* had high leaf SLA and low WUE relative to other species, presumably essential for interspecific competition in a relatively water-rich regeneration niche. In nature, the coincidence of large-scale disturbance and adequate soil moisture, that facilitates significant eucalypt regeneration, may be rare (Yates et al. 2000).

Conclusions

Although other studies have shown significant benefits of plastic tree guards in preventing browsing damage to seedlings, our results show that the prevailing temperature within these guards creates an unfavorable microclimate for seedling establishment in a Mediterranean-type environment. In contrast, shadecloth tree guards, although having similarly beneficial effects on preventing browsing to seedlings, create a beneficial microclimate for seedlings that supports higher rates of photosynthesis and growth. We conclude that shadecloth tree guards are likely to increase the success of ecological restoration efforts where tubestock is planted in Mediterranean-type environments, although they are not commercially available. Our results may be widely applicable to a range of restoration settings where seedling tubestock is planted, except those where plants are low temperature limited.

Implications for Practice

- Restoration using tubestock is necessary for reasons such as low seed supply, unpredictable rainfall, or long hot summers such as those of Mediterranean-type environments.
- Commonly used plastic tree guards increased air temperatures by an average of 6.7°C over a summer, with a maximum of 53.5°C compared to 47.9°C in controls, leading to elevated mortality of seedlings.
- Shadecloth tree guards increased photosynthesis, SLA, survival, and growth relative to those in controls and plastic tree guards in a range of species planted in a Mediterranean-type environment.

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Figure 1. (a) Mean height and mortality of *Eucalyptus gomphocephala* and *Banksia attenuata* under control and plastic tree guard treatments of the 2003 restoration trial at the Zamia site (*n*= 3 plots, 20 seedlings per plot; ± 1 SE), (b) percent mortality, and (c) and height of *E. gomphocephala*, *B. attenuata*, and *B. menziesii* under control and shadecloth tree guard treatments of the 2004 restoration trials at the Corner Hovea/Zamia (*n*= 3 plots, 22 *E. gomphocephala* and 30 of each of *B. attenuata* and *B. menziesii* per plot; ± 1 SE) and East Zamia (*n*= 3 plots, 22 *E. gomphocephala* per plot; ± 1 SE) sites.

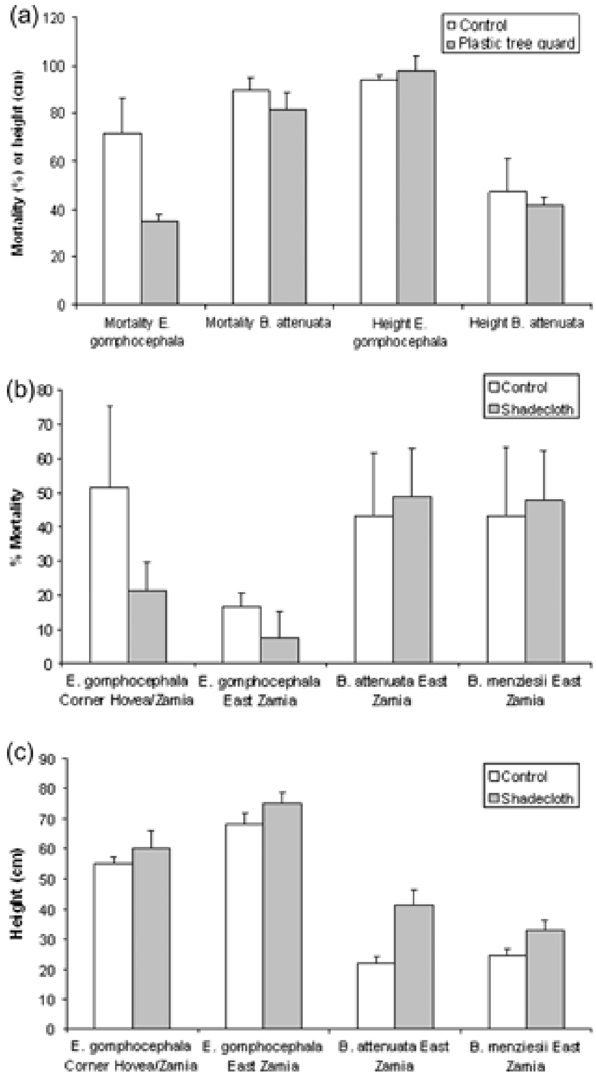

Figure 2. (a) Photosynthesis, (b) transpiration, and (c) WUE of seedlings of four co-occurring tree species (*n*= 12 because species data are pooled for clarity, except in summer where *n*= 9 because *Eucalyptus rudis* was not measured due to mortality; ± 1 SE) under establishment technique treatments of control, plastic tree guards, and shadecloth tree guards in winter (24 May 2005), in spring (20 October 2005), and at the end of summer (4 March 2006).

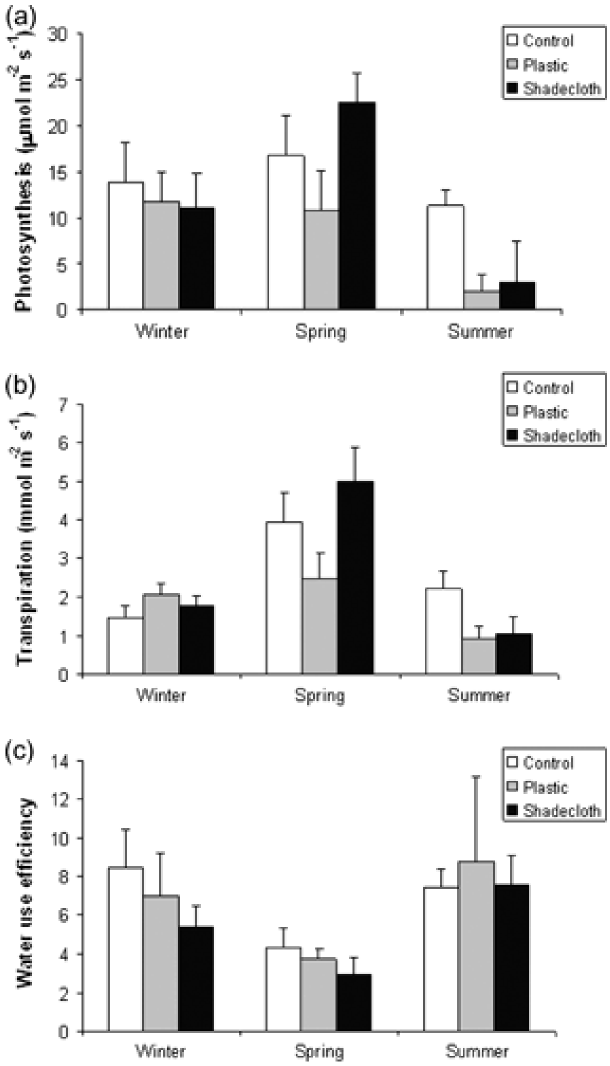

Figure 3. Midday photochemical efficiency (F_v/F_m) of seedlings of four co-occurring tree species (n= 12 because species data are pooled for clarity, except in summer where n= 9 because *Eucalyptus rudis* was not measured due to mortality; ± 1 SE) under establishment technique treatments of control, plastic tree guards, and shadecloth tree guards at preplanting (10 May 2005) in winter (24 May 2005), in spring (20 October 2005), and at the end of summer (4 March 2006).

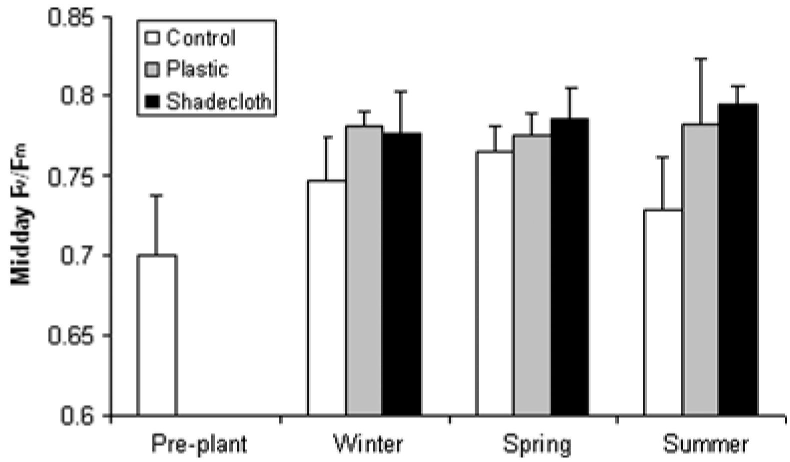

Figure 4. SLA of seedlings of four co-occurring tree species (*n*= 12 because species data are pooled for clarity; ± 1 SE) under establishment technique treatments of control, plastic tree guards, and shadecloth tree guards at preplanting (10 May 2005) in winter (24 May 2005), in spring (20 October 2005), and at the end of summer (4 March 2006).

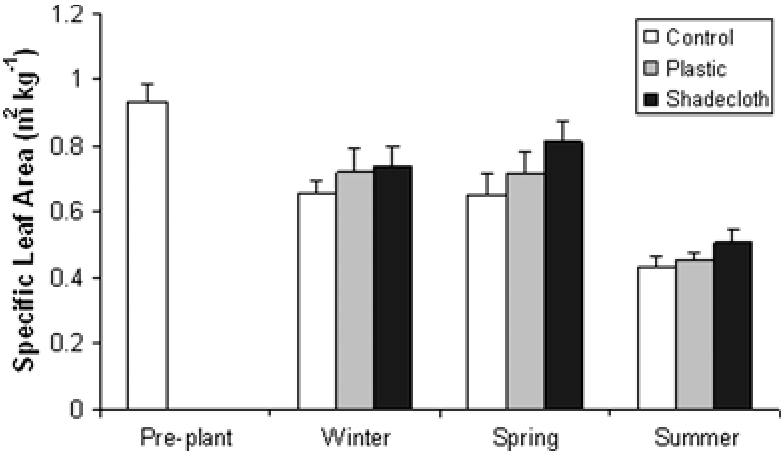

Table 1. PAR (400–750 nm; ± 1 SE) measured in winter (May 2005) and spring (October 2005) simultaneously with gas exchange by the quantum sensor of the CIRAS-2 infrared gas analyzer, and average maximum (*n*= 12; ± 1 SE) and absolute maximum temperature measured at 0.15 m above soil level from 27 October 2003 to 29 January 2004 with a TinyTag temperature probe and data logger for control, plastic, and shadecloth tree guard treatments.

	Control	***Plastic Guard***	***Shadecloth Guard***
Winter PAR	1,030 ± 152	551 ± 104	416 ± 83
Spring PAR	1,540 ± 99	683 ± 140	532 ± 113
Average maximum temperature (°C)	33.7 ± 0.5	40.4 ± 0.6	32.3 ± 0.5
Absolute maximum temperature (°C)	47.9	53.5	46.5

Table 2. Mean mortality (%) and height (cm) of *Eucalyptus gomphocephala*, *Banksia attenuata*, *E. marginata*, and *E. rudis* seedlings under control, plastic tree guard, and shadecloth tree guard treatments of the 2005 ecophysiology trial at Camel Lake (*n*= 3 plots, 20 seedlings per plot; ± 1 SE).

	Control	***Plastic***	***Shade***	***$F_{[2,6]}$ Value***	***p Value***
Mortality					
E. gomphocephala	23.3[a]± 10.1	30.0[a]± 7.6	5.0[a]± 2.9	2.923	0.130
B. attenuata	43.3[a]± 14.8	41.7[a]± 10.1	20.0[a]± 8.7	1.273	0.346
E. marginata	31.7[a]± 15.9	46.7[a]± 13.0	10.0[a]± 5.8	2.141	0.1987
E. rudis	81.7[a]± 10.9	93.3[a]± 4.4	88.3[a]± 3.3	0.491	0.6347
Height					
E. gomphocephala	61.5[a]± 0.8	63.4[ab]± 1.6	68.9[b]± 2.6	4.674	0.0598
B. attenuata	26.6[a]± 1.0	27.8[a]± 1.2	35.0[b]± 0.4	25.159	0.0012
E. marginata	42.1[a]± 1.0	44.6[ab]± 1.1	46.8[b]± 0.1	7.310	0.0246
E. rudis	68.4[a]± 2.5	54.2[a]± 1.2	67.6[a]± 7.6	1.834	0.2527

Superscript letters indicate significant differences within species.