Climate suitability of diverse provenances of a widely-distributed eucalypt: Testing the 'local is best' paradigm under climate warming

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Environmental suitability of local provenances under climate warming

It is commonly recommended that revegetation efforts use local provenances (seed sources) of tree species, as they will be well-adapted to the local environment. As climate warms, local provenances may cease to be well adapted. It is argued that assisted migration through translocation of seeds or plants originating in warmer climates will ensure that local vegetation is 'climate ready.' There are myriad factors that can potentially shape the environmental suitability of a local provenance, including rainfall, soil type, fire frequency or competition, among others. However, for many tree species, the importance of temperature in determining environmental suitability is not known.

Moreover, it is generally unknown whether adaptation to temperature varies among provenances within a species. For widespread tree species, it may be argued that provenances should be suitable for planting anywhere within their native climatic range. However, widespread tree species often exhibit substantial variation within their range, with differences in morphology and growth observed along environmental gradients. If this variation is the result of spatially structured genetic differentiation along climatic gradients, then matching provenance to local climate might be important even when planting widespread species. Local adaptation to temperature in a provenance would represent a genetically based constraint on climatic tolerance and thus environmental suitability in the face of climate warming.

Thus, to determine whether consideration of temperature adaptation is important when choosing provenances, there are two key questions to address: first, how sensitive is the species to temperature; and second, how does this sensitivity vary among different provenances? Exploring these two questions in controlled temperature experiments provides a test of the 'local is best' prediction for provenances under climate warming.

Climate warming experiments with Forest Red Gum (*Eucalyptus tereticornis*)

We examined these questions in a series of glasshouse warming experiments with different provenances of *E. tereticornis*. This tree species is widely-distributed along the eastern coast of Australia, with a native range spanning approximately 2,500 kilometres and approximately 13°C in mean annual temperature from temperate climates in the south to tropical climates in the north. We used twelve diverse provenances originating from locations spanning the geographic and climatic range of this species (Figure 1).

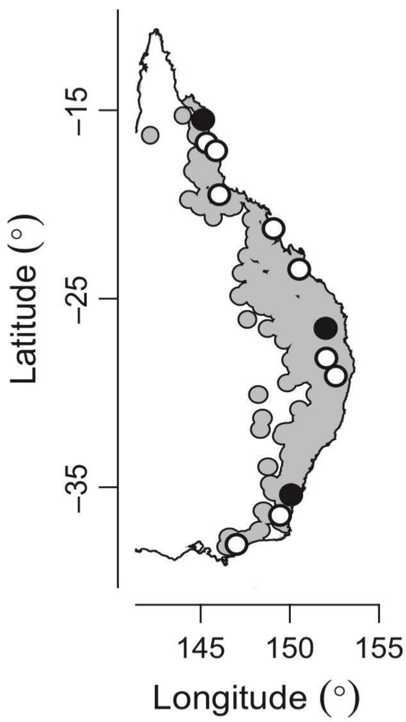

Figure 1. The distribution of *Eucalyptus tereticornis* in geographic space. Grey symbols reflect the species' native range as determined by occurrence records in the Atlas of Living Australia. White and black circles together denote provenances studied in a climate-shift experiment reported in Drake *et al*. (2015). Three of those provenances were selected and studied in a comparison of provenances experiment in Drake *et al*. (2017); these are denoted by black circles (reproduced with permission).

Climate shift experiment

In the first experiment (Drake *et al*., 2015), we grew 12 diverse provenances from seed in an array of common-garden environments designed to represent local (home) as well as warmed (home + 3.5°C) conditions. Provenances were divided into four groups, which were each assigned to two glasshouses: one, a 'home' environment where the temperature mimicked mean summertime temperature conditions at the seed origin and two, a 'warmed' environment representing a climate shift of + 3.5°C. The range of home environments collectively spanned the native climatic range of the species.

We found that the 12 provenances differed in response to experimental warming of 3.5°C relative to their home climate-of-origin in a manner that depended on their geographic origin. Warming increased photosynthetic capacity and growth in southern cool-origin provenances, whereas the opposite was observed in northern warm-origin provenances, which exhibited reduced photosynthetic capacity and growth. Consequently, the capacity to cope with climate warming declines from temperate to tropical latitudes in this species. However, this experiment did not establish whether provenances from different parts of the species' range are locally adapted and thus differ in ability to cope with warming, particularly if translocated far from their provenance of origin.

Comparison of provenances experiment

We designed a follow-up study to distinguish whether or not cool-origin, central and warm-origin provenances were adapted to local temperature or shared a broad climatic suitability irrespective of climate of origin (Drake *et al*., 2017). In this second study, the provenances were each grown in a full array of six mean summertime daily temperature regimes that spanned and exceeded the native geographic range of the species. We found that the temperature responses of photosynthesis and growth were equivalent across the three provenances (Figure 2), reflecting a nearly identical response to temperature despite a 2,200-km geographic distance and 13°C difference in mean annual temperature at seed origin. The climatically diverse provenances did not exhibit local adaptation to temperature in terms of their temperature sensitivity of photosynthesis and growth.

Conclusions

These two experiments demonstrate that *E. tereticornis* exhibits a broad and peaked response of photosynthesis and growth to temperature that mirrors the widespread native geographic and climatic range of the species. This leads to the prediction that increasing temperatures expected with climate warming will enhance growth in local provenances in the southern, cooler portions of the species' range, whereas local provenances in the northern, warmer portions of the range will exhibit little change or even declines in growth with warming (Figure 3).

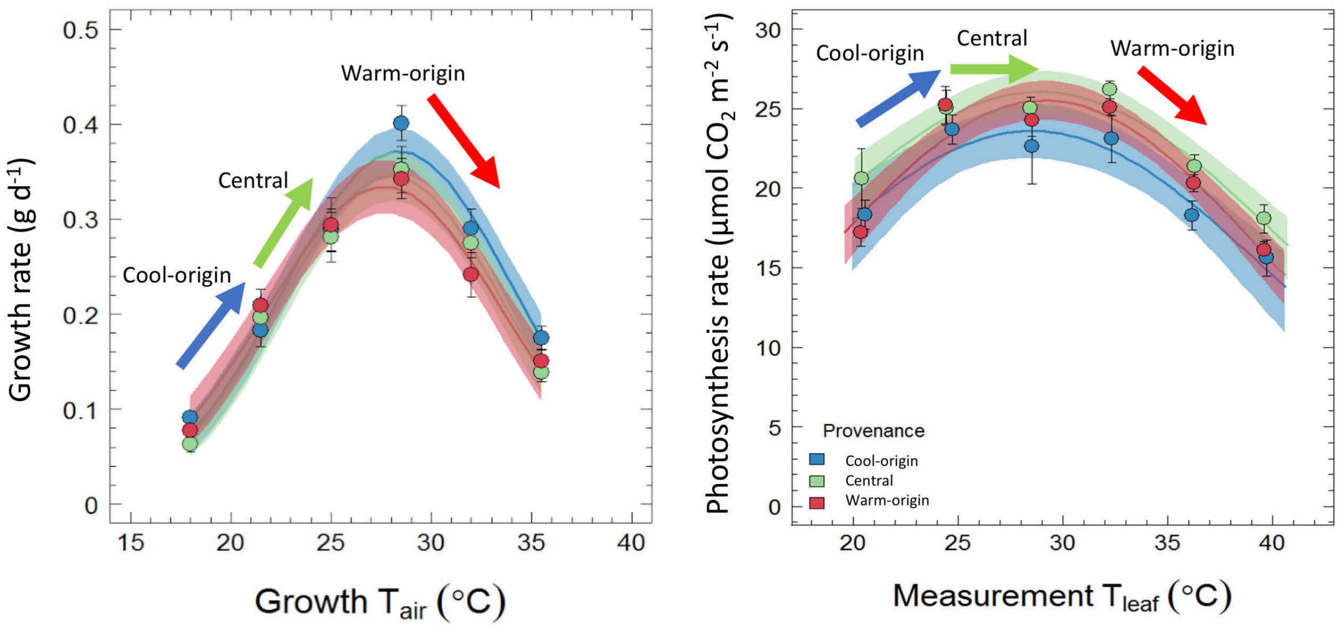

Figure 2. Temperature sensitivity of growth and photosynthesis in response to temperature of the growing environment in widely-distributed *E. tereticornis*. Each point represents either a cool-origin (blue, 18°C mean summer temperature), central (green, 21.5°C) or warm-origin (red, 28.5°C) provenance grown in each of six mean daily summertime growth temperatures that together span the entire native geographic range of the species. Growth was measured as dry mass growth rate (grams per day) and photosynthesis as light-saturated net photosynthesis of leaves (μmol CO_2 m^{-2} s^{-1}) for plants measured under growth conditions. Symbols are the mean ± SE. Growth and photosynthesis respond to temperature with a peak near 28°C and temperature sensitivity did not differ among contrasting cool-origin, central, and tropical warm-origin provenances of *E. tereticornis* (Drake *et al*., 2017). Arrows show direction and magnitude of each provenance's response to +3.5°C warming relative to their local climate.

Furthermore, the experiments provide evidence that provenances of *E. tereticornis* are not locally adapted in their temperature responses of photosynthesis and growth. The provenances all shared the same underlying temperature response functions. Consequently, in terms of temperature sensitivity of growth at the seedling stage, provenance choice for revegetation should not matter. In other words, we found no evidence that 'local is best' with respect to direct temperature effects on growth. Despite the lack of provenance differentiation in underlying temperature sensitivity, the impacts of climate warming will nonetheless vary across the geographic range of this widespread eucalypt species, depending on each provenance's local climate position on the species' temperature response curves for photosynthesis and growth.

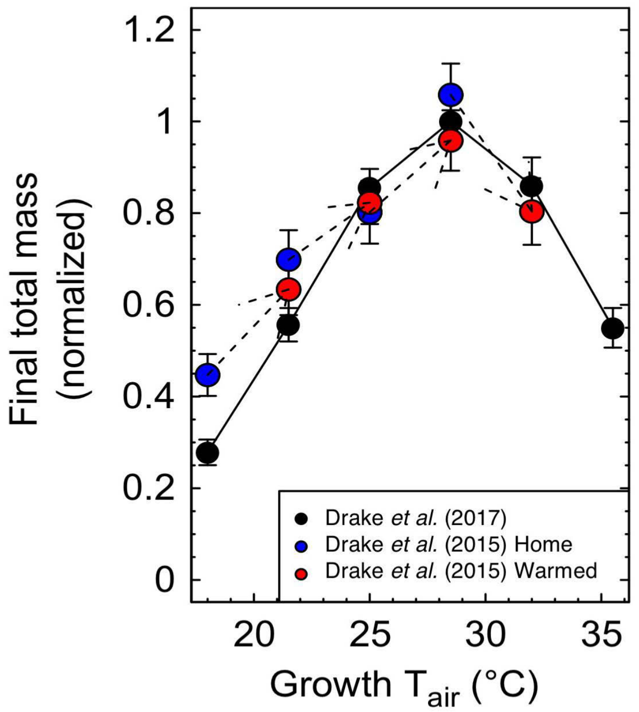

Figure 3. A comparison of temperature sensitivity of growth in two experiments with *E. tereticornis*. Growth was measured as final dry mass of harvested plants and was normalized to mean final mass at the peak growth temperature of 28.5°C. Points reflect the means and error bars reflect 1 SE. The data from Drake *et al*. (2017) are the combined and averaged responses of three provenances grown at all six temperatures, whereas the data from Drake *et al*. (2015) are the combined and averaged responses of four groups of three provenances grown in their respective temperature environments ('home' and warmed by +3.5°C). Dashed arrows show the directional effect of +3.5°C warming for each of the four provenance home groups.

The lack of local adaptation among provenances in temperature sensitivity of growth is perhaps surprising. Even though seed dispersal is typically rather poor in eucalypts, which in effect would preserve local genetic differences, long distance movement of pollen by bats and birds is one possible means for more widespread genetic mixing. In addition, the existence of abundant genetic variation within local provenances or weak selection pressure by temperature could also explain the lack of local adaptation along environmental temperature gradients.

Our studies were designed to isolate the direct effects of temperature. Other factors such as water and nutrient availability may modify the temperature sensitivity of growth or influence survival. In addition, our study examined seedlings, arguably a critical and environmentally sensitive bottleneck in terms of plant establishment. Yet temperature sensitivity in other life stages and processes, such as reproduction, remains an open question.

Nonetheless, these findings provide evidence that local adaptation to temperature among provenances in a widely-distributed species is less important than previously thought. Furthermore, provenance choice for replanting or translocation does not appear to be restricted by temperature of origin, perhaps expanding opportunities for wider seed source utilisation with climate warming.

Acknowledgements

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References

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