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A multistressor, multitrait approach to assessing the effects of wind and dust on *Eucalyptus tereticornis*¹

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PREMISE OF THE STUDY: Plants are routinely subjected to multiple environmental stressors, and the ability to respond to these stressors determines species survival and ecological breadth. Despite stressors such as wind and dust significantly influencing plant development, morphology, and chemistry, the combined influence of these factors is yet to be investigated.

METHODS: We used a manipulative glasshouse approach to compare the morphological, physiological, and biomechanical responses of *Eucalyptus tereticornis* to the independent and combined effects of wind and dust.

KEY RESULTS: Wind decreased both *E. tereticornis* height and stem flexural stiffness. Additionally, wind had no effect on leaf physiology, nor did dust have any significant effect on any of the traits measured.

CONCLUSIONS: Our results suggest that wind and dust in combination may have an additive effect on several plant traits and provide new insight into the effects and importance of studying wind, dust, and different stress combinations.

KEY WORDS dust; flexural stiffness; height; leaf biomass; multistress; Myrtaceae; photosynthesis; stem diameter; transpiration; wind

In nature, organisms encounter a multitude of natural and anthropogenic stressors simultaneously. The ecological response to these stressors can be positive or negative and will ultimately influence species abundance, survival, growth, and reproduction (Côté et al., 2016; Teichert et al., 2016). Although we generally assume the impact of multiple stressors is an additive accumulation of the impacts of each separate stressor (Crain et al., 2008), the cumulative effects of stressors can be additive, synergistic, or antagonistic (Folt et al., 1999). Multiple stressors can intensify negative impacts when acting in combination (e.g., synergistic effect). For example, UV radiation substantially increases the negative effects of anthropogenic pollutants including polyaromatic hydrocarbons (Steevens et al., 1999). However, multiple stressors may also have antagonistic impacts, such as when water pollution reduces the effects of a second stressor including oxygen depletion (Teichert et al., 2016). Given the diversity of stressor combinations that co-occur in nature and our limited understanding regarding the frequency of additive, synergistic and antagonistic interactions among stressors

(Côté et al., 2016), it remains difficult to predict the ecological impact multiple stressors may have.

Wind and dust are two stressors whose combined influence should be investigated. Despite being underestimated for their ecological importance, both factors significantly disturb the physical and biological environment, affecting nutrient cycling, species interactions and ultimately species mortality (Barton, 2014; Smith and Ennos, 2003; Field et al., 2010). For terrestrial plants, wind and dust are particularly important because as independent stressors they inhibit development and reproductive yield and alter morphology and leaf chemistry (Borka, 1984; Cleugh, 1998; Cleugh et al., 1998; Hirano et al., 1995). Because wind can significantly affect the occurrence and concentration of ambient dust, these factors have huge potential to act as a stress combination in nature. Furthermore, unlike temperature, UV radiation, and pollution, wind and dust has been ignored in multistress research.

Wind mechanically stimulates plants and induces a suite of morphological and developmental responses, which include reduced height, aboveground biomass, and leaf area and increased cuticle thickness, leaf toughness, and stem diameter and flexibility (Cordero, 1999; Anten et al., 2005, 2010; Kern et al., 2005; McArthur et al., 2010). In addition to changing morphology, wind also decreases boundary layer thickness and leaf temperature, factors

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that influence the amount of carbon dioxide available to photosynthetically active tissue and ultimately decrease rates of photosynthesis. (Cordero, 1999; Smith and Ennos, 2003; Wadsworth, 1959).

Dust is emitted from artificial and natural processes including industrial processing, road traffic, and suspension of weathered rock and soil. A combination of wind, rain, and gravity transports and deposits dust on vegetation and soil surfaces. Deposition on vegetation is spatially heterogenous, with significantly more dust depositing on abaxial compared with adaxial surfaces (Tomašević et al., 2005). Once deposited, dust can physically block the stomata of plants, shade leaves, increase leaf temperature, and degrade cuticular waxes (Borka, 1984; Eveling and Bataillé, 1984; Hirano et al., 1995; Thompson et al., 1984). Consequently, dust deposition can decrease photosynthesis and increase transpiration. The elemental composition of deposited dust can influence the concentrations of heavy metals (e.g., Pb, Mn) and nutrients found on leaf surfaces and in soil, which if taken up into plant tissue may alter the development or morphology of plant stems and reproductive structures (Borka, 1984).

We investigated the impacts of wind and dust independently and in combination on *Eucalyptus tereticornis* morphology, physiology, and biomechanics. We asked the question: Do wind and dust stresses have additive, synergistic, or antagonistic impacts? Or in other words, are the effects of wind worse or reduced in the presence of dust? Because *E. tereticornis* has traits that enhance wind drag (e.g., large leaves) and wind drag may influence several morphological and biomechanical characteristics (Vogel, 1989), we predicted a significant number of traits to differ between wind and control treatments.

MATERIALS AND METHODS

Study species and seedling purchase—*Eucalyptus tereticornis* Sm., in the subgenus *Eucalyptus* (Brooker, 2000) is a broadly distributed tree species endemic to and occurring along the coastline of eastern Australia (Boland et al., 2006). It can grow between 20 m and 50 m high, is up to 2 m in diameter at breast height (dbh), and at maturity, leaves are 10–20 cm long, 1–3 cm wide, and waxy. Its latitudinal distribution combined with its common occurrence along roads (R. J. Leonard, personal observation) predisposes it to a range of wind and dust regimes. We obtained ~100 8-mo-old seedlings of *E. tereticornis* from Greening Australia, Richmond Production Nursery on the 15 November 2012. All seedlings were sourced from Camden provenance seed and maintained at 25°C ± 2°C, natural light conditions (LD ~14 h light/10 h dark) and 65% relative humidity at the University of Sydney.

Seedling maintenance—We transplanted 96 *E. tereticornis* seedlings into individual pots using native soil mix (Osmocote Professional Native potting and planting mix; Scotts, Marysville, Ohio, USA) and grew seedlings for 1 wk under glasshouse conditions before starting treatments. For the duration of the experiment, we applied water directly to the soil layer to avoid washing particles from leaf surfaces.

Experimental design—We set the study up as a randomized block design, with six treatment blocks and 16 seedlings per block. Within each block, we allocated four individuals to one of four treatments: (1) wind with dust, (2) wind without dust, (3) no-wind with dust, or

(4) no-wind without dust. We used a seedling density of ~8 seedlings per square meter to limit possible density-dependent effects of wind or dust on plant traits (Retuerto et al., 1996). Plots (treatments within blocks) and blocks were separated by ~0.8 m high dividers made with bamboo frames and clear plastic sheeting. We imposed wind and/or dust treatments on seedlings for 8 wk, from 26 November 2012 to 21 January 2013. Every second day, we rotated pots by 45° about their axes to ensure that plants received airflow from all directions. We also moved plants within their rows to ensure that each wind-blown plant was subjected to a similar mean wind speed. To eliminate potential shading or temperature differences inherent in the glasshouse, we shifted blocks once weekly.

Wind and dust manipulation—We imposed two levels of wind (presence/absence) and two levels of dust (presence/absence) treatment on *E. tereticornis* seedlings. The no-wind treatment was ambient conditions within the glasshouse (i.e., very little air movement). The wind treatment was generated using pedestal fans (diameter: 350 mm pedestal fans; Blackwoods, Sydney, Australia) applied 3 h daily between 13:00 and 16:00 hours using one fan per block on the third speed setting of ~3 m·s⁻¹. We used this wind speed and exposure time because it reflected wind speed and wind peak data in areas where *E. tereticornis* are dominant (McArthur et al., 2010). To eliminate any effect of the fan, we rotated fans daily.

For the dust treatment, we prepared artificial dust from soil samples collected at eight sites in the Greater Sydney Region. From each site, we collected duplicate samples of the top 5 cm of soil. To prepare dust, we first oven-dried soil for 48 h. We then ground the samples using a mortar and pestle and finally passed them through metal sieves until particles were <100 μm. This process meant artificial dust was within the same size range as dust encountered in the field (R. J. Leonard, The University of Sydney, unpublished data). Based on upper limits of leaf dust deposition in representative Australian flora (R. J. Leonard, unpublished data), we applied 0.02 ± 0.005 g dust to each plant daily at ~1610 h for the duration of the experiment. We used metal sieves (retention size < 100 mm) to apply dust from a height of 10 cm above each plant.

Morphological characteristics—Before starting the treatments, we recorded seedling height, branch number, and leaf number for each plant. We also recorded petiole length and leaf length on six plants per treatment, taking measurements on leaf pairs at the third and fourth node. At the end of 8 weeks, we recorded these same six variables, as well as, whole plant leaf biomass and root biomass on six plants per treatment. We took seedling height as the distance from the soil surface to the base of the apical bud and determined leaf length and petiole length on the third leaf pair down from the apical bud. We also noted any seedling mortality.

Biomechanical characteristics—To measure stem flexibility, we calculated flexural stiffness (defined as EI in N·m², where E is Young's modulus and I is the area moment of inertia,) using a three-point bending test on six plants per treatment (Anten et al., 2005). In each case, we used the lower half of the stem because older tissue is more important for stability and its thigmomorphogenetic responses to wind are weaker than in younger tissue (Chehab et al., 2009). We cut all stem sections ~20 cm long, starting 20 cm below the third node to ensure that stem sections were approximately uniform in diameter. We removed leaves before measurements and

completed all measurements within 20 min of cutting stems. To determine EI, we rested stems on two support clamps padded with styrofoam and measured the distance between clamps (L). We then placed an empty water bottle halfway along the stem section, weighed $100 \times g$ of water (F) and added this to the bottle. We measured the vertical displacement of stem sections (y) from photographs taken before and after the water (force) was added to the stem using the ImageJ analysis program (National Institutes of Health, Bethesda, Maryland, USA; <http://rsb.info.nih.gov/ij/download>). We calculated EI, using the equation (Hibbeler, 2011):

$$EI = \frac{FL^3}{48y}$$

where EI ($N \cdot m^2$) is flexural stiffness, F is the force applied in Newtons, L is the distance in meters between supports, and y is the deflection in meters.

Physiological characteristics—We measured leaf physiological traits (leaf photosynthesis, transpiration, stomatal conductance, and intracellular CO_2 concentration) using a portable, open-flow gas exchange system LI-6400 (Li-Cor, Lincoln, Nebraska, USA). For each plant, we measured two leaves. Due to damage in some leaves, we took measurements on either the third, fourth, or fifth leaf below the youngest expanded leaf. We measured six plants per treatment combination daily, starting ~11:00 hours, between 14 to 21 January 2013. For each measurement, we set the photosynthetically active photon flux density to $2000 \mu mol \cdot m^{-2} \cdot s^{-1}$, equivalent to a sunny day (Ying et al., 2002). To minimize the system response time to a change in leaf exchange rate and to mimic ambient temperature and CO_2 concentration in the glasshouse, we set the flow rate of air through the chamber and sample-side infrared gas analyzer (IRGA) to $500 \mu mol \cdot s^{-1}$, maintained the leaf temperature at $26^\circ C$ and kept intake air at 400 ppm (Ying et al., 2002).

Statistical analyses—We used a factorial multivariate analysis of variance (MANOVA) to assess differences in variables between treatments. Upon testing MANOVA assumptions, we found one

key requirement was violated—several of the dependent variables were not moderately correlated (e.g., $0.2 < \text{Pearson's } r < 0.9$) and in some cases not correlated at all (e.g., Pearson's $r < 0.1$) (Field, 2009). To ensure the assumption of at least moderate correlation between dependent variables was not violated, we used Pillai's trace (V) because it is robust to multicollinearity violations (Field, 2009) and conducted only MANOVAs on dependent variables that were moderately correlated (Pearson's $r > 0.2$). In total we conducted three separate MANOVAs: (1) whole-plant traits including height change, basal diameter, branch number, and root biomass; (2) leaf traits including petiole length, leaf biomass, leaf number and leaf length; and (3) physiological traits including photosynthesis, transpiration, stomatal conductance and intercellular CO_2 . To assess differences in treatment groups for flexural stiffness and for posthoc MANOVA analyses, we used factorial analyses of variances (2-way ANOVAs). Since leaf physiological measurements were done in duplicate, we used the average values for each plant in the statistical analyses. For all analyses, we used the statistical package SPSS version 21 (SPSS, Chicago, Illinois, USA) and data were transformed to conform to homogeneity of variance where necessary.

RESULTS

We found a significant main effect of wind but not dust on the whole-plant category (wind: $V = 0.50$, $F_{4,17} = 4.22$, $P = 0.02$; dust: $V = 0.28$, $F_{4,17} = 1.61$, $P = 0.22$; interaction: $V = 0.20$, $F_{4,17} = 1.06$, $P = 0.41$; Table 1). Within this category, wind treatment only affected plant height ($F_{1,92} = 6.38$, $P = 0.01$; all other traits $P > 0.05$). At the end of the treatment, wind-exposed individuals had grown significantly less than their nonwind counterparts (Fig. 1). Although the change in height for plants growing in the wind and dust treatment suggested an antagonistic effect of the two factors in combination, we found no significant interaction ($F_{1,92} = 0.02$, $P = 0.89$).

We found no significant main effect of wind or dust on leaf (wind: $V = 0.16$, $F_{4,17} = 0.78$, $P = 0.55$; dust: $V = 0.14$, $F_{4,17} = 1.27$, $P = 0.32$) or physiological (wind: $V = 0.06$, $F_{4,17} = 0.25$, $P = 0.90$; dust: $V = 0.14$, $F_{4,17} = 0.68$, $P = 0.62$) categories.

We found a significant main effect of wind ($F_{1,16} = 22.34$, $P < 0.001$) but not dust ($F_{1,16} = 0.51$, $P = 0.48$) on flexural stiffness

TABLE 1. Mean (\pm SE) values for traits of *Eucalyptus tereticornis* seedlings grown in the presence or absence of wind (+W, -W) and/or dust (+D, -D).

Characteristic	+W, +D	+W, -D	-W, +D	-W, -D
Whole plant				
Δ Height (cm)*	34.52 ± 2.85	27.33 ± 2.11	39.77 ± 2.33	33.37 ± 2.11
Basal diameter (cm)	0.80 ± 0.04	1.04 ± 0.29	0.74 ± 0.03	0.71 ± 0.04
Branch number	7.25 ± 0.58	5.92 ± 0.68	6.75 ± 0.98	6.75 ± 1.38
Root biomass (g)	23.07 ± 2.67	22.89 ± 2.23	19.00 ± 3.53	29.95 ± 4.81
Petiole length (cm)	1.31 ± 0.17	1.58 ± 0.11	1.60 ± 0.19	1.67 ± 0.18
Mechanical				
Flexural stiffness ($N \cdot m^2$)	0.0027 ± 0.0005	0.0027 ± 0.0005	0.0086 ± 0.0031	0.0114 ± 0.0022
Leaf				
Leaf biomass (g)	18.64 ± 1.41	15.91 ± 1.36	17.64 ± 1.99	16.71 ± 0.93
Leaf number	63.21 ± 4.44	57.21 ± 8.08	59.95 ± 1.89	68.00 ± 5.27
Leaf length (cm)	8.70 ± 0.97	9.33 ± 0.69	10.31 ± 0.56	10.10 ± 1.00
Physiological				
Photosynthesis ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	8.08 ± 0.35	7.36 ± 0.55	7.64 ± 0.19	7.84 ± 0.38
Transpiration ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	2.77 ± 0.24	2.61 ± 0.30	2.76 ± 0.17	2.41 ± 0.26
Stomatal conductance ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	0.17 ± 0.02	0.16 ± 0.03	0.16 ± 0.01	0.15 ± 0.02
Intercellular CO_2 ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	286.58 ± 7.70	289.27 ± 7.70	287.55 ± 5.41	274.34 ± 11.01

* Significant difference between treatments ($P < 0.05$).

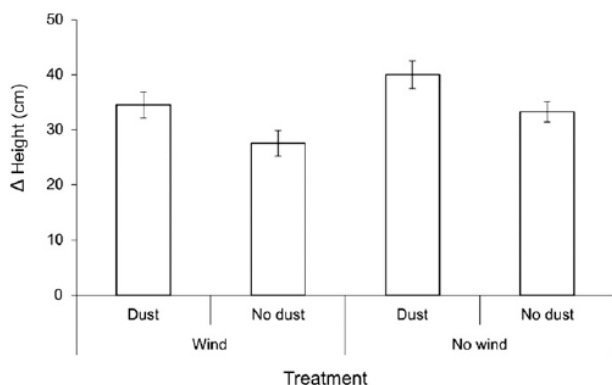


FIGURE 1 Mean (\pm SE) change in plant height for *Eucalyptus tereticornis* seedlings exposed to one of four treatment conditions: with or without wind and/or with or without dust.

(Fig. 2). Stems of wind-exposed plants were less stiff than their non-wind counterparts. For this trait, there was also no significant interaction effect ($F_{1,16} = 0.67$, $P = 0.42$).

DISCUSSION

We found a significant effect of wind but not dust on *E. tereticornis* height and flexural stiffness; wind-exposed plants were significantly smaller and their stems less stiff than control plants. These findings confirm previous work that shows that wind is an important environmental stress affecting plant morphology and mechanical behavior (Cleugh, 1998; Ennos, 1997). Additionally, our results are the first to suggest a possible antagonistic effect of wind and dust on plant height; plants exposed to the two factors grew taller than plants exposed to wind alone. This finding, however, requires further research. Ultimately, our study highlights the unpredictability of interactions among stressors and the need for additional multi-stress studies.

For the majority of traits analyzed, we found no significant difference between the independent effects of wind and dust and the

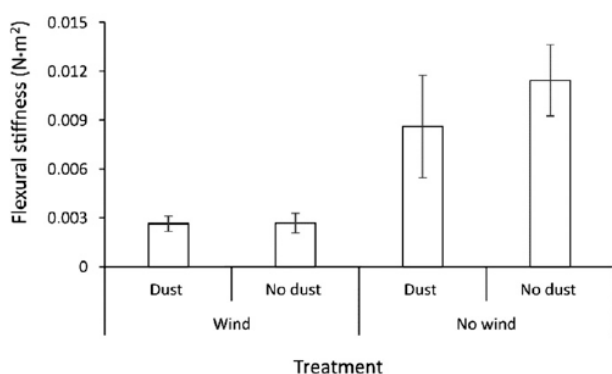


FIGURE 2 Mean (\pm SE) flexural stiffness for *Eucalyptus tereticornis* seedling stems exposed to one of four treatment conditions: with or without wind and/or with or without dust.

effects of the control treatment. Additionally, our results, with the exception of plant height, indicate that wind and dust in combination are not more stressful than either one is by itself. These findings suggest that wind and dust independently and in combination have an overall net effect of zero on the majority of plant traits quantified. Our results therefore suggest an additive effect of wind and dust on *E. tereticornis* because the product of an additive interaction between two stressors whose net independent effects are zero will also be zero (Piggott et al., 2015). Synergistic and antagonistic interactions require a net effect of -1 and $+1$, respectively, and usually a significant interaction term. Given that we found a possible antagonistic, albeit nonsignificant effect of wind and dust in combination on plant height, our results again highlight the unpredictability of interactions between stressors. Furthermore, the method we used to apply dust could have influenced our findings and possible interactions among stressors. We applied dust after wind; however, dust can also deposit on plants during wind. Although we suspect both application methods led to similar amounts of dust deposition, the possibility that they influence traits differently is an interesting question that requires further research.

Plants exposed to wind were smaller than control plants. Wind is known to reduce the height of various trees species (Smith and Ennos, 2003; Kern et al., 2005) including *E. tereticornis* (McArthur et al., 2010). Wind exposure decreased stem height but not leaf number, indicating a thigmomorphogenetic response (Niesenbaum et al., 2006).

Despite finding no statistically significant effect of dust on stem height, results suggest dust may increase plant height, but additional research is warranted (Fig. 1). We dusted plants with particulate matter containing trace metals. Plant height may be positively affected by the addition of these metals to the soil surface as demonstrated for annuals including *Phaseolus vulgaris* and *Gomphrena globosa* (Rai et al., 2010).

Notably, we found an effect of wind on flexural stiffness but not stem diameter or petiole length. Reduced flexural stiffness in wind-exposed stems meant stems were more flexible and, therefore, less prone to mechanical failure or stem breakage (Anten et al., 2010). Plants can further prevent mechanical failure by producing larger petioles, thicker stems, and smaller leaf areas, which reduce drag forces (Anten et al., 2010; Vogel, 1989). Our results did not support this. Given the inverse relationship between efficiency of water transport (particularly important in seedlings) and mechanical strength (e.g., stem thickness) (Wagner et al., 1998), we suspect there was a trade-off between the relative investment of hydraulic and mechanical tissue within *E. tereticornis* stems (Kern et al., 2005; Rowe et al., 2004). Consequently, stem thicknesses were similar between wind and non-wind treatments. Given that wind affected flexural stiffness but not stem diameter, our results suggest a potential effect on stems shape or material properties including the thickness of particular tissues which requires further research. Furthermore, although flexural stiffness was different between wind treatments, the wind speed used may not have been sufficient to create enough drag force to cause an increase in petiole length or decrease in leaf area (Anten et al., 2010). Stem, compared with leaf or petiole properties may therefore be more susceptible to the effects of the wind speed used in this study.

We also found no effect of wind on root biomass. It is possible that shorter and more flexible stems transfer a smaller bending moment to the anchorage root system; therefore, plant anchorage could be maintained without increased root biomass (Anten et al., 2006).

We found no effect of wind on stomatal conductance, transpiration, or photosynthesis. These results are consistent with physiological measurements of vegetation exposed to similar wind speeds (Retuerto and Woodward, 1992). This response could indicate *E. tereticornis* is well adapted to cope with mean wind speeds ($\sim 3 \text{ m}\cdot\text{s}^{-1}$) encountered in the field. Because leaf physiology was unaffected by the wind speed used, it would be interesting to quantify physiological responses to the maximum wind speeds encountered in the field (e.g., $>10 \text{ m}\cdot\text{s}^{-1}$).

Contrary to our expectations, we also found no effect of dust on leaf physiology. Based on this result, it is unlikely dust particles blocked stomata or entered leaf tissues and increased cell alkalinity and chlorophyll degradation (contrary to the findings of Hirano et al. [1995]). As experiments were conducted in summer, the light intensity may have been high enough to compensate for dust shading caused by dust deposition (Gale and Easton, 1979). The possibility that season or variation in climatic factors like light might influence the effect of dust again highlights the importance of multifactor studies. In addition, given that smaller dust sizes (e.g., $<10 \mu\text{m}$) typically contain chemicals capable of entering and adversely impacting plant cells (Lau and Luk, 2001; Watmough et al., 1999), we suspect the deposition of these dust sizes on leaves was not sufficient to cause changes in leaf physiology. The effects of different dust sizes on leaf physiology is an exciting avenue for future research, especially given ambient dust sizes vary according to proximity to cities, factories, and roads.

CONCLUSIONS

Studies integrating multiple stressors are necessary to further our understanding of how organisms are affected by their multivariate environment. For plants and other organisms, the interaction and effect of multiple stressors can be additive, synergistic, or antagonistic. This study highlights the complex additive and potentially antagonistic interactions that wind and dust have on *E. tereticornis*. Our findings suggest that the type of interaction between two stressors may depend on the trait analyzed, thereby highlighting the unpredictability and need for additional multistress studies. Ultimately, our findings show that for a majority of *E. tereticornis* traits wind and dust are not more stressful in combination than either one is by itself.

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AUTHOR CONTRIBUTIONS

Study conception and design: R.L., C.M., and D.H.; data acquisition, analysis, and interpretation: R.L.; manuscript draft and revision: R.L., D.H., and C.M. All authors approved the publication and have no competing interests.

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