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# The capacity to cope with climate warming declines from temperate to tropical latitudes in two widely distributed *Eucalyptus* species

JOHN E. DRAKE[1], MICHAEL J. ASPINWALL[1], SEBASTIAN PFAUTSCH[1], PAUL D. RYMER[1], PETER B. REICH[1,2], RENEE A. SMITH[1], KRISTINE Y. CROUS[1], DAVID T. TISSUE[1], OULA GHANNOUM[1] and MARK G. TJOELKER[1]

[1]*Hawkesbury Institute for the Environment, University of Western Sydney, Locked Bag 1797, Penrith, NSW 2751, Australia*
[2]*Department of Forest Resources, University of Minnesota, St. Paul, Minnesota, USA*

## Abstract

As rapid climate warming creates a mismatch between forest trees and their home environment, the ability of trees to cope with warming depends on their capacity to physiologically adjust to higher temperatures. In widespread species, individual trees in cooler home climates are hypothesized to more successfully acclimate to warming than their counterparts in warmer climates that may approach thermal limits. We tested this prediction with a climate-shift experiment in widely distributed *Eucalyptus tereticornis* and *E. grandis* using provenances originating along a ~2500 km latitudinal transect (15.5–38.0°S) in eastern Australia. We grew 21 provenances in conditions approximating summer temperatures at seed origin and warmed temperatures (+3.5 °C) using a series of climate-controlled glasshouse bays. The effects of +3.5 °C warming strongly depended on home climate. Cool-origin provenances responded to warming through an increase in photosynthetic capacity and total leaf area, leading to enhanced growth of 20–60%. Warm-origin provenances, however, responded to warming through a reduction in photosynthetic capacity and total leaf area, leading to reduced growth of approximately 10%. These results suggest that there is predictable intraspecific variation in the capacity of trees to respond to warming; cool-origin taxa are likely to benefit from warming, while warm-origin taxa may be negatively affected.

*Keywords:* acclimation, climate change, *Eucalyptus grandis*, *Eucalyptus tereticornis*, phenotypic plasticity, photosynthesis, respiration, temperature

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## Introduction

The global mean surface temperature has increased by 0.85 °C from 1880 to 2012 (Hartmann *et al*., 2013), and warming of 2–4 °C is likely to occur this century (Meinshausen *et al*., 2009; Solomon *et al*., 2009; Huntingford *et al*., 2012; Collins *et al*., 2013). Quantifying and understanding the capacity of organisms to cope with warming is important for the conservation of biodiversity, the management of natural resources, and the accurate prediction of future climate conditions (Sala *et al*., 2000; Mawdsley *et al*., 2009; Mcguire *et al*., 2009). Because forests dominate the terrestrial C cycle and climate projections are sensitive to C cycle feedbacks (Dixon *et al*., 1994; Friedlingstein *et al*., 2006; Pan *et al*., 2011), the response of forest trees to warming is particularly important.

The capacity of forest trees to successfully cope with warming critically depends on their phenotypic plasticity- the ability of a given genotype to express different phenotypes as a function of the environment (Bradshaw, 1965; Nicotra *et al*., 2010). Many plants respond to warming by altering photosynthetic and respiratory physiology in a manner that maintains or enhances net C gain; this process of physiological acclimation is a type of phenotypic plasticity. Potentially greater respiratory losses of C in response to warming are often minimized through acclimation, particularly a reduction in the rate of mitochondrial respiration in the dark (R) at a common temperature (Tjoelker *et al*., 1999; Atkin & Tjoelker, 2003; Bolstad *et al*., 2003; Lee *et al*., 2005; Ow *et al*., 2008; Crous *et al*., 2011). Similarly, photosynthetic C gain is often maintained or enhanced with warming through an increase in photosynthetic capacity, an increase in the temperature optimum of photosynthesis, or an increase in total plant leaf area (Kattge & Knorr, 2007; Sage & Kubien, 2007; Ghannoum *et al*., 2010a,b; Gunderson *et al*., 2010; Way & Oren, 2010; Smith & Dukes, 2013). These physiological acclimation responses are often related to a suite of other co-varying traits such as specific leaf area (SLA, $m^2$ leaf area $g^{-1}$ leaf dry mass), foliar nitrogen (N)

Correspondence: John E. Drake, tel. +61 02 4570 1018, fax +61 02 4570 1103, e-mail: je.drake@uws.edu.au

content, and nonstructural carbohydrates (Weih & Karlsson, 2001; Tjoelker *et al.*, 2008), but there are no consistent morphological or stomatal trait responses when warming experiments are summarized by meta-analysis (Way & Oren, 2010).

How a plant responds to warming may vary depending on the taxa's climate-of-origin. Many studies suggest that warming of 2–4 °C is likely to increase the growth of temperate and boreal trees of relatively cool origin, where temperature is thought to limit growth (Schmidtling, 1994; Carter, 1996; Rehfeldt *et al.*, 1999, 2002; Mckenzie *et al.*, 2001; Bunn *et al.*, 2005; Savva *et al.*, 2007; Williams *et al.*, 2010). In contrast, warming is likely to reduce the growth of warm-temperate and tropical trees, where high temperatures are thought to approach physiological limits such that further warming is detrimental, rather than beneficial (Clark *et al.*, 2003, 2010; Feeley *et al.*, 2007; Doughty & Goulden, 2008; Way & Oren, 2010). A similar pattern was observed for Scots pine (*Pinus sylvestris*) populations grown across a wide-range of common gardens, although reduced growth and/or survival in populations grown at sites warmer than their home origin may have been due to indirect (e.g., moisture related) as well as direct warming effects (Reich & Oleksyn, 2008). Thus, the literature suggests that tree responses to warming vary across large geographic scales. However, the underlying mechanisms have not been tested in a rigorous experiment that separates phenotypic plasticity to warming from other confounding factors that occur across biomes.

It is widely recognized that the genetics and functional traits of populations vary along environmental gradients, suggesting that the effect of warming may vary biogeographically across populations of a given species (Slayter & Morrow, 1977; Joshi *et al.*, 2001; Jump & Peñuelas, 2005; Albert *et al.*, 2010; Breza *et al.*, 2012; Aspinwall *et al.*, 2013). For example, the foliar N content of widely distributed trees often declines clinally with increasing temperature at seed origin, and this variation can be heritable (Oleksyn *et al.*, 1998; Tjoelker *et al.*, 2008). Intraspecific variation related to climate-of-origin has also been observed for water-use-efficiency, specific leaf area, growth rate, reproductive traits, and chemical defense traits (Moore *et al.*, 2004; Koehler *et al.*, 2012; Woods *et al.*, 2012; Pratt & Mooney, 2013). How this intraspecific variation in functional traits influences the capacity of trees to respond to climate warming is largely unknown.

Climate warming may negatively affect trees near the warm edge of a species' distribution more than trees from moderate- or cool-origins. First, trees from moderate- or cool-origins may contain the genetic material enabling growth at warmer temperatures via gene flow from warm-origin populations. Warm-origin trees have not received genes from trees in warmer climates, as such trees do not exist, and may thus have limited capacity to respond to warming (Davis & Shaw, 2001; Jump & Peñuelas, 2005; Savolainen *et al.*, 2007; Sexton *et al.*, 2011). Secondly, climate warming will expose warm-origin trees to higher temperatures than cool- and moderate-origin trees, and these high temperatures may inhibit physiological processes necessary for growth (Sage & Kubien, 2007; Doughty & Goulden, 2008; Clark *et al.*, 2010; Way & Oren, 2010). Therefore, we hypothesize that warm-origin trees are more likely to be operating near their upper thermal limit and will thus have a constrained capacity to cope with additional warming.

Australian eucalypts provide a useful model system to test these concepts. Some *Eucalyptus* species are widely distributed and inhabit warm-temperate, subtropical, and tropical climatic regions. This provides the opportunity to compare the temperature response of temperate and tropical populations within species. Additionally, these warm climate regions are underrepresented in the literature regarding acclimation to climate warming (Way & Oren, 2010). Studying eucalypts also provides a somewhat independent test of the conceptual models of intraspecific variation in response to warming developed through research with Northern Hemisphere conifers, primarily *Pinus contorta*, *Pinus sylvestris*, and *Pseudotsuga menziesii* (e.g., Rehfeldt *et al.*, 1999, 2002; Reich & Oleksyn, 2008). Thus, Australian eucalypts provide a useful model system in which to study intraspecific variation in response to warming across large biogeographic gradients from the temperate zone to the tropics.

In this study, we performed a +3.5 °C climate-shift experiment using 21 provenances of two widely distributed *Eucalyptus* species. We tested two hypotheses: (i) cool-origin provenances will physiologically acclimate photosynthesis and respiration in response to warming, leading to maintained or enhanced growth; and (ii) warm-origin provenances will be operating closer to their maximum thermal limit and will have a constrained capacity to acclimate, leading to reduced growth with warming. Thus, we predict an interaction between warming and home climate across large geographic scales.

## Materials and methods

### *Study species*

We selected *Eucalyptus grandis* and *E. tereticornis*, as these species are widely distributed across a common latitudinal gradient in eastern Australia (Fig. 1). The distribution of *E. tereticornis* is nearly continuous across eastern Australia, while *E. grandis* has a disjunct distribution consisting of a core south-

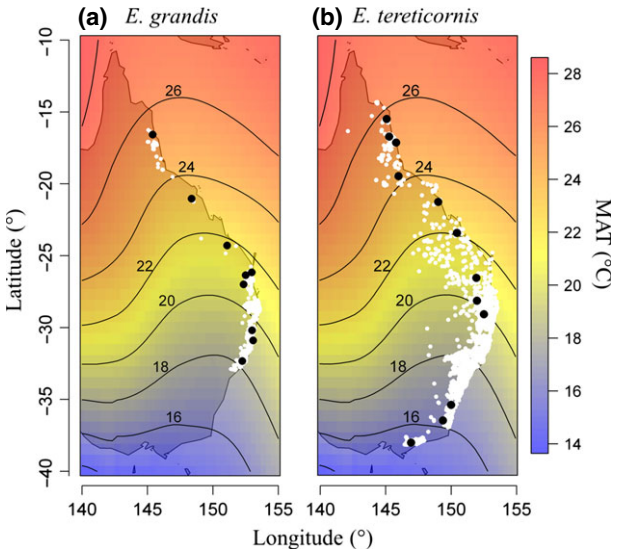


**Fig. 1** Distribution map of the study species and provenance locations in relation to mean annual temperature (MAT). Climate data are from the National Centers for Environmental Prediction (NCEP) reanalysis 2 product. White circles reflect occurrence records from the Atlas of Living Australia. Black circles show the seed source locations for the 9 *Eucalyptus grandis* (a) and 12 *E. tereticornis* (b) provenances used in this study.

ern range and a smaller range in the far-north, separated by a few sporadic occurrences (Fig. 1).

We obtained seed collected from native trees that were coastal (east of the Great Dividing Range), low elevation (<500 m above sea level) and of known geographic origin from the Australian Tree Seed Centre (CSIRO, Canberra, Australia). We refer to plants of known and common seed origin as a 'provenance'. We selected 9 provenances of *E. grandis* and 12 provenances of *E. tereticornis*, spanning the geographic range of both species (Fig. 1). Seeds were germinated in a common shade house on the University of Western Sydney campus (Richmond, NSW, Australia) and grown for 2 months in small cone pots. These seedlings were then transplanted into the experimental growth conditions described below.

### *Soil*

Soil was collected from the A horizon of a local dry sclerophyllous forest in Menangle, NSW, Australia. The soil was a sandy loam with moderate fertility. The soil had the following characteristics: pH = 5.0 (0.01 M CaCl), organic carbon content = 1.4%, total Kjeldahl N = 1300 mg $kg^{-1}$, total P = 217 mg $kg^{-1}$, C : N : P = 65 : 6 : 1, Ca < 10 mg $kg^{-1}$, Mg < 10 mg $kg^{-1}$, Na = 20 mg $kg^{-1}$, K < 10 mg $kg^{-1}$, Al = 5560 mg $kg^{-1}$, Fe = 14800 mg $kg^{-1}$ (ALS Laboratory Group, Analytical Chemistry and Testing Services, Smithfield, NSW, Australia). Nine kilograms of soil was added to each of 420 cylindrical pots (PVC pipes, 15 cm diameter by 40 cm length). The bottom of each pot consisted of a PVC cap with four drilled drainage holes covered with 2 mm mesh.

### *Experimental design*

We implemented a 'climate-shift' experimental design by growing individual seedlings of each provenance under a temperature regime mimicking the summer climate-of-origin for each provenance (hereafter 'home') or its climate-of-origin +3.5 °C (hereafter 'warmed'). This was accomplished using seven naturally lit, adjacent, and temperature-controlled glasshouse bays that have been described previously (Ghannoum *et al*., 2010a,b; Lewis *et al*., 2013). This experimental design isolates the effect of temperature and maintains a common light and soil environment; this eliminates some of the limitations of common garden field experiments (Reich & Oleksyn, 2008) but excludes ecological interactions that may occur in the natural environment. The air temperature of each bay was controlled at three set-points over a day-night cycle to approximate a natural diel cycle with an average temperature range of 9 °C (i.e., a night-time minimum temperature from 20:00 to 06:00 hours, a mid-day maximum temperature from 10:00 to 16:00 hours, and a moderate temperature value from 06:00–10:00 to 16:00–20:00 hours). These temperature set-points were designed to achieve diel mean temperature values in 3.5 °C increments of 18, 21.5, 25, 28.5, and 32 °C. As there were seven glasshouse bays but five temperature conditions, the 21.5 and 28.5 °C temperatures were repeated in two bays. The mean air temperature of each bay was highly correlated with the temperature target throughout the course of the experiment (observed air temperature = 1.69 + 0.95 × target temperature, $r^2 = 0.99$, $P < 0.0001$; slope not different than 1.0, major axis regression, $P > 0.1$).

Provenances were assigned to home temperature conditions based on spatially interpolated climate records from a network of weather stations across Australia (Jeffrey *et al*., 2001). Mean air temperature over the past 20-years during the summer months of November to February was calculated for each provenance and used to bin the provenances into home temperature conditions of 18, 21.5, 25, or 28.5 °C. The mean temperature in the glasshouse bays exhibited a 1 : 1 correspondence with the mean summer temperature at the seed origin of the provenances within the bays ($y = 1.048x$, $P < 0.001$, $r^2 = 0.99$, slope not significantly different than 1.0, major axis regression, $P = 0.08$). Thus, the growth temperatures in the home treatment successfully recreated the temperature at seed origin for these provenances. Note that no *E. grandis* provenances were assigned to a home temperature of 18 °C, as the distribution of *E. grandis* does not extend as far south as the distribution of *E. tereticornis* (Fig. 1). Plants were randomly rotated within glasshouse bays fortnightly.

Thirty of the most uniform seedlings of each provenance were selected from the shade house material and the stem length and basal diameter of all seedlings was recorded. These thirty seedlings of each provenance were grouped into triplets of similar stem length and then randomly assigned into one of three groups. The first group was destructively harvested for measurement of initial aboveground biomass. The second and third groups were transplanted into soil-filled pots and placed into home and warmed climate conditions. This selection process ensured that home and warmed plants did not differ in initial size and that the plants used to characterize initial

aboveground biomass were representative of the plants in both temperature treatments. Plants were kept well-watered and fertilized every 3 weeks with a commercial liquid fertilizer (500 ml Aquasol, at 1.6 g $l^{-1}$; 23% N, 4% P, 18% K, 0.05% Zn, 0.06% Cu, 0.0013% Mo, 0.15% Mn, 0.06% Fe, 0.011% B; Yates Australia, Padstow, NSW, Australia).

In summary, 10 plants of each provenance were grown in home and warmed temperature environments for 90 days during the summer (24 October 2012–11 January 2013) under well-watered and fertilized conditions. The experiment consisted of 420 individual potted plants (21 provenances × 2 temperature treatments × 10 replicate plants = 420 plants).

### *Growth metrics*

We measured two metrics of plant growth: (i) the final biomass of leaves, stems, and roots on the 11 January 2013 harvest and (ii) aboveground biomass production during the 90-day experiment.

We destructively harvested 210 individual plants at the end of the experiment on 11 January 2013, after recording the stem length and basal diameter of all 420 plants. Five to six of the 10 replicate plants growing in each experimental condition were randomly selected, harvested, and separated into leaf, stem, and root components. After 90 days, plants had grown from an initial stem length of 9.6 ± 3.7 cm (standard deviation) to 97 ± 29 cm. The entire root system was washed free of soil, oven dried, and weighed. The total fresh leaf and stem mass was recorded and dry weights of these components were calculated based on the fresh : dry weight ratio of representative subsamples. The fresh mass, dry mass, and total area was measured on a ten-leaf-subsample of each harvested plant (Li-3100C Area Meter, Li-Cor Inc., Lincoln, NE, USA), which allowed for the calculation of total plant leaf area and dry mass. Two provenances of *E. tereticornis* and one provenance of *E. grandis* were not harvested, as these plants were part of a subsequent experiment.

Aboveground biomass production was calculated as the absolute difference between final and initial aboveground biomass. These values were calculated for every pot in the experiment using an allometric approach. Initial aboveground biomass was estimated for each plant based on an allometric relationship between basal diameter, stem length, and aboveground dry mass using data from the 24 October 2012 harvest,

$$\log_{10}(\mathrm{ADM}) = a + b \times \log_{10}(\mathrm{SL} \times \mathrm{BD}) \quad (1)$$

where ADM is aboveground dry mass, SL is stem length, and BD is basal diameter. Fitted parameters of $a$, $b$, and adjusted $r^2$ values were −1.88, 1.93, and 0.80 for *E. tereticornis* and −1.94, 1.04, and 0.81 for *E. grandis*. Final ADM was calculated using Eqn (1) and data from the 11 January 2013 harvest, with $a$, $b$, and adjusted $r^2$ values of −1.01, 0.787, and 0.70 for *E. tereticornis* and −0.458, 0.626, and 0.71 for *E. grandis*. These relationships differed across species and initial vs. final harvests (ANCOVA, $P < 0.001$), but there was no evidence of intraspecific differences (*not shown*). Absolute growth rate (AGR) was calculated as the absolute difference between final and initial ADM as predicted by Eqn (1). This approach has the advantage of using data for all 420 plants, rather than the 210 plants harvested on 11 January 2013; statistical analyses of AGR with all 420 plants as predicted by Eqn (1) and with the 210 directly measured plants produced the same results (mixed model ANOVAs; *not shown*). Roots were not included in these calculations because it was not feasible to separate and measure the initial root biomass of seedling transplant stock grown together in cone stock.

We tested whether there were likely to be effects of particular glasshouse bays by comparing the absolute growth rates of provenances assigned to the replicated 21.5 and 28.5 °C bays. Growth rates did not differ significantly between plants of either species in the replicated 21.5 °C bays (mixed model ANOVA with random provenance, main effect of bay, $P = 0.17$, $n = 35$), or the replicated 28.5 °C bays ($P = 0.68$, $n = 35$). Plant growth was equal across different glasshouse bays of the same temperature, suggesting that the treatment effects were unlikely to be driven by unmeasured artifacts of particular glasshouse bays. Plants from the replicate bays at 21.5 and 28.5 °C were pooled for all subsequent analysis.

### *Physiological acclimation*

To quantify physiological acclimation to warming, we measured leaf-level rates of light-saturated photosynthesis at ambient $CO_2$ concentration ($A_{sat}$), light- and $CO_2$-saturated photosynthesis ($A_{max}$), and mitochondrial respiration in the dark (R). Acclimation of these processes in response to warming was assessed by separating the direct short-term temperature sensitivity of each process from long-term physiological adjustment to growth temperatures (Atkin *et al.*, 2005b).

For each provenance, we measured $A_{sat}$, $A_{max}$, and R in three conditions: (i) home-grown plants were measured at their average growth temperature; (ii) warm-grown plants were measured at their average growth temperature; and (iii) home-grown plants were measured at the temperature of the warm-grown plants (i.e., +3.5 °C). Home-grown plants were physically moved into the corresponding warmed temperature bay one hour prior to the measurements at the warmed temperature. The short-term temperature response was assessed by comparing (i) and (iii), while physiological acclimation was assessed by comparing (ii) and (iii), which reflect measurements at a common temperature. This method of assessing acclimation follows the set temperature method as described by Atkin *et al.* (2005b). We analyzed all photosynthetic and respiration data on an area and mass basis, and the overall results and interpretation did not depend upon the normalizing unit. Thus, we express photosynthetic traits on an area basis and R on a mass basis, following Osnas *et al.* (2013).

We measured $A_{sat}$ and $A_{max}$ from mid-morning to early afternoon (10:00–14:00 hours, local time) on 3–5th December 2012 on six randomly chosen plants within each condition for each provenance using six identical open gas exchange systems (Li-6400 with Li-6400-02B LED light source, Li-Cor Inc.). It was not feasible to measure all plants on the same day, so the sampling was designed to insure that treatments were not confounded with day of measurement. That is, home and

warmed plants of each individual provenance were measured on the same day, and provenances from all temperature treatments were measured on each day. The youngest fully expanded leaf of each replicate plant was marked and used for all gas exchange measurements ($A_{sat}$, $A_{max}$, and R). The leaf was enclosed in the gas exchange chamber and exposed to saturating light (1800 μmol $m^{-2}$ $s^{-1}$), 400 ppm $CO_2$ in the reference cell, and a flow rate of 500 μmol $s^{-1}$. Measuring $A_{sat}$ with a light level of 1800 μmol $m^{-2}$ $s^{-1}$ is consistent with previous studies and our own preliminary measurements of photosynthesis at a range of light levels (J. E. Drake, personal observation; Kallarackal & Somen, 1997; Pinkard *et al*., 1998; Crous *et al*., 2013). A system of humidifiers and dehumidifiers were used to control the vapor-pressure-deficit (VPD) of each glasshouse bay to minimize co-variation between air temperature and VPD; the leaf VPD during measurement was maintained between 0.8 and 1.8 kPa. Leaf temperature was controlled at ±1 °C of the bay midday temperature by controlling the chamber block temperature. After recording $A_{sat}$ and the associated stomatal conductance ($g_s$), the concentration of $CO_2$ in the reference cell was increased to 1800 ppm for the measurement of $A_{max}$.

We measured leaf R on the same set of leaves from 11 to 14th December 2012 at least 2 h after sunset (22:00–02:00 hours). By measuring at night, our observations of R directly reflect the environmental and physiological conditions that are relevant for leaf dark respiration, and we avoid the repression of mitochondrial respiration in the light or light-enhanced dark respiration (Atkin *et al*., 1998, 2000; Barbour *et al*., 2007). As for the photosynthetic measurements, home and warmed plants of each individual provenance were measured on the same night, provenances from all temperature treatments were measured on each night, and the order of measurements was randomized such that time was not confounded with any provenance or treatment. For each observation, an entire leaf was enclosed in a large gas exchange chamber (Li-6400-22L, Li-Cor Inc.) which allowed for the accurate measurement of large $CO_2$ differentials without leak artifacts (e.g., Jahnke & Krewitt, 2002). The cuvette block temperature was maintained at the ambient nighttime temperature of the glasshouse bay, the reference $CO_2$ concentration was controlled at 400 ppm, and a flow rate of 350 μmol $s^{-1}$ was used. Note that R was measured at lower leaf temperatures than $A_{sat}$ and $A_{max}$. The leaves were detached, fresh leaf area was measured (Li-3100C Area Meter, Li-Cor Inc.), leaf dry mass was recorded after drying at 70 °C, and specific leaf area (SLA) was calculated as the ratio of leaf area to dry mass. Leaves were ground with mortar and pestle and analyzed for C and N content with an elemental analyzer (TruSpec Micro, Leco, St. Joseph, MI, USA).

### *Statistical analysis*

To characterize the average response across all provenances, data were analyzed using a mixed model analysis of variance (ANOVA) framework. As the provenances were sampled from an underlying distribution of all possible seed sources, provenance was included as a random effect. Temperature treatment (home vs. warmed) and species were included as categorical fixed effects and home temperature category was included as a fixed effect. Because there were no *E. grandis* provenances at a home temperature of 18 °C, the *E. tereticornis* data at 18 °C were excluded from the mixed model ANOVAs to avoid missing elements in the design matrix. We also fit species-specific mixed model ANOVAs so that the *E. tereticornis* provenances from 18 °C could be included, and this altered the statistical interpretation for only two variables (foliar N concentration and R at a common temperature; see below). All mixed model ANOVAs were performed using the 'lme4' and 'nlme' packages (Pinheiro *et al*., 2013) in R v. 3.0.1 (R Development Core Team, 2012) and $r^2$ values of mixed models were computed as in Nakagawa & Schielzeth (2013). Logarithmic and power transformations were often necessary to satisfy the analysis assumptions of residual normality and homoscedasticity. Tests of the relationship between the glasshouse bay air temperatures and mean summer air temperature at seed origin were implemented using major axis regression in the 'smatr' R package following the recommendations of Warton *et al*. (2006).

We estimated the phenotypic plasticity of ten variables by calculating the response ratio with warming, or the mean value measured in the warmed environment divided by the mean value measured in the home environment. The variables included growth metrics (absolute growth rate: AGR and relative growth rate: RGR), leaf area variables (total leaf area: TLA, total leaf mass: TLM, and specific leaf area: SLA), and traits related to photosynthesis ($A_{max}$, $A_{sat}$, $g_s$, R, and foliar N content). We used the response ratio because it summarizes the effects of warming and, for this experimental design, the absolute value of the response ratio subtracted from 1.0 is equivalent to a commonly used metric of plasticity, the relative difference plasticity index (Valladares *et al*., 2006).

## Results

### *Growth metrics*

Experimental warming of +3.5 °C increased the biomass of provenances of *E. tereticornis* and *E. grandis* from cool and moderate-home temperatures (18, 21.5, and 25 °C) by 20–60% but decreased biomass in the warmest home temperature by ~10% (28.5 °C, Fig. 2). This interaction between home temperature and warming treatment was statistically significant for absolute growth rate (AGR; Table 1), total final biomass (Fig. 2, $P < 0.05$), leaf biomass (Fig. 2, $P = 0.01$), stem biomass (Fig. 2, $P < 0.0001$), and there was a nonsignificant trend for root biomass (Fig. 2, $P > 0.1$). Stem biomass tended to increase most strongly with warming in cool-origin provenances (increases of 63%, 20%, and 11% for stem, leaves, and roots, respectively, at 21.5 °C), while all biomass components decreased with warming in warm-origin provenances (decreases of 8%, 10%, and 18% for stem, leaves, and roots, respectively, at

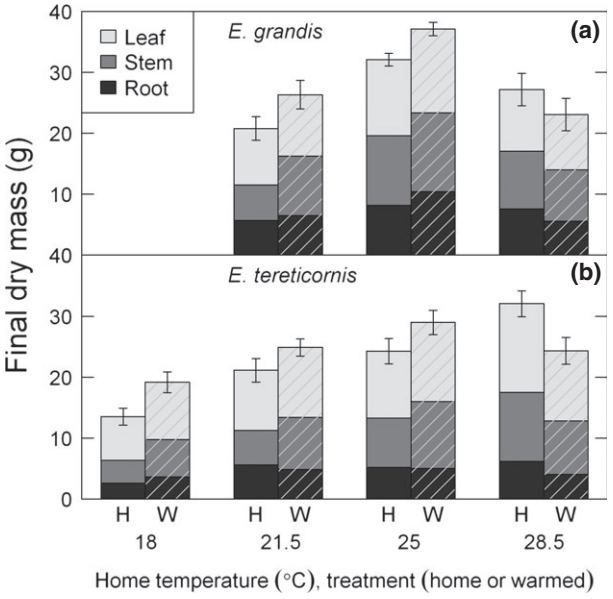


**Fig. 2** Final dry mass components of nine provenances of *Eucalyptus grandis* (a) and 12 provenances *E. tereticornis* (b) in a climate shift experiment. The four home temperature categories and the experimental treatments (H: home vs. W: warmed) are shown on the *x*-axis. The warmed treatments are also denoted with gray hashing. Each bar reflects the mean of six observations for each of three provenances; error bars reflect ±1 SEM. Note that there were no *E. grandis* provenances assigned to a home temperature of 18 °C, as the distribution of *E. grandis* does not extend as far south as the distribution for *E. tereticornis*.

**Table 1** Statistical analysis of absolute growth rate (AGR). The marginal $r^2$ value (fixed effects only) was 0.34 and the conditional $r^2$ value (fixed and random effects) was 0.41

| Term | DF (num/den) | Sums of Squares | Mean Square | *F*-value | *P*-value |
|---|---|---|---|---|---|
| S | 1/11 | 498 | 498 | 5.4 | 0.04 |
| T | 1/413 | 4786 | 4786 | 85.4 | <0.0001 |
| H | 2/11 | 1535 | 767 | 8.9 | 0.004 |
| S × T | 1/413 | 313 | 313 | 2.9 | 0.09 |
| S × H | 2/11 | 7 | 4 | 0.03 | 0.97 |
| T × H | 2/413 | 8658 | 4329 | 49.6 | <0.0001 |
| S × T × H | 2/413 | 468 | 234 | 2.7 | 0.1 |

Terms of the statistical analysis are abbreviated as follows: S, species; T, warming treatment; H, home temperature. Interactions are shown as combinations of terms. All terms were fixed effects in a linear mixed model; provenance was included as a random effect. Numerator (num) and denominator (den) degrees of freedom (DF) were estimated by the Satterthwaite approximation.

28.5 °C). The three-way interaction between species, warming, and home temperature was not significant for any metric of growth or biomass (Table 1), indicating that the two-way interaction between warming and home temperature was similar for *E. grandis* and *E. tereticornis*.

### *Physiological measurements and acclimation*

Photosynthetic capacity ($A_{max}$), realized light-saturated photosynthetic rates ($A_{sat}$), and stomatal conductance ($g_s$) all responded to warming in a correlated manner that significantly depended on the home temperature environment (Table 2; all treatment × home temperature interactions at growth temperature *P*-values <0.001). Values of $g_s$ were high and $C_i/C_a$ was nearly constant at ~0.8 (Table 2), suggesting that stomatal limitation of photosynthesis was minor in these well-watered plants (Long & Bernacchi, 2003). Additionally, $A_{sat}$ was highly correlated with $A_{max}$ ($A_{sat} = 8.7 + 0.44 \times A_{max}$, $P < 0.0001$, $r^2 = 0.51$), suggesting that acclimation of photosynthetic capacity ($A_{max}$) directly affected realized leaf-level C uptake at high light ($A_{sat}$).

Acclimation of photosynthetic capacity ($A_{max}$) in response to warming was dependent on the provenance's climate-of-origin (Fig. 3, gray vs. black symbols, warming treatment × home temperature interaction at a common temperature, $P < 0.01$). Recall that acclimation was assessed by separating the short-term effect of +3.5 °C warming (i.e., the direct effect of temperature without acclimation) from the effects of long-term growth at +3.5 °C (i.e., possibly including acclimation). Cool-origin provenances of both species (18 °C for *E. tereticornis*, 21.5 °C for *E. grandis*) acclimated to warming by increasing photosynthetic capacity, as the long-term temperature response to warming (Fig. 3, solid line) exceeded what could be explained by the short-term temperature response (Fig. 3, dashed line). In contrast, warm-origin provenances (28.5 °C) of both species acclimated to warming by reducing photosynthetic capacity, as the long-term temperature response to warming (Fig. 3, solid line) was negative and lower than predicted by the positive short-term temperature response (Fig. 3, dashed line). Provenances from intermediate home temperatures showed minimal or slight down-regulation in $A_{max}$ with warming, as the short-term temperature response and the long-term temperature response were similar (compare solid and dashed lines, Fig. 3). A nearly identical pattern was evident in photosynthetic data expressed per unit leaf mass (Figure S1).

Acclimation of R also varied across the provenances of contrasting climatic origin, although this effect was significant for *E. tereticornis* only (Fig. 4, gray vs. black symbols, warming treatment × home temperature interaction at a common temperature, $P < 0.01$). There was no evidence of R acclimation in response to warm-

**Table 2** Leaf-level gas exchange characteristics of two *Eucalyptus* species, including light-saturated photosynthesis ($A_{sat}$), stomatal conductance ($g_s$), and the ratio of $CO_2$ concentration inside leaves relative to the atmosphere ($C_i/C_a$). Each value reflects the mean (standard error) of six replicate plants across each of three provenances. Treatments include plants grown and measured at their home temperature ('HH'), plants grown at home but measured at a warmed temperature of +3.5 °C ('HW'), or plants grown and measured at a warmed temperature of +3.5 °C ('WW')

| Species (S) | Home temperature (H) (°C) | Treatment (T) | $A_{sat}$ (μmol $m^{-2}$ $s^{-1}$) | $g_s$ (mol $m^{-2}$ $s^{-1}$) | $C_i/C_a$ (mol $mol^{-1}$) |
|---|---|---|---|---|---|
| *E. grandis* | 21.5 | HH | 23.0 (0.8) | 0.72 (0.03) | 0.81 (0.01) |
| | | HW | 21.3 (1.1) | 0.68 (0.07) | 0.80 (0.01) |
| | | WW | 24.4 (0.8) | 0.87 (0.06) | 0.80 (0.02) |
| | 25.0 | HH | 23.1 (0.8) | 0.73 (0.05) | 0.80 (0.01) |
| | | HW | 21.5 (1.3) | 0.67 (0.06) | 0.80 (0.01) |
| | | WW | 21.9 (1.1) | 0.67 (0.08) | 0.76 (0.02) |
| | 28.5 | HH | 23.3 (1.0) | 0.87 (0.04) | 0.83 (0.01) |
| | | HW | 21.3 (1.1) | 0.80 (0.04) | 0.83 (0.01) |
| | | WW | 20.7 (0.8) | 0.78 (0.05) | 0.82 (0.01) |
| *E. tereticornis* | 18.0 | HH | 20.4 (0.7) | 0.53 (0.04) | 0.79 (0.01) |
| | | HW | 19.8 (0.6) | 0.53 (0.03) | 0.78 (0.01) |
| | | WW | 24.4 (0.7) | 0.76 (0.05) | 0.80 (0.01) |
| | 21.5 | HH | 26.2 (0.6) | 0.81 (0.05) | 0.80 (0.01) |
| | | HW | 25.3 (0.8) | 0.69 (0.06) | 0.77 (0.02) |
| | | WW | 24.2 (0.7) | 0.75 (0.06) | 0.79 (0.01) |
| | 25.0 | HH | 20.6 (0.9) | 0.77 (0.04) | 0.79 (0.02) |
| | | HW | 25.6 (0.6) | 0.84 (0.05) | 0.81 (0.01) |
| | | WW | 27.1 (0.4) | 1.12 (0.08) | 0.83 (0.01) |
| | 28.5 | HH | 26.5 (0.9) | 0.95 (0.04) | 0.82 (0.01) |
| | | HW | 24.1 (0.6) | 0.97 (0.04) | 0.83 (0.01) |
| | | WW | 23.7 (0.8) | 0.84 (0.04) | 0.82 (0.01) |
| Significant effects, comparisons at growth temperature only (HH vs. WW)* | | | T × H, S × T × H | T × H, S × T × H | – |
| Significant effects, comparisons at a common temperature only (HW vs. WW)* | | | T × H | T × H, S × T × H | – |

*Statistical results (ANOVA). 'S', 'H', and 'T' indicate statistically significant effects of species, home temperature, and warming treatment, respectively. Significant interactions are denoted by a combination of abbreviations (e.g., T × H indicates that the treatment effect interacted with home temperature).

ing in the provenances from the coolest home climate of either species, as the short- and long-term temperature responses were equivalent (Fig. 4). However, moderate- to warm-origin provenances acclimated R in response to warming through reductions in R, as the short-term temperature response of R exceeded the long-term temperature response (compare solid and dashed lines, Fig. 4). Thus, except for the cool-origin provenances, acclimation to warming reduced R relative to the rates predicted by the direct short-term effect of temperature.

### *Leaf and plant traits*

Experimental warming significantly reduced foliar N content from an average of 3.16% to 2.96% across home environments of both species ($P = 0.0005$, Table 3). Foliar N also significantly declined with increasing home temperature ($P < 0.0001$), but the effect of warming on foliar N did not depend on the home temperature environment (interaction $P = 0.52$). However, when the *E. tereticornis* data were analyzed separately, there was a significant interaction between warming treatment and home temperature environment ($P = 0.04$, Table 3); warming increased leaf N in the 18 °C provenances from 3.10% to 3.35%, but decreased leaf N in the other provenances from 3.34% to 3.02%. Foliar N content was high for both species relative to the global mean of ~1.7% for broadleaf evergreen trees (Kattge *et al.*, 2011) and significantly higher for *E. grandis* relative to *E. tereticornis* (3.2% vs. 2.9%, main effect of species, $P < 0.0001$; Table 3).

There was a significant interaction between home temperature and warming treatment on specific leaf

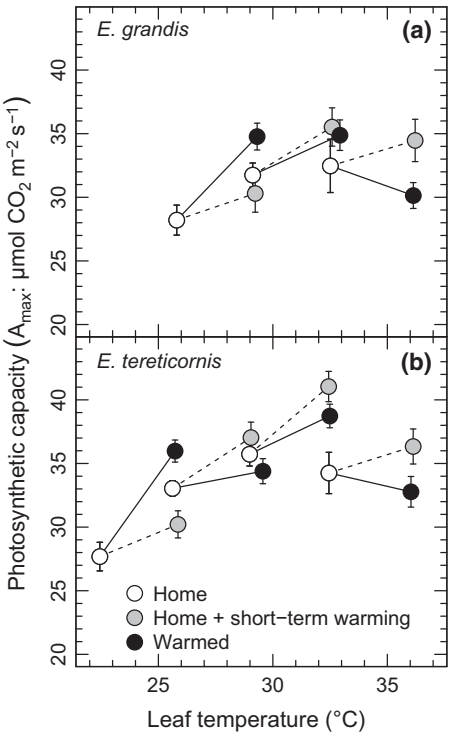


**Fig. 3** Acclimation of photosynthetic capacity to +3.5 °C warming depended on home climate *E. grandis* (a) and *E. tereticornis* (b). Each symbol reflects a home temperature category and was calculated as the mean of six observations for each of three provenances; error bars reflect ±1 SEM. Open symbols reflect plants grown and measured in their home climate. Gray symbols reflect plants grown in their home climate but measured in the warmed climate of +3.5 °C. Black symbols reflect plants that were grown and measured in the warmed climate condition. The dashed line reflects the short-term effect of temperature and the solid line reflects the long-term effect of temperature, which potentially includes acclimation. Photosynthetic fluxes are shown on an area basis, but the results were equivalent when expressed per unit leaf mass.

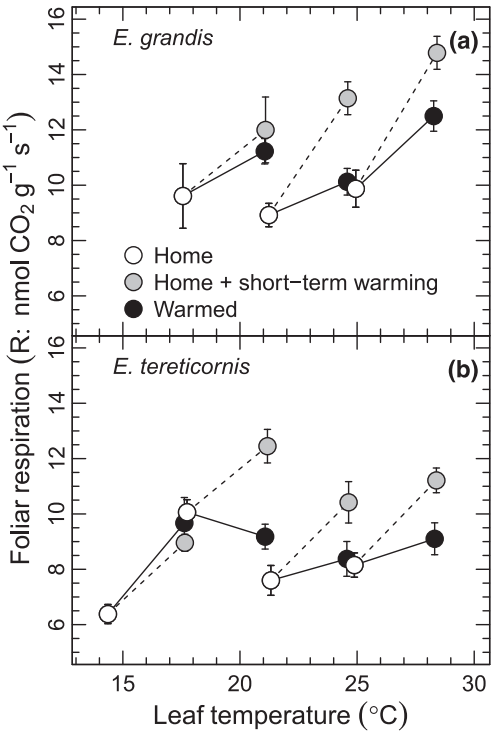


**Fig. 4** Acclimation of foliar respiration (R) to +3.5 °C warming depended on home climate for *E. grandis* (a) and *E. tereticornis* (b). Each symbol reflects a home temperature category and was calculated as the mean of six observations for each of 3 provenances; error bars reflect ±1 SEM. Open symbols reflect plants grown and measured in their home climate. Gray symbols reflect plants grown in their home climate but measured in the warmed climate of +3.5 °C. Black symbols reflect plants that were grown and measured in the warmed climate condition. The dashed line reflects the short-term effect of temperature and the solid line reflects the long-term effect of temperature, which potentially includes acclimation. Respiration rates are shown on a mass basis, but the results were equivalent when expressed per unit leaf area.

area (SLA; $P = 0.03$), but this effect was variable across the home temperatures. SLA increased with warming in the 21.5 °C provenances of both species and the 28.5 °C provenances for *E. grandis*, but not for *E. tereticornis* (Table 3). SLA values were relatively high for both species relative to the global mean of ~95 $cm^2$ $g^{-1}$ for broadleaved evergreen trees (Kattge *et al.*, 2011) and was significantly higher for *E. grandis* relative to *E. tereticornis* (290 vs. 227 $cm^2$ $g^{-1}$, $P < 0.0001$; Table 3).

Similar to the whole-plant biomass response (Fig. 2), the effect of experimental warming on total plant leaf area was highly dependent on the home temperature environment (Table 3, interaction $P = 0.001$). In the coolest-origin provenances of both species (18 °C for *E. tereticornis*, 21.5 °C for *E. grandis*), warming lead to an increase in total plant leaf area of 30.5% and 34.5%, respectively. However, warming lead to a decrease in leaf area in the warmest-origin provenances of both species (28.5 °C) of 13.1% and 5.9% for *E. tereticornis* and *E. grandis*, respectively. The effect of warming on total plant leaf area appeared to be a simple function of plant size, as warming had no effect on leaf area ratio (ratio of total plant leaf area to total biomass, *not shown*, all *P*-values >0.1).

### *Phenotypic plasticity to climate shifting*

The capacity of plants to alter growth, leaf area, and leaf gas exchange variables with +3.5 °C warming was strongly dependent on climate-of-origin (Fig. 5). Note that for this experimental design, the absolute value of

**Table 3** Leaf and plant characteristics of two *Eucalyptus* species grown at home and warmed (+3.5 °C) temperature treatments. Each value reflects the mean (standard error) of six to 10 replicate plants of three provenances. See text and Fig. 5 for variable abbreviations

| Species (S) | Home temperature (H) (°C) | Treatment (T) (Home or Warmed) | N (%) | SLA ($cm^2\ g^{-1}$) | TLA ($m^2$) | TLM (g) | AGR (g) | RGR ($mg\ g^{-1}\ d^{-1}$) |
|---|---|---|---|---|---|---|---|---|
| *E. grandis* | 21.5 | H | 3.64 (0.12) | 262 (12) | 0.23 (0.02) | 9.3 (0.8) | 15.9 (0.7) | 48.3 (1.2) |
| | 21.5 | W | 3.42 (0.1) | 321 (13) | 0.32 (0.02) | 10 (0.7) | 23.9 (0.7) | 51.5 (1.3) |
| | 25.0 | H | 3.09 (0.09) | 307 (15) | 0.37 (0.01) | 12.5 (0.5) | 22.5 (0.6) | 45.7 (0.8) |
| | 25.0 | W | 2.86 (0.11) | 273 (7) | 0.37 (0.01) | 13.8 (0.5) | 23.8 (0.6) | 46.0 (0.7) |
| | 28.5 | H | 3.18 (0.09) | 291 (19) | 0.29 (0.02) | 10.1 (0.8) | 23.5 (0.4) | 48.8 (0.6) |
| | 28.5 | W | 3.13 (0.1) | 285 (17) | 0.27 (0.03) | 9.1 (1) | 22.1 (0.5) | 46.9 (0.6) |
| *E. tereticornis* | 18.0 | H | 3.11 (0.08) | 221 (8) | 0.16 (0.02) | 7.2 (0.7) | 10.5 (0.3) | 49.5 (1.2) |
| | 18.0 | W | 3.36 (0.11) | 224 (8) | 0.21 (0.02) | 9.4 (0.9) | 13.9 (0.6) | 51.4 (1.2) |
| | 21.5 | H | 3.34 (0.13) | 203 (9) | 0.2 (0.02) | 9.8 (0.9) | 14.6 (0.8) | 44.9 (0.8) |
| | 21.5 | W | 3.02 (0.13) | 236 (11) | 0.27 (0.02) | 11.5 (0.8) | 21.8 (0.8) | 48.0 (0.7) |
| | 25.0 | H | 2.96 (0.12) | 229 (7) | 0.25 (0.02) | 10.9 (0.9) | 19.6 (0.8) | 44.3 (0.7) |
| | 25.0 | W | 2.71 (0.06) | 222 (11) | 0.28 (0.02) | 13 (1) | 24 (0.6) | 46.2 (0.9) |
| | 28.5 | H | 2.78 (0.1) | 231 (13) | 0.33 (0.02) | 14.5 (1.1) | 21 (0.6) | 50.7 (0.8) |
| | 28.5 | W | 2.63 (0.09) | 252 (12) | 0.29 (0.02) | 11.5 (1) | 21.1 (0.5) | 51.1 (0.8) |
| Significant effects* | | | T, H, T × H† | S, H, T, T × H | S, T × H | S, T, T × H | T × H | T × H |

*Statistical results (ANOVA). 'S', 'H', and 'T' indicate statistically significant effects of species, home temperature, and warming treatment, respectively. Significant interactions are denoted by a combination of these abbreviations (e.g., T × H).
†Significantly different for *E. tereticornis* only.

the response ratio subtracted from 1.0 is equivalent to the normalized difference plasticity index (Valladares *et al.*, 2006). Absolute and relative growth rates (AGR and RGR) were increased by warming in provenances in 18, 21.5, or 25 °C home environments, but AGR and RGR were either reduced or did not change with warming for provenances in a home environment of 28.5 °C (Fig. 5a–d). Total plant leaf area (TLA) increased with warming in provenances from cool- and moderate-home temperatures, but total leaf area did not change or was reduced with warming in warm-origin provenances (Fig. 5e and f). The increase in total plant leaf area in cool-origin provenances was related to an increase in total plant leaf mass (TLM) and, to some extent, an increase in SLA (Fig. 5g–j). Variables related to leaf photosynthesis ($A_{max}$, $A_{sat}$, $g_s$, foliar N) tended to increase with warming in cool-origin provenances and decrease with warming in warm-origin provenances of both species (Fig. 5k–p). Despite the acclimation of R to warming in all but the coolest home origin provenances (Fig. 4), realized rates of R tended to be higher in warmed vs. home treatments (Fig. 5q and r), thus acclimation was not complete. The overall trend was for high response ratios in cool home temperatures while response ratios were more constrained or <1.0 at warm home temperatures, suggesting that phenotypic plasticity to +3.5 °C warming was lower in provenances from warm home climates relative to provenances from cool home climates.

### *Biogeographic pattern of responses to warming*

Across all provenances, the growth response to warming followed a marked clinal trend for both species (Fig. 6). The species responded similarly in the general pattern of biomass response +3.5 °C warming, with strong increases in biomass in cool-origin provenances and small reductions in biomass in warm-origin provenances (Fig. 6b and d). The positive biomass growth response to warming was widespread for *E. tereticornis*, except for provenances at the warm edge of the distribution (Fig. 6d). In contrast, the positive growth response to warming was constrained to provenances near the cool edge of the distribution for *E. grandis* (Fig. 6b); all of the *E. grandis* provenances north of the distribution discontinuity showed a small reduction in biomass with warming. Clinal trends in the response of $A_{max}$ and total plant leaf area to warming were also observed (Figure S2), given the strong correlation between these variables and growth.

## Discussion

The results of this climate-shift experiment supported both hypotheses: (i) plants responded to warming through physiological acclimation in photosynthetic and respiratory metabolism; and (ii) the degree of acclimation depended on home climate. Cool- and moderate-origin provenances responded to +3.5 °C warming

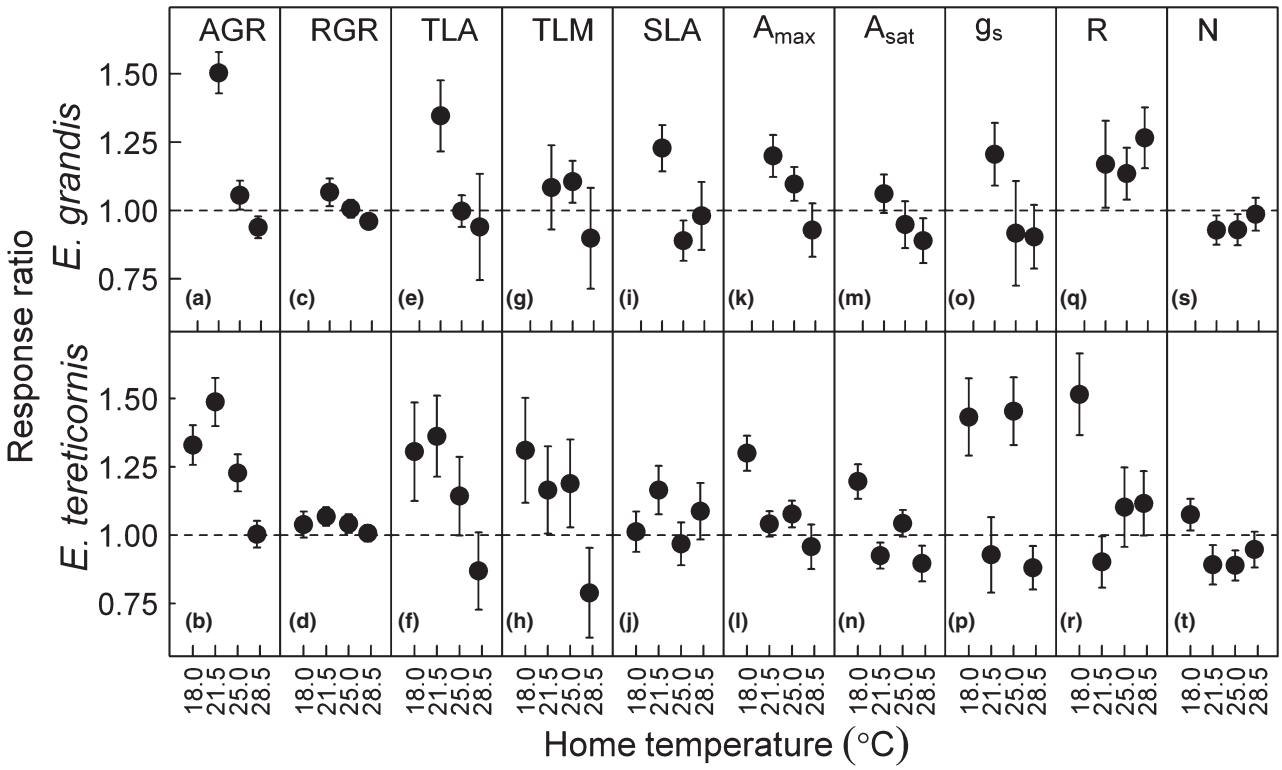


**Fig. 5** The response of ten variables to experimental warming for two *Eucalyptus* species of four home temperature categories (18, 21.5, 25, and 28.5 °C). The variables were: AGR, absolute growth rate; RGR, relative growth rate; TLA, total plant leaf area; TLM, total plant leaf mass; SLA, specific leaf area; $A_{max}$, maximum photosynthetic rate with saturating light and $CO_2$; $A_{sat}$, light-saturated photosynthetic rate at ambient $CO_2$ concentration; $g_s$, stomatal conductance; R, foliar mitochondrial respiration in the dark; and N, foliar N concentration (%). Values reflect the mean of 6–10 observations for each of three provenances; error bars reflect the 95% confidence interval. Response ratios greater than 1.0 indicate that the value was higher in the warmed treatment relative to the home environment.

through a substantial increase in photosynthetic capacity and leaf area, resulting in increased growth. Thus, warming had a positive effect on growth across much of the species' ranges in these well-watered conditions. Warm-origin provenances, in contrast, reduced photosynthetic capacity, leaf area, and growth in response to +3.5 °C warming. These results suggest that the effects of warming are likely to vary across the range of widely distributed species; cool-origin plants likely have the flexibility to alter physiological and structural traits leading to a positive growth response to warming, while warm-origin plants are likely to have a constrained ability to alter traits and will thus be negatively affected by warming.

### *Physiological acclimation to climate warming*

We observed substantial acclimation of respiration and photosynthesis to long-term growth with +3.5 °C warming, but the magnitude and direction of acclimation was dependent on home climate.

The acclimation of R reported here is broadly consistent with the literature, which shows that acclimation of foliar R to growth temperature is widespread and that warming typically leads to a reduction in R measured at a common temperature (Atkin & Tjoelker, 2003; Atkin *et al*., 2005a; Lee *et al*., 2005; Smith & Dukes, 2013). Tjoelker *et al*. (2008) studied 20 provenances of a widespread conifer (*Pinus banksiana*) grown in common gardens and found widespread acclimation of R to seasonal temperature variation, and the degree of acclimation did not appear to vary across the provenances. However, a subsequent detailed analysis of four cold-origin and four warm-origin provenances indicated that the degree of acclimation of R to seasonal temperature variation was higher in the warm-origin relative to the cold-origin provenances, possibly because of increased cold hardening in cold-origin provenances (Tjoelker *et al*., 2009). Remarkably, our observations with two *Eucalyptus* species show a pattern similar to this boreal conifer from the Northern Hemisphere (Tjoelker *et al*., 2008, 2009), with widespread acclimation of R and more extensive acclimation of R in warm-origin relative to cool-origin provenances (Fig. 4). However, cold hardening is unlikely to account for the lack of respiratory acclimation in the cool-origin prove-

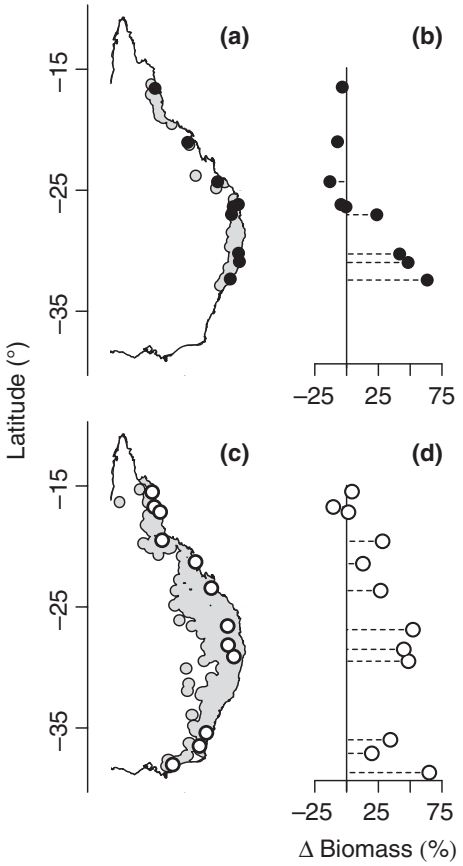


**Fig. 6** Clinal response of *Eucalyptus grandis* (a and b) and *E. tereticornis* (c and d) to experimental warming. The percentage change in total final biomass in response to +3.5 °C warming (b and d) is shown for 9 provenances of *E. grandis* (filled circles) and 12 provenances of *E. tereticornis* (open circles). The gray shaded area reflects the natural distribution of each species.

nances studied here (Fig. 4), given the relatively warm temperatures during the experimental period and at seed origin. These cool-origin provenances had substantially higher growth and photosynthetic rates when grown with +3.5 °C warming (Figs 2, 3, 5, and 6); we suggest that the metabolic demands of supporting these processes necessitated higher rates of mitochondrial respiration in these plants such that R did not acclimate to warming.

We observed an interaction between home temperature and warming for photosynthetic variables; cool-origin plants up-regulated $A_{max}$, $A_{sat}$ and $g_s$ with warming while warm-origin plants down-regulated these traits (Figs 3 and 5, Table 3). To our knowledge, this is the first study to demonstrate predictable intraspecific variation in the acclimation of photosynthetic variables to warming. However, this pattern is consistent with literature suggesting that tropical plants are likely to be more negatively affected by climate warming relative to species from temperate environments (Cunningham & Read, 2002; Clark *et al*., 2003; Wang *et al*., 2014), but see Cheesman & Winter (2013), and literature showing constrained acclimation to warming at the warm edge of species' distributions (Way & Sage, 2008a,b; Wertin *et al*., 2011; Crous *et al*., 2013). The literature on photosynthetic acclimation to warming is discordant; many studies indicate that the temperature optimum of photosynthesis ($T_{opt}$) increases in response to warming in many species (Slatyer & Ferrar, 1977; Read & Busby, 1990; Kattge & Knorr, 2007; Sage & Kubien, 2007; Gunderson *et al*., 2010; Smith & Dukes, 2013), however, other studies suggest that photosynthetic capacity and $T_{opt}$ do not acclimate to changes in growth temperature (Ferrar *et al*., 1989; Way & Oren, 2010; Lin *et al*., 2012) or that acclimation potential is reduced at high temperatures (Crous *et al*., 2013). Thus, plants vary in their capacity to acclimate photosynthetic traits in response to warming and some of this variation appears to be explained by major life history adaptations related to intrinsic relative growth rate and plant functional type (Read & Busby, 1990; Tjoelker *et al*., 1998; Atkin *et al*., 2006; Bunce, 2008; Volder *et al*., 2010; Cheesman & Winter, 2013; Smith & Dukes, 2013). We suggest that intraspecific variation in phenotypic plasticity of leaf gas exchange traits is also an important source of variation in plant acclimation to warming and appears to be arrayed along biogeographic clines of population origin.

While acclimation of leaf-level photosynthesis was correlated with the growth response across provenances, the accumulation of total plant leaf area was a stronger predictor of growth response to warming (e.g., Fig. 5, Figure S2). Warming likely altered meristem and leaf development; while these processes were not the focus of this study, they are clearly important in this and other warming experiments with trees (e.g., Hänninen *et al*., 2007; Way & Oren, 2010; Fu *et al*., 2012).

### *Implications for climate warming effects on tropical forests*

There is considerable concern regarding negative effects of climate change on tropical forests, particularly regarding drought effects on forest dieback (Cramer *et al*., 2001; Phillips *et al*., 2009; Allen *et al*., 2010). For example, increasing sea surface temperatures in the tropical North Atlantic can lead to reduced dry-season precipitation in Amazonia through a northwards shift in the intertropical convergence zone (Cox *et al*., 2008) and these drought events are associated with widespread tree mortality and reductions in growth rate (Phillips *et al*., 2009). Thus, climate warming is expected to have indirect negative effects on tropical forest C-sinks associated with drought. This is most extensively documented in the Amazon, but similar

patterns have been documented or predicted across the globe (Hughes, 2003; Allen *et al*., 2010).

The current study, however, suggests that climate warming may negatively affect C uptake and growth of tropical trees independent of drought. Even in well-watered conditions, photosynthetic capacity (Fig. 3), light-saturated photosynthesis (Fig. 5), absolute growth rate, relative growth rate, and total biomass (Figs 5 and 6) were all reduced by +3.5 °C warming in warm-origin taxa of tropical origin. Warming of +3.5 °C in 2100 relative to 1900 is well-within predictions for a range of representative pathways of rising greenhouse gas concentrations (Collins *et al*., 2013). Thus, this study adds to the growing understanding that increased temperatures are likely to directly reduce tree C uptake in warm forests (Cunningham & Read, 2002; Clark *et al*., 2003, 2010; Doughty & Goulden, 2008) and that increased water stress is likely to accentuate the negative effect of rising temperature on photosynthetic carbon gain (e.g., Wang *et al*., 2014). Eastern Australia is projected to receive more variable rainfall in the future, potentially with increased annual amounts in the north but reduced amounts in the south (Teng *et al*., 2012; Sillmann *et al*., 2013); these patterns of altered precipitation, in association with other climate factors such as elevated $CO_2$, are likely to further influence the direct effects of increased temperature studied here.

In this climate-shift experiment, we found that the effect of +3.5 °C warming on tree growth and physiology strongly interacted with the taxa's climate-of-origin, suggesting that climate warming during this century is likely to have differential effects across the range of widely distributed species. Cool-origin plants likely have the flexibility to alter physiological and structural traits to cope with warming, while warm-origin plants are likely to have a constrained ability to alter traits and may be negatively affected by warming. These results have widespread implications for the survival and persistence of warm-origin trees, as well as the treatment of photosynthetic and respiratory acclimation potential in ecosystem and earth system models (Smith & Dukes, 2013).

## Acknowledgements

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Acclimation of photosynthetic capacity to +3.5 °C warming depended on home climate. Here, photosynthesis is expressed per unit leaf mass for *E. grandis* (a) and *E. tereticornis*. Each symbol reflects a home temperature category and was calculated as the mean of 6 observations for each of 3 provenances; error bars reflect ±1 SEM. Open symbols reflect plants grown and measured in their home climate. Gray symbols reflect plants grown in their home climate but measured in the warmed climate of +3.5 °C. Black symbols reflect plants that were grown and measured in the warmed climate condition. The dashed line reflects the short-term effect of temperature and the solid line reflects the long-term effect of temperature, which potentially includes acclimation. Plants from cool origins (left sides of graphs) acclimated to warming by increasing photosynthetic capacity, while plants from warm-origins (right sides of graph) acclimated to warming by reducing photosynthetic capacity. Plants from intermediate origins (middle of each graph) displayed little acclimation to warming, as the short-term and long-term effects of warming were similar.

**Figure S2.** Clinal response of the change in absolute growth rate (AGR; a), total plant leaf area (b), and photosynthetic capacity ($A_{max}$; c) to experimental warming of +3.5 °C in relation to the mean annual temperature (MAT) at the seed source of each provenance. All data are expressed as a percentage change in the warmed treatment relative to the home treatment. Nine provenances of *E. grandis* and twelve provenances of *E. tereticornis* were studied. Plotted lines reflect the best fits. (a) The AGR response of *E. tereticornis* followed a second order polynomial ($y = -270 + 36.5x - 1.04\ x^2$, $r^2 = 0.65$, $P < 0.01$) while the relationship for *E. grandis* followed a segmented linear regression (intercept = 622, break point = 19.37 °C, slope below break point = −32.7, slope above break point = 1.6, $r^2 = 0.92$, $P < 0.01$). (b) Similarly, the leaf area response of *E. tereticornis* followed a second order polynomial ($y = -242.4 + 32.0x - 0.91\ x^2$, $r^2 = 0.54$, $P < 0.05$) while the relationship for *E. grandis* followed a segmented linear regression (intercept = 360, break point = 19.23 °C, slope below break point = −19.0, slope above break point = 0.66, $r^2 = 0.67$, $P < 0.05$). (c) The $A_{max}$ response followed a linear relationship for *E. tereticornis* ($y = 63.7 - 2.7x$, $r^2 = 0.25$, $P < 0.05$) and followed a nonsignificant trend for *E. grandis* ($y = 72.1 - 3.2x$, $r^2 = 0.1$, $P = 0.2$).