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WIND AFFECTS MORPHOLOGY, FUNCTION, AND CHEMISTRY OF EUCALYPT TREE SEEDLINGS

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Wind is a powerful abiotic influence on plants that is predicted to increase with global warming. The resulting changes to plant function and interaction with herbivores are likely to have significant ecological, forestry, and agricultural consequences. We used a glasshouse manipulative study to test the effects of wind exposure on a range of morphological, functional, and chemical characteristics of seedlings of *Eucalyptus tereticornis*, a widespread coastal tree. Chronic wind exposure (6 wk of 3 h d^{-1}) resulted in reduced height growth and leaf area, thicker leaf cuticle, slightly higher leaf dry matter, and greater phenolic concentration. Chronic and acute (single 3-h pulse) exposure to wind induced greater variability in minimum epidermal water conductance. The changes that occurred to seedlings show the significance of wind as an active abiotic agent in shaping plants. The changes, particularly if they are maintained or enhanced over time, may alter rates of herbivory and have the potential to lead to cascading ecological consequences that are especially relevant as climate changes.

Keywords: abiotic factors, climate change, cuticle, growth, herbivory, phenolics.

Introduction

Wind is a powerful abiotic influence that has affected the function and evolution of plants since the colonization of land (Niklas 1998). It has been argued to have slowed ecosystem transitions in the geological time frame (Arens 2001) and has catastrophic effects on forests in an ecological time frame (Ennos 1997). It is particularly salient at present, because wind is predicted to increase, especially along coastlines, as climates change during the next century (IPCC 2007). Understanding the resulting proximal changes to plants is important not only from a fundamental ecological perspective but also because these changes are likely to have significant forestry and agricultural consequences.

Wind can influence patterns of natural, agricultural, and forestry ecosystems by modifying plant assemblages (Rae et al. 2006), crop yield (Nuberg 1998), and tree viability (Ennos 1997) and by altering nutrient input to remnant forest in agricultural landscapes (Duncan et al. 2008). Whole plants and their leaves are typically smaller and more compact in higher-energy regimes (Whitehead 1962; Ennos 1997). Leaf shape can strongly affect drag (Vogel 1989) and so may in part be an adaptation to wind.

Wind can shape whole plant and leaf characteristics by moving and distorting foliage and by altering boundary layers, leading to direct effects and induced responses. The direct consequences include mechanical damage and altered photosynthetic rates, transpiration (Koehl and Alberte 1988; Roden and Pearcy 1993*a*; Haring and Carpenter 2007), and respiration (Todd et al. 1972). These changes are a direct result not only of leaf movement (pitching and flapping) but also of changes in irradiation resulting from sunflecks (brief periods of intense light; Roden and Pearcy 1993*b*) or self-shading (Haring and Carpenter 2007). Alteration of the boundary layer affects mass transfer, hence gas exchange and thermal balance of leaves (Jones 1992). As well as these purely passive effects of wind, movement can induce short-term physiological adjustment to altered gas exchange (Caldwell 1970) and thigmomorphogenesis, morphological and physiological responses of plants to mechanical stress (Jaffe and Forbes 1993; Goodman and Ennos 1996).

Research on the effects of wind on plants has emphasized functional and/or morphological changes in response to high winds (Vogel 2009). Few studies have explored impacts of wind on plant chemistry, despite overwhelming evidence for the influence of other abiotic factors on phytochemistry. Changes in both morphology and chemistry are likely to be particularly significant in an ecological context because of the effects of these changes on herbivory and consequent cascading effects on ecological communities. Thus, differences in cuticle thickness and leaf area—both traits that may be altered by wind—are associated with different herbivore assemblages (Peeters 2002). Wind-induced enzymes in the common bean *Phaseolus vulgaris* L. enhance lignin accumulation and increase resistance to at least one arthropod herbivore and one leaf pathogen (Cipollini 1997). Short-term (9–12 d) wind-induced mechanical stress alters enzyme activity in tomato *Lycopersicon esculentum* and cucumber *Cucumis sativus* L. plants, tending to reduce relative growth rate of the invertebrate herbivore *Manduca sexta* larvae in the former and reducing reproduction in melon aphids *Aphis gossypii* in the latter (Cipollini and Redman 1999; Moran and Cipollini 1999).

Here, we aimed to test the effects of wind exposure on morphology, function, and chemistry of seedlings of a widespread, coastal eucalypt tree species *Eucalyptus tereticornis*,

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using a manipulative glasshouse study. Specifically, compared with control plants, we hypothesized the following under windy conditions. (1) Seedling height growth and leaf area would be less, a pattern seen in many other plant species (Jaffe and Forbes 1993; Niklas 1996). (2) Leaf cuticle would be thicker as an adaptive response to provide protection from mechanical damage (Grace and Van Gardingen 1996). (3) Leaf minimum epidermal conductance of water would be greater in at least some plants, because the mechanical damage by wind gusts would compromise the cuticle and perhaps stomatal closure. Although cuticles of leaves can self-repair, it is likely that the time frame of our study (6 wk) was too short for the crystalline state of the epicuticular wax to be fully formed (Knight et al. 2004). (4) Leaf soluble nitrogen would be lower and leaf soluble phenolics would be higher, because terrestrial plants often respond to wind by reducing stomatal aperture, decreasing photosynthesis (Caldwell 1970) and increasing oxidative pressure (Close and McArthur 2002).

In light of previously established relationships between leaf chemistry and herbivory, we consider our results in terms of their potential consequences on ecological interactions.

Material and Methods

Study Species, Seed Germination, and Seedling Maintenance

Eucalyptus is a diverse genus of trees (more than 700 species) that dominates most forest and woodland communities in Australia (Boland et al. 2006). For this study, we chose *Eucalyptus tereticornis* because its extensive latitudinal distribution along the coastline of eastern Australia and into New Guinea (Brooker and Kleinig 1999) makes it relevant to our broader question of the biological consequences of the predicted increase in wind associated with climate change. We used seedlings because of their relevance to plant fitness. Adult eucalypt trees are vulnerable to invertebrate and arboreal marsupial herbivores, but seedlings are also consumed by terrestrial marsupial herbivores (pademelons [genus *Thylogale*], wallabies and kangaroos [genera *Wallabia* and *Macropus*]), and herbivory can be a major cause of seedling death (Moles and Westoby 2004*a*, 2004*b*).

About 200 g of *E. tereticornis* seed (Australian Seed Company, Hazelbrook) was lightly coated in a copper oxychloride fungicide (Amgrow, Silverwater) before being surface sown into 96 plastic seed trays (350 mm × 295 mm × 50 mm) in autumn (March 9, 2006). The seed was germinated in a commercial seed raising mix (Amgrow) and allowed to grow for 1 mo in a perspex glasshouse at the University of Sydney, Camperdown campus. The glasshouse was permanently covered with 50% shade cloth (light intensity measured to be ~15% of full sunlight in spring). The temperature was set at 18°C at night and 24°C during the day.

Between April 10–17, 2006, the seedlings were transplanted into a native soil mix (Martins Soil, Sydney) and grown in individual forestry seedling tubes (50 × 50 × 123 mm) in 128 crates of 40 seedlings each at the same facility for a further 2 wk before treatments began. Plants were watered daily. Fertilizer was applied once a week at a rate of 1 tablespoon of Peter's Excel fertilizer (N : P : K 20 : 2.2 : 6.6; Scotts, Baulkham Hills) in 9 L of water among 32 seedling crates.

Experimental Design and Wind Treatments

The study was set up as a randomized block design. Seedlings (mean starting 3.5 cm height, 5.8 leaves; in crates of 40, $n = 128$ crates) were randomly and equally divided between eight blocks in the glasshouse. The density of 400 seedlings m^{-2} was low enough to minimize physical interference between plants throughout the trial, which can otherwise modify responses to wind (Retuerto et al. 1996). Plants were then randomly allocated into no wind ($n = 8$) or chronic wind ($n = 8$) treatment plots. Plots were separated by 1.85-m-high dividers made with timber frames and clear plastic sheeting.

We imposed a no wind or chronic wind treatment on seedlings for 6 wk (May 2–June 15, 2006). The no wind treatment was ambient conditions within the glasshouse, with very little air movement. We generated the chronic wind treatment using large pedestal fans (650-mm pedestal fans, Blackwoods, Sydney) applied 3 h daily, with 1 fan $plot^{-1}$ on the first speed setting of 3 m s^{-1}, measured using a 3-cup anemometer (Casella, model 1307). This speed was relatively conservative but was chosen for several reasons. It reflected monthly wind speed data at three sites around Sydney (Penrith Lakes, Holsworthy, and Horsley Park; mean annual wind speed 3.13 m s^{-1}, SD 0.18; maximum wind speed [peak at 1500 hours] 4.73 m s^{-1}, SD 0.40; Australian Bureau of Meteorology) where *E. tereticornis* occurs as a dominant species. Also, the physical bending of seedlings at 3 m s^{-1} appeared realistic without being extreme, and it enabled comparison with previous experiments (Cipollini 1997; Moran and Cipollini 1999). The meteorological data showed an afternoon peak in wind speed, so we applied the wind treatment between 1400 and 1700 hours daily. Crates were rotated weekly within plots to minimize differences between seedlings. Plants were watered daily and similarly across treatments with a handheld sprinkler. Soil was maintained around field capacity. Fertilizer was applied twice per week as described earlier.

An index of light intensity was calculated to account for spatial variation in the glasshouse, which could affect plant characteristics. This was calculated as the average of multiple measures per plot over 3 d (September 12–14, 2006), using a Li-Cor light meter (model LI-250A). We assumed that the relative difference between plots over time would be reflected by this index, even if the absolute intensity changed.

Morphological Characteristics of Plants

We quantified six morphological characteristics of plants: seedling height, number of leaves per plant, leaf area, leaf specific mass, leaf thickness, and cuticle thickness. Seedling height and the number of leaves per stem were measured ($n = 32$ per plot) at the beginning and end of the 6-wk treatment period. Seedling height was measured from the base of the stem at soil level to the base of the apical bud.

Leaf area and specific leaf mass (i.e., leaf mass area; g cm^{-2}) were determined on the third leaf pair down from the apical bud, which uses the youngest part of the plant as the reference point. We chose this set of leaves as an index for comparison between treatments because they were relatively fully developed in size but had always been produced during the time frame of the wind treatments. As a second comparison, we also measured leaf area and specific leaf mass for the leaves of the fifth paired node from the bottom of the seedling (i.e., matched for node number), which uses the oldest part of the plant as the reference point. These leaves were always below the third leaf pair down. Leaf area was measured with a flatbed scanner and the Image J image analysis program (http://rsb.info.nih.gov/ij/download). Specific leaf mass was calculated after drying the leaves that were used to measure leaf area in an oven at 70°C for 3 d before cooling and weighing.

Leaf thickness was determined from a microtome-cut transverse section ~20 μm thick, using a Carl Zeiss light microscope at ×400 magnification. Measured leaves were taken from the third leaf pair down from 1–2 plants per plot and sectioned using a freeze microtome (School of Plant Sciences, University of Tasmania). Cuticle thickness of the adaxial surface was also measured on these sections at ×2500 magnification, using a Nikon DS-L1 digital camera. We measured cuticle thickness three times on three parts per leaf, but these were averaged per plot for statistical analyses.

Leaf Minimum Epidermal Conductance to Water

To estimate the chronic and acute effects of wind, epidermal conductance at stomatal closure ($g_{\min}$) was measured gravimetrically from three treatments. One treatment was the control (no wind), the second was a test of acute effects (acute wind), and the third was the chronic wind treatment. This acute effect involved moving one plant per block from the no wind controls into the chronic wind blocks on the last day of the 6-wk treatment period so that they were exposed to the last 3-h application of wind. Immediately after this exposure, $g_{\min}$ was measured on all treatments.

The measurements were made on one leaf from one plant from each of the eight no wind plots ($n = 8$) and two plants from each of the eight chronic wind plots, as well as the eight acute wind plants. The leaf was one of the leaves from the third leaf pair from the top, making the results directly relevant to the cuticle thickness data. The leaf was carefully excised and its petiole sealed with Vasoline, taking care to minimize damage from handling. The leaf was then placed in an open-topped wire frame, which was weighed every 40 min over a 9-h period. Time, temperature, and relative humidity were recorded at each interval and $g_{\min}$ calculated following the method of Jordan and Brodribb (2007), which involves graphically identifying the inflection point at which conductance stopped decreasing rapidly. This inflection point is inferred to be the point of stomatal closure. The $g_{\min}$ measured at stomatal closure represents the sum of the conductance through the cuticle and residual conductance through stomata (stomatal incompetence). It is not possible to discriminate between these components of $g_{\min}$ with these methods because leaves of *E. tereticornis* have stomata on both surfaces.

Chemical Characteristics of Leaves

Fifty plants from each plot were randomly sampled June 14–15, 2006, for quantification of plant primary and secondary chemistry. Standard biochemical and gravimetric assays were used to quantify leaf chemistry. All leaves were cut from the stems at the petiole and mixed well. Two grab samples were dried for 3 d in an oven at 55°C and then ground in a ball mill (Retsch MM301, Haan) and stored in a desiccator.

Dry matter (as a percent of fresh mass) was quantified by weighing the grab sample of leaves per plot before (fresh mass) and after (dry matter) drying as described above. Amino acids (an index of total nitrogen) were quantified using a ninhydrin assay (Starcher 2001). Five milligrams of each sample were hydrolyzed in 500 μL of 6 N HCl at 100°C for 24 h before cooling and evaporating off the HCl in a concentrator (Christ, Osterode). The samples were then redissolved in 1 mL of distilled water, vortexed, and centrifuged down. The extracted amino acids were then assayed against a bovine serum albumin standard (Sigma-Aldrich) that had been similarly hydrolyzed. Soluble carbohydrates were extracted from 20-mg leaf samples in 0.1 M H_2SO_4 for 1 h in a heat bath at 100°C following Smith et al. (1964). Extracts were then quantified against a glucose standard by colorimetric determination following the phenol-sulfuric acid assay of Dubois et al. (1956).

Total soluble phenolics were extracted in 70% acetone following Hagerman (1988) and quantified using the colorimetric Prussian blue assay of Price and Butler (1977), as modified by Graham (1992). Samples of 20 mg were extracted with 1 mL 70% acetone four times. After each addition of acetone, the samples were sonicated for 30 min and centrifuged. The supernatants of each extraction per sample were combined and an aliquot assayed against a gallic acid (product G7384–100G, Sigma-Aldrich) standard.

Total fiber was measured gravimetrically as neutral detergent fiber (van Soest et al. 1991; van Soest and Wine 1967) on 50-mg samples after preextraction of total phenolics. Five milliliters of neutral detergent solution were added to preextracted sample in a test tube and heated for 3 h at 120°C. Samples were centrifuged and the neutral detergent solution decanted. Samples were then washed nine times with distilled water heated to 90°C, centrifuged, and the water removed. Following this, samples were washed twice with 100% acetone, dried in an oven at 100°C overnight, and cooled to room temperature before weighing. Results are presented proportional to dry matter (g dry matter^{-1}) and leaf area (g cm^{-2}).

Statistical Analyses

For the morphological and chemical characteristics (dependent variables), univariate analyses were conducted using the general linear model procedure in SAS (PROC GLM; SAS Institute 2003). The model included light index (covariate), block, and wind as independent variables. Residuals were checked for normality and homoscedacity, and no transformations were necessary. The change in height data was tested with and without one block (an apparent outlier with considerably faster growth), but the patterns and significance of factors were similar. Data are presented as least squares means ± 1 SE.

The effects of wind damage on minimum water loss may be indicated by increased variability associated with a higher incidence of high values of minimum epidermal conductances. Bartlett's test of homogeneity of variances was therefore used to test for differences in variance between treatments (Sokal and Rohlf 1995). Mean scores for treatments were also compared using a randomization test (Manly 1997). Both analyses were performed with macros specially written in SAS (ver. 9.1; SAS Institute 2003).

Results

Morphological Characteristics of Plants

Neither height nor number of leaves was significantly different between treatment groups at the beginning of the experiment ($P = 0.1131$ and 0.6222, respectively). Seedlings grew 32% taller in the no wind than in the chronic wind treatment over the 6-wk experiment (fig. 1*a*; $F_{1,6} = 27.98$, one-tailed $P = 0.0009$), with mean increases in height of 5.0 and 3.8 cm, respectively. The number of leaves per plant did not differ between treatments at the end (fig. 1*b*; wind effect $F_{1,6} = 0.95$, $P = 0.3669$).

Leaf area (third leaf pair from top) was 32% greater in the no wind than in the chronic wind treatment after the 6-wk experiment (fig. 1*c*; wind effect $F_{1,6} = 4.60$, one-tailed $P = 0.0379$) and 31% greater in the no wind than in the chronic wind treatment for the fifth leaf pair from the bottom (wind effect $F_{1,6} = 5.61$, one-tailed $P = 0.0278$). Specific leaf mass did not differ between treatments (third leaf pair from top [fig. 1*d*]; wind effect $F_{1,6} = 2.17$, $P = 0.1910$; fifth leaf pair from the bottom; wind effect $F_{1,6} = 2.85$, $P = 0.1593$).

Leaf thickness (third leaf pair from top) did not differ between treatments (fig. 1*e*; wind effect $F_{1,6} = 0.49$, $P = 0.5081$), but leaf cuticle was 68% thicker in the chronic wind than in the no wind treatment (fig. 1*f*; wind effect $F_{1,6} = 157.39$, one-tailed $P < 0.0001$).

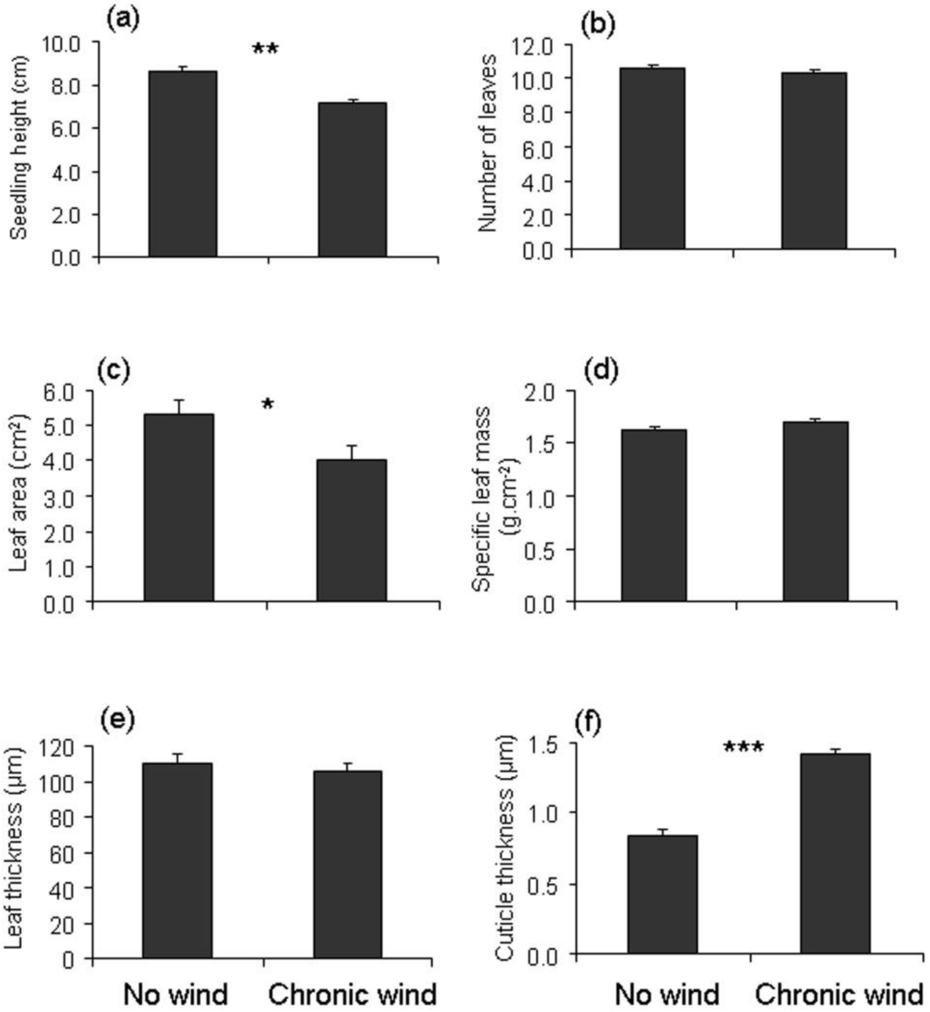

Fig. 1 Morphological characteristics of *Eucalyptus tereticornis* seedlings as a function of wind treatment after a 6-wk exposure. *a*, Seedling height. *b*, Number of leaves. *c*, Leaf area. *d*, Specific leaf mass. *e*, Leaf thickness. *f*, Cuticle thickness. One asterisk, $P < 0.05$; two asterisks, $P < 0.01$; three asterisks, $P < 0.0001$. Values are least squares means + SE.

Leaf Minimum Epidermal Conductance to Water

Plants exposed to chronic wind conditions over 6 wk had much greater variability in minimum epidermal conductance ($g_{\min}$) than those in no wind conditions, with acute wind conditions intermediate ($\sigma^2 = 28.63$ for chronic wind plants, $\sigma^2 = 3.33$ for acute wind plants, $\sigma^2 = 0.24$ for No wind plants; fig. 2). All three variances were significantly different from each other ($P < 0.01$). From the distributions, it is clear that this was due to very high $g_{\min}$ in some but not all of the wind-treated plants: all three treatments arise from similar baselines, but the upper tails for acute wind– and especially chronic wind–treated plants are inflated. The median score for acute wind–treated plants was significantly higher than that for no wind plants ($P < 0.05$), and those for chronic wind plants were marginally higher than those for no wind plants ($P = 0.09$).

Chemical Characteristics of Leaves

There was a small (4%) but statistically significant increase in leaf dry matter in the chronic wind than in the no wind treatment over the 6-wk experiment (fig. 3*a*; wind effect $F_{1,6} = 10.17$, one-tailed $P = 0.0095$). Amino acids (fig. 3*b*; wind effect $F_{1,6} = 1.61$, $P = 0.2513$), soluble carbohydrates (fig. 3*d*; wind effect $F_{1,6} = 0.18$, $P = 0.6897$), and fiber as a proportion of dry matter (fig. 3*e*; wind effect $F_{1,6} = 1.52$, $P = 0.2641$) or in relation to leaf area (fig. 3*f*; wind effect $F_{1,6} = 0.19$, $P = 0.6797$) did not differ between the chronic wind and the no wind treatments. In contrast, total phenolic concentration was 7% higher in the chronic wind than in the no wind treatment (fig. 3*c*; wind effect $F_{1,6} = 4.02$, one-tailed $P = 0.0459$).

Discussion

Wind-Induced Morphological, Functional, and Chemical Characteristics of Plants

The changes that occurred to *Eucalyptus tereticornis* seedlings as a result of wind confirm its significance as an active abiotic agent in shaping plants, since wind reduced the size of both whole plants and leaves, induced thickening of leaf cuticle, and increased the leakiness of leaves. Wind also altered leaf dry matter and phenolic concentration.

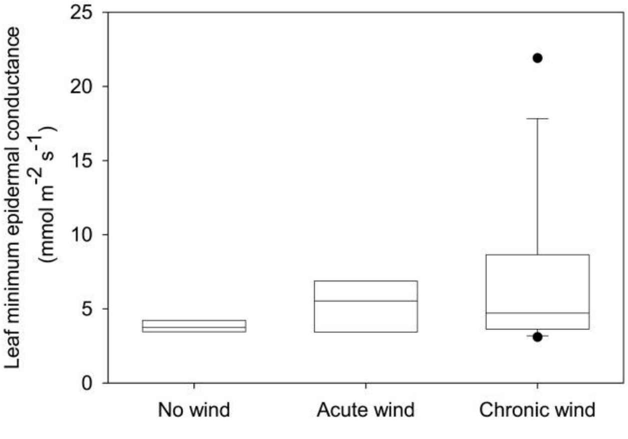

Fig. 2 Box plots of leaf minimum epidermal conductance from *Eucalyptus tereticornis* seedlings exposed to no wind, acute wind, and chronic wind conditions. Horizontal line within the box, median; box, twenty-fifth and seventy-fifth percentiles; whiskers, tenth and ninetieth percentiles; circles, outliers.

At the whole plant level, the reduced height growth in the chronic wind treatment was consistent with our expectations. Although this reduced height growth could involve lower productivity in chronic wind, the fact that number of leaf pairs did not decrease implies a thigmomorphogenetic response. Reduction in internode length is typical of thigmomorphogenesis (Liu et al. 2007), regardless of whether it is associated with reduced growth (e.g., Whitehead 1962) or not (e.g., Niesenbaum et al. 2006).

The substantial increase in cuticle thickness in chronic windy conditions is consistent with its role in reducing mechanical damage and so could be argued to be an adaptive response. While the cuticle was thicker (1.4 cf. 0.8 μm), in absolute terms it was still quite thin, less than half the thickness of cuticle in juvenile leaves and less than 20% of that in adult leaves of *Eucalyptus nitens* saplings grown in the field (Loney et al. 2006). This could be due to differences in developmental stage of the plant and the relatively unstressed, low-light growing conditions in our experiment, since leaf cuticle is usually thinner in shade than in sunny conditions (Osborn and Taylor 1990; Ashton and Berlyn 1992). The difference in cuticle thickness between our chronic wind and no wind conditions is unlikely to be the consequence of differences in developmental age of the leaves, even though thickness can increase for an extended period after leaves are fully expanded (G. J. Jordan, unpublished data). The similar rates of accumulation of leaf pairs, implied by figure 1*b*, suggest that both chronic wind and no wind leaves were of similar absolute and developmental ages. Although there is little relationship between cuticle thickness and cuticular permeability at the interspecific level (Riederer and Schreiber 2001), it is possible that within-species variation in cuticle thickness influences cuticular permeability (e.g., Ristic and Jenks 2002), especially in cuticles as thin as those observed here. This is because cuticles are compound structures, with the resistance to conduction of water primarily residing in a thin outer layer (the cuticle proper; Jeffree 2006; Schreiber 2006). The cuticle proper is often of similar thickness to the cuticle thicknesses observed in our experiment (Jeffree 2006), implying that the thicker cuticles in wind-exposed plants may be associated with thicker waterproof layers.

The patterns in leaf minimum epidermal conductance ($g_{\min}$), across treatments are entirely consistent with stochastic damage caused by wind. The increased variance observed in the acute wind compared with the no wind treatment is most simply interpreted as the result of some leaves being damaged (and thereby "leaking" more water) and not others. The even higher variance in the chronic wind treatment strengthens this argument: we would expect that cuticle of some leaves would be damaged repeatedly, giving them very high conductance, but some may have remained undamaged. That many of the leaves sampled from chronic wind exposure showed high $g_{\min}$ highlights the ineffectiveness of the induced thicker cuticle in these leaves to protect against water loss. In spite of the capacity of cuticles to self-repair (Riederer and Schreiber 2001), accumulated damage over a leaf's lifetime can significantly increase

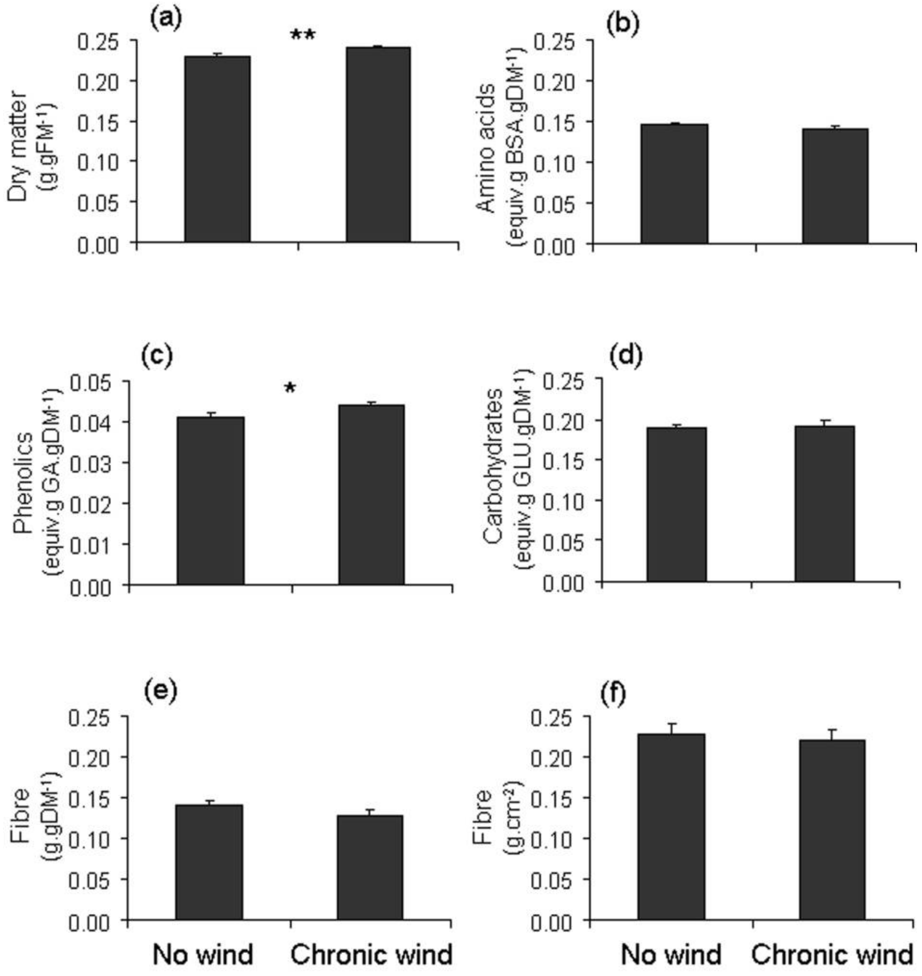

Fig. 3 Chemical characteristics of *Eucalyptus tereticornis* leaves as a function of wind treatment after a 6-wk exposure. *a*, Dry matter. *b*, Amino acids. *c*, Total phenolics. *d*, Soluble carbohydrates. *e*, *f*, Fiber. One asterisk, $P < 0.05$; two asterisks, $P < 0.01$. Values are least squares means + SE.

both g_{min} and astomatal cuticular conductance (Jordan and Brodribb 2007).

The reduced leaf area and slightly higher dry matter content in windy conditions may reflect effective acclimation or may simply be passive consequences of wind. Potential adaptive advantages of smaller leaves include reduced biomechanical stress resulting from lower leverage under wind shear; better heat shedding and therefore lower water demand (Givnish 1979); and faster leaf expansion, which reduces the duration of a vulnerable period for the leaf (Moles and Westoby 2000). However, most studies indicating adaptive effects of leaf size have been based on considerably larger differences in leaf size than those observed changes in this study. Smaller leaves may therefore simply reflect decreased leaf expansion as a result of a leaf water deficit. Slightly higher dry matter content without increasing specific leaf mass could similarly reflect greater water deficit in chronic wind leaves as a result of the greater leakiness of the damaged leaves.

The chemical changes to leaves in windy conditions were relatively subtle. The lack of change to the concentration of amino acids and fiber contrasted with our expectations. Partitioning nitrogenous compounds into Rubisco, free amino acids, and others may elucidate any more subtle changes that may have occurred. It is possible that leaves of young seedlings do not alter fiber allocation because they are constrained by rapid plant growth requirements (Read et al. 2003) along with relatively short leaf life span. These results, along with the lack of difference in soluble carbohydrates, suggest a lack of substantial change to primary biochemical processes in response to the conditions we imposed.

The small increase in soluble phenolics is the first empirical demonstration of such a change in response to wind. Other studies examining chemical responses have quantified elemental changes (e.g., carbon; Niesenbaum et al. 2006) or leaf enzymes and lignin (Cipollini 1997; Cipollini and Redman 1999). Our result is consistent with the concept that phenolics, as antioxidants, increase to minimize oxidative pressure that otherwise leads to photodamage (Close and McArthur 2002) and that can occur as a result of a range of abiotic factors, potentially including wind. The absolute phenolic levels were relatively low, however, presumably because of the high-nutrient and low-light conditions in the glasshouse (Lawler et al. 1997). Higher phenolic levels and possibly greater difference between treatments may occur in plants grown in wind for longer, particularly in higher-light conditions.

Ecological Consequences

Phenotypic changes to plants may be relaxed if plants are no longer exposed to wind (Retuerto and Woodward 2001). However, under sustained windy conditions, the patterns of morphological and chemical change that we found for *E. tereticornis* seedlings—particularly if they persist or are even enhanced in the longer term—may affect rates of herbivory and therefore have ecological implications beyond the direct wind-plant interaction. Interestingly, conflicting predictions arise from the patterns we found. Reduced growth rates should extend the period of vulnerability of seedlings to terrestrial mammalian herbivores, but increased phenolics (at higher concentrations than we found) can reduce palatability (O'Reilly-Wapstra et al. 2005). The influence of leaf chemistry on intake can be determined from experiments with captive herbivores, but the net outcome of these two characteristics—vulnerability to being visited plus palatability once there—need to be determined from field studies. Presumably, the impact of any vulnerability to browsing is outweighed by the benefits of reduced wind damage resulting from the more aerodynamic profile of compact plants grown under wind conditions. Changes in cuticle thickness may also have ecological consequences. Since the cuticle provides a physical barrier against pathogens and small herbivores (Riederer 2006), increased thickness may alter the heterotrophic communities associated with plants. This could be particularly significant in cases of plant species with relatively thick cuticles if wind induces a proportional increase in thickness to that observed here. Certainly, among-species comparisons have demonstrated such differences in invertebrate herbivore communities associated with leaf cuticle thickness (Peeters 2002).

Many abiotic factors, including sunlight, water availability, and soil nutrients, can have profound effects on ecosystems, resulting in dramatic shifts in plant and animal communities. Their influence extends far beyond the morphological, functional, and chemical responses of plants and beyond the interaction between plants and herbivores. Given the effects of wind on plant characteristics demonstrated here and in other studies, combined with the known influence of these characteristics on herbivory, the ecological consequences of wind may also be profound and far reaching. The predicted increase in coastal winds with climate change adds a complexity that deserves attention, not only from a fundamental perspective but also because it has consequences for crop production via altered plant growth rates and resistance to pests.

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