



Geographic range size, seedling ecophysiology and phenotypic plasticity in Australian *Acacia* species

Catherine L. Pohlman^{1*}, Adrienne B. Nicotra¹ and Brad R. Murray²

¹School of Botany and Zoology, Australian National University, Canberra, ACT, and

²Institute for Water and Environmental Resource Management, University of Technology, Sydney, Gore Hill, New South Wales, Australia

ABSTRACT

Aim The degree to which eco-physiological traits critical to seedling establishment are related to differences in geographic range size among species is not well understood. Here, we first tested the idea that seedling eco-physiological attributes associated with establishment differ between narrowly distributed and geographically widespread plant species. Secondly, we tested the notion that species occupying wide geographic ranges have greater phenotypic plasticity in response to the environment than contrasted species with more restricted distributions.

Location Eastern Australia.

Methods We compared five pairs of geographically restricted and widespread *Acacia* species grown under glasshouse conditions for differences in seedling relative growth rate and associated allocational, morphological and physiological traits. We then examined whether widespread species displayed greater phenotypic plasticity in these traits than narrowly distributed species in response to changes in soil water availability.

Results Neither relative growth rate nor any measure of biomass accumulation or allocation differed significantly between seedlings of narrowly distributed and widespread species. In addition, the plasticity of biomass allocation was not greater in widespread species. However, the leaflets of widespread species had higher photosynthetic capacity and greater plasticity of water use efficiency than the leaflets of narrowly distributed species.

Main conclusions We demonstrated fundamental differences in the physiology and plasticity of leaflets of widespread and narrowly distributed species. The greater plasticity of these seedling leaflet traits may allow widespread *Acacia* species to utilize a wider range of environmental conditions in relation to soil moisture than restricted *Acacia* species. However, we did not find corresponding differences in mean or plasticity of seedling growth and allocational traits. In general, we suggest that relationships between rarity and species traits are both context and taxon specific.

Keywords

Acacia, Australia, phenotypic plasticity, range size, relative growth rate, seedling, specific leaf area, water availability.

*Correspondence and present address:
Catherine L. Pohlman, School of Tropical Environment Studies & Geography (TESAG), James Cook University, PO Box 6811, Cairns, Queensland 4870, Australia.
E-mail: catherine.pohlman@jcu.edu.au

INTRODUCTION

Although plant species vary widely in the size of their geographic ranges, there is a paucity of studies investigating the degree to which ecophysiological traits linked to seedling establishment

are related to differences in range size (e.g. Baskauf & Eickmeier, 1994; Robson & Maze, 1995; Sultan *et al.*, 1998). In contrast, numerous studies have explored how plant life-history and ecological traits relate to interspecific variation in range size (reviewed in Bevill & Louda, 1999; Murray *et al.*, 2002a). With

the exception of a few traits (e.g. seed size), these studies have yet to demonstrate general correlations with range size (Murray *et al.*, 2002a). Yet, physiological attributes influencing seedling establishment clearly have considerable potential for shaping the geographic extents of species (e.g. Brändle *et al.*, 2003, but see Thompson & Ceriani, 2003).

Furthermore, the potential for phenotypic plasticity in seedling attributes to differ between narrowly distributed and widespread flowering plant species has received very little attention (e.g. Rapson & Maze, 1994; Bell & Sultan, 1999). Phenotypic plasticity is the range of variation individuals of a given genotype may show in response to the environment (Bradshaw, 1965; Schlichting, 1986). By altering traits in response to environmental conditions, plants are able to respond adaptively to a range of environments and thus utilize a wider range of habitats than would be possible if all traits were 'fixed' (Sultan, 1995). Widespread species are likely to face a variety of conditions throughout their ranges, and to show genotypic differentiation within the range (Gaston, 2003). In addition to such variation in genotypic variation, widespread species may show greater phenotypic variation, or plasticity, in response to environmental factors.

In the present study, we tested two hypotheses. First, we tested the idea that seedling ecophysiological attributes associated with establishment differ between narrowly distributed and geographically widespread plant species. We compared potential relative growth rates (RGRs) and associated biomass allocation and physiological traits between seedlings of narrowly distributed and widespread *Acacia* species of eastern Australia. Second, we tested the notion that species occupying wide geographic ranges differ in extent of phenotypic plasticity in response to the environment relative to species with more restricted distributions. We made no *a priori* predictions as to the direction of mean differences in eco-physiological traits between widespread and narrowly distributed species, as previous research indicates these are not highly predictable (reviewed in Beville & Louda, 1999; Murray *et al.*, 2002a). However, we predicted that the plasticity of response would be greater in widespread than narrowly distributed species. The plasticity of the seedling traits was assessed in response to differing water availability. Water availability is an important factor influencing plant growth (e.g. McConnaughay & Coleman, 1999; Poorter & Nagel, 2000), particularly in the context of the dry Australian environment. We predicted that widespread species would demonstrate greater plasticity in their traits in response to the imposition of different experimental soil water availabilities.

METHODS

Study species

Five pairs of narrowly distributed and widespread Australian *Acacia* species were compared. Species were paired geographically, such that the entire distribution of each narrowly distributed species was contained within the range of the

widespread species. Potential species distributions were modelled using the program BIOCLIM (Busby, 1986, Fig. 1). Where more than one combination for a species was possible, species pairs were chosen on the basis of similar habitat requirements (according to the habitat descriptions given in Stanley & Ross, 1983; Harden, 1991) and where there still remained more than one possible combination, species pairs were assigned arbitrarily. All ten species are either trees or small trees in growth form. The widespread species *Acacia melanoxylon* (R. Br.) was paired with the narrowly distributed species *A. cincinnata* (F. Muell.). Similarly, *A. irrorata* (Sieber ex Spreng.) was paired with *A. elata* (A. Cunn. Ex Benth.), *A. implexa* (Benth.) with *A. fulva* (Tindale), *A. dealbata* (Link) with *A. trachyphloia* (Tindale) and *A. mearnsii* (de Willd.) with *A. silvestris* (Tindale) (Table 1). Three of the species had phyllodinous leaves: *A. cincinnata*, *A. melanoxylon*, and *A. implexa*.

A complete molecular phylogeny that distinguishes the relationships between species does not yet exist for the genus *Acacia* (J. Miller, pers. comm.). Current work demonstrates that even sectional delineations in the *Acacias* are not always monophyletic (Miller *et al.*, 2003), as such the existing taxonomy (as presented in CSIRO, 1999) cannot be used to infer phylogenetically independent contrasts (PICs). Thus, we chose to work with geographic rather than phylogenetic pairs.

For each species pair, five seedling provenances were chosen to cover the range of the restricted species' geographic distribution. The seedling provenances of the widespread species were chosen to occur as close to those of the restricted species as possible (Table 2). Seeds were obtained from the Australian Tree Seed Centre (CSIRO Forestry and Forest Products, Canberra, Australia) and were bulk samples originally sourced from multiple parents at each seed provenance. Provenance A for *A. fulva* was excluded from the analysis when it was found to belong to another *Acacia* species. Each pair of species was assigned to a single experimental block.

Provenance pairs were compared to ensure that pairs did not differ in mean annual temperature or mean annual precipitation. We used the program BIOCLIM (Busby, 1986) to generate estimates of mean annual temperature and annual precipitation for each provenance of each species. Paired *t*-tests indicated that there were no significant differences in mean annual temperature or annual precipitation between narrowly distributed and widespread members of pairs ($t = -0.56$, d.f. = 23, $P = 0.581$ and $t = -1.091$, d.f. = 23, $P = 0.287$ for mean annual temperature and annual precipitation, respectively).

Experimental design

To allow the determination of potential RGR, six replicate plants from each of five seedling provenances per species were grown at high soil water availability ($n = 6$ replicates \times five provenances \times 10 species). Half the seedlings were harvested between weeks 8 and 10 of the experiment and the remaining seedlings were harvested between weeks 16 and 17. To

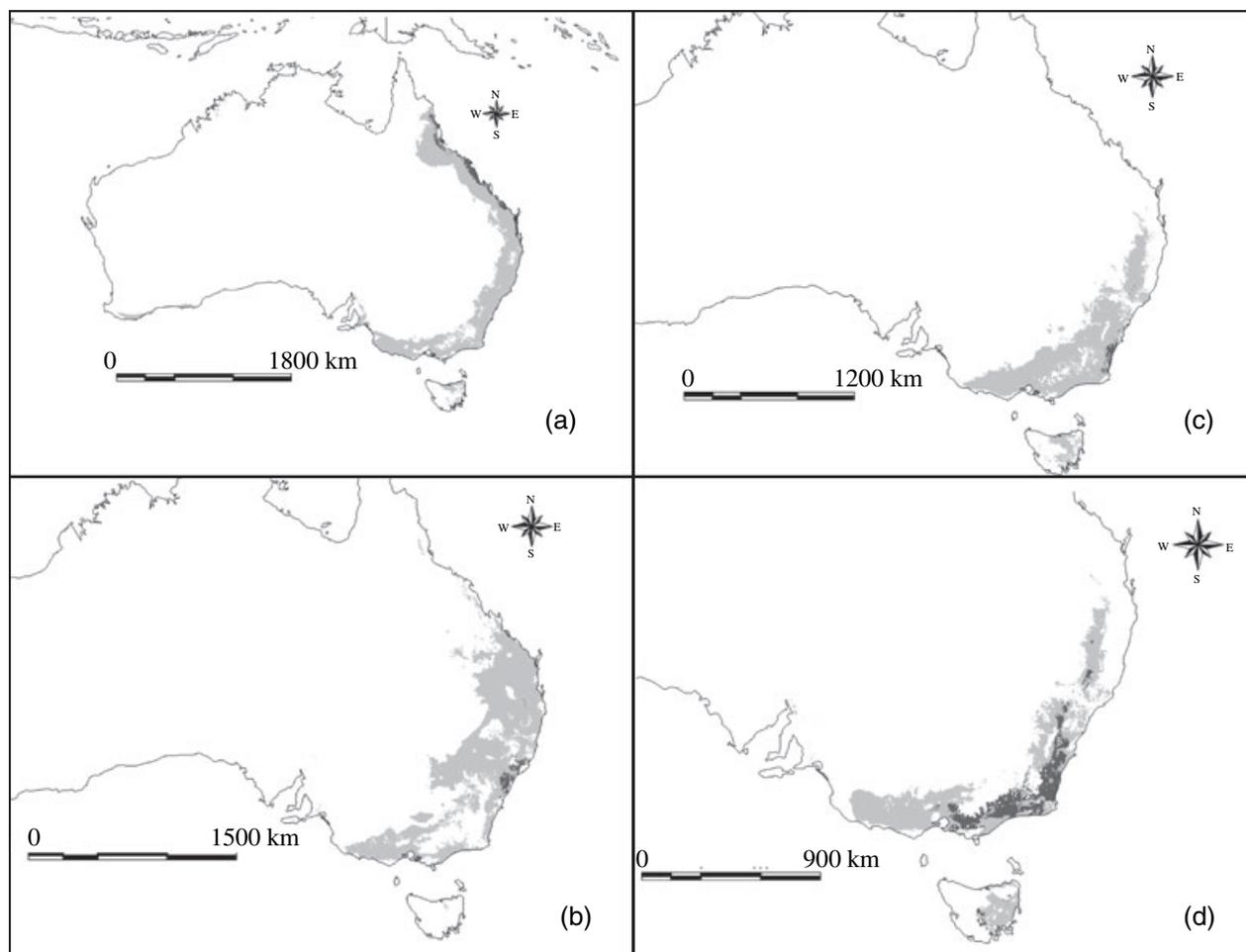


Figure 1 Contrasting geographic distributions of four of the five species pairs used in the study. A comparative map for *A. elata* (rare) and *A. irrorata* (common) is not shown, as the small number of distribution records for *A. irrorata* precluded the construction of a useful BIOCLIM map. Ranges of restricted (dark shading) and widespread (light shading) species are represented by potential climatic ranges calculated using the program BIOCLIM (Busby, 1986). (a) *A. cincinnata* (rare) and *A. melanoxyton* (common), (b) *A. fulva* (rare) and *A. implexa* (common), (c) *A. trachyphloia* (rare) and *A. dealbata* (common) and (d) *A. silvestris* (rare) and *A. mearnsii* (common).

Table 1 Pairings of geographically restricted (R) and widespread (W) *Acacia* species examined in the present study. Taxonomy, life-history and habitat information from Harden (1991) and Stanley & Ross (1983)

Pairing	Rarity	Species	Growth form	Height (m)	Leaf design	Habitat
1	R	<i>A. cincinnata</i>	Small tree	To 8 m	Phyllodineous	Wet sclerophyll and rainforest
	W	<i>A. melanoxyton</i>	Tree	6–30 m	Phyllodineous	Wet sclerophyll and rainforest
2	R	<i>A. silvestris</i>	Tree	8–30 m	Bipinnate	Dry sclerophyll
	W	<i>A. mearnsii</i>	Tree	7–10 m	Bipinnate	Dry sclerophyll
3	R	<i>A. trachyphloia</i>	Tree	4–18 m	Bipinnate	Dry sclerophyll
	W	<i>A. dealbata</i>	Tree	5–12 m	Bipinnate	Coastal communities
4	R	<i>A. fulva</i>	Tree	3–10 m	Bipinnate	Dry sclerophyll
	W	<i>A. implexa</i>	Tree	5–12 m	Phyllodineous	Coastal communities
5	R	<i>A. elata</i>	Tree	8–18 m	Bipinnate	Wet sclerophyll and rainforest
	W	<i>A. irrorata</i>	Tree	4–12 m	Bipinnate	Dry sclerophyll

compare the plasticity of narrowly distributed and widespread species in response to soil water availability, an additional three replicate plants per seedling provenance from each species were grown at low soil water availability and harvested

at the same time as the second RGR harvest. Plants grown at low and high soil water availability were then compared ($n = 3$ replicates \times five provenances \times 10 species \times two treatments).

Table 2 Seedling provenances for each of the geographically restricted (R) and widespread (W) study species. Seeds were supplied by the Australian Tree Seed Centre and CSIRO Plant Industry

Pr	Restricted					Widespread				
	Species	Provenance	Location	Latitude	Longitude	Species	Provenance	Location	Latitude	Longitude
1	<i>A. cincinnata</i>	A	Mossman	16° 35'	145° 25'	<i>A. melanoxydon</i>	A	WSW Atherton	17° 18'	145° 25'
		B	Kuranda SF	16° 42'	145° 42'		B	Ravenshoe	17° 35'	145° 25'
		C	Lake Cootharaba	26° 17'	152° 17'		C	Cascade	30° 13'	152° 49'
		D	Gympie	26° 11'	152° 40'		D	Mt Mee-Sellins Rd	27° 06'	152° 44'
		E	Tuan SF	25° 44'	152° 44'		E	Bli Bli	26° 37'	153° 02'
2	<i>A. silvestris</i>	A	WNW Narooma	36° 11'	150° 01'	<i>A. mearnsii</i>	A	East Lynne	35° 36'	150° 17'
		B	Deua River	35° 43'	149° 50'		B	Araluen	35° 39'	149° 49'
		C	W of Narooma	36° 14'	149° 48'		C	Brogo River	36° 28'	149° 35'
		D	Wadbilliga NP	36° 16'	149° 38'		D	Mt Gladstone	36° 14'	149° 08'
		E	Bruthen	37° 43'	147° 50'		E	Wattle Cir Omeo	37° 27'	147° 50'
3	<i>A. trachyphloia</i>	A	Batemans Bay	35° 44'	150° 15'	<i>A. dealbata</i>	A	Bemboka	36° 38'	149° 35'
		B	Currowan Creek	35° 35'	150° 03'		B	Tidbinbilla.	35° 27'	148° 57'
		C	Monga SF	35° 36'	149° 55'		C	Boorowa	34° 38'	148° 48'
		D	Monga SF	35° 34'	149° 55'		D	Abercrombie River	34° 14'	149° 47'
		E	Braidwood	35° 29'	149° 55'		E	Kandos	35° 52'	149° 48'
4	<i>A. fulva</i>	A*				<i>A. implexa</i>	A	Sofala	33° 05'	149° 41'
		B	Mt Yengo	32° 59'	150° 51'		B	Bylong	32° 37'	150° 03'
		C	Howes	32° 51'	150° 51'		C	Bermagui	36° 24'	150° 02'
		D	Wollemi NP	32° 35'	150° 52'		D	Moonan	31° 55'	151° 14'
		E	Singleton	32° 34'	151° 10'		E	Swansea	33° 05'	151° 37'
5	<i>A. elata</i>	A	Brimstone Creek	34° 03'	150° 29'	<i>A. irrorata</i>	A	Stony Creek	36° 06'	150° 03'
		B	Buxton	34° 15'	150° 32'		B	Bodalla	36° 06'	150° 38'
		C	Gloucester Tops	32° 05'	151° 38'		C	Karuah-Newcastle	32° 39'	151° 57'
		D	Mount Boss SF	31° 14'	152° 22'		D	Gloucester	32° 01'	151° 58'
		E	Wauchope	31° 28'	152° 44'		E	Girard	28° 18'	152° 56'

**A. fulva* originally had five seedling provenances but provenance A was eliminated from the analysis when it was found to belong to another *Acacia* species.

Seedling germination and growth

Seeds were sterilized with 2% bleach, soaked in boiling water, placed in sterile Petri dishes in a growth cabinet (25 °C/16 °C, 12 h/12 h day/night) and irrigated with distilled water until germination. On germination, seedlings were transferred into pots of sterilized sand (4 cm × 4 cm × 8 cm depth), placed under automatic watering and grown under benign conditions in the greenhouse until they were large enough to be transplanted into the main experiment. All seedlings except those of *A. cincinnata* and *A. melanoxydon* were transplanted in the first week of July, 2000. *Acacia cincinnata* seedlings required an extra 2 weeks' growth before they were large enough to survive the transfer. Each pair of restricted and widespread species was planted on the same day. Plants were randomized within each block (species pair) in the greenhouse.

High soil water-treatment plants were potted in a sand-vermiculite mixture whilst the lower soil water-treatment plants were potted into pure sand. Pilot tests determined that the high water mixture had approximately twice the water holding capacity of sand alone (0.018 and 0.041 mL cm⁻³ for sand and sand-vermiculite mixes, respectively). Pots were 9 cm in

diameter and c. 45 cm deep to avoid root restriction. All plants were fertilized with Osmocote (Scotts Australia, Pty Ltd, Baulkham Hills, Australia) slow release fertilizer, which was supplemented approximately fortnightly with Aquasol [Hortico (Aust.) Pty Ltd, Homebush, Australia]. Plants were grown in the presence of ample nitrogen in sterile potting media to minimize likelihood of forming nodules with symbiotic nitrogen fixing *Rhizobium* bacteria. For 9 weeks following transplanting, plants were watered daily or twice daily as needed. The difference in the water holding capacity of the two sand mixes was expected to produce a difference in water availability. Once the seedlings were established, watering frequency was altered to increase the difference in water availability between the two treatments: the high water treatment plants were watered twice a day whilst the low water treatment plants were watered once every 2 days. From 3 October (13 weeks into the experiment) onwards, high water treatment plants were watered twice a day and low water treatment plants were watered only when they appeared to be experiencing some degree of water stress.

The seedlings were grown in a greenhouse with a thermostat set at a temperature of 20 °C, however, on hot days the system could not maintain these cool temperatures. Towards the end

of the experiment, the temperature regularly exceeded 30 °C on clear days and on two occasions, technical problems led to overheating events (> 40 °C). Light levels in the glasshouse reached c. 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ on clear days.

The first harvest to determine RGR occurred between weeks 8 and 10. The harvest to determine plasticity and RGR was conducted between weeks 16 and 17. The first harvest was timed to allow the three species that produced phyllodes to pass through the transitional stage between juvenile leaves and phyllodes. Although there was some persistence of leaflets, most plants had attained their adult leaf types by the time of the harvest. Seedlings of *Acacia* species from arid and mesic environments still exhibit exponential growth at 13 weeks (Atkin *et al.*, 1998, 1999) and, as phyllode production may affect the average growth rate of seedlings (Atkin *et al.*, 1998), we decided to wait until phyllode production had begun, before measuring RGR.

Seedling growth measurements

At harvest, the leaflets, phyllodes, stems and roots of each plant were dried between 60 ° and 75 °C to constant mass and weighed. Total leaflet area and total foliage area (leaflets and phyllodes) were measured for each plant by scanning foliage with a flatbed computer scanner and then analysing the images with NIH Image (US National Institutes of Health and available at <http://rsb.info.nih.gov/nih-image/>). From these measurements, it was possible to calculate the total dry mass, root to shoot ratio (g root/g shoot), foliage mass ratio (g foliage/g total plant biomass), specific leaflet area (cm^2 leaflet area/g leaflet mass) and specific foliage area (SFA) [$(\text{cm}^2 \text{ phyllode} + \text{cm}^2 \text{ leaflet area})/(\text{g phyllode mass} + \text{g leaflet mass})$] for each plant. Seedling RGR of each seedling provenance was calculated according to the following formula:

$$\frac{\text{average } \ln(\text{total dry mass, harvest two}) - \text{average } \ln(\text{total dry mass, harvest one})}{\text{time (harvest two)} - \text{time (harvest one)}}$$

Leaf level physiology

Physiological measurements were taken on the leaves of plants from both soil water availability treatments between weeks 12 and 15. An initial set of gas exchange measurements was made on the youngest fully expanded leaf of one randomly selected plant per treatment for each seedling provenance for all 10 species ($n = 5$ seedling provenances \times 10 species \times two water treatments = 100 plants) using a LI-6400 Portable Photosynthesis System (Li-Cor, Lincoln, NB, USA). Measurements were made at a light intensity of 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, which was determined to be a saturating light intensity for all species. Reference CO_2 concentration was set at 400 ppm, relative humidity controlled at 60%, block temperature at 25 °C and measurements were made between sunrise and midday. The measurements of interest were CO_2 assimilation (A_{max}), stomatal conductance, transpiration rate, C_i/C_a and water

use efficiency ($\text{WUE} = \text{unit carbon gained through photosynthesis/unit water lost through transpiration}$).

Dark and light chlorophyll fluorescence parameters were measured on the youngest fully expanded leaf of all plants ($n = 5$ seedling provenances \times 10 species \times two water treatments \times three replicates = 300 plants), using a WALZ Photosynthesis Yield Analyzer MiniPAM portable chlorophyll fluorometer (Walz, Effeltrich, Germany). Fv/Fm was measured several hours after sunset on leaves that had been left in darkness in order to ensure that all reaction centres of photosystem II were fully open (dark-adapted leaves). Fv/Fm is the ratio of variable fluorescence to maximal fluorescence of a dark-adapted leaf and represents the potential quantum yield of photosystem II. Electron transport rate (ETR) was measured on leaves under illumination by sunlight and thus actively photosynthesising (light-adapted leaves) in early to mid-afternoon. ETR is the rate of electron transport from the reaction centres of photosystem II and is another measure of photosynthetic capacity (Walz, 1999). The leaves were measured at ambient temperature in the greenhouse (slightly below 20 °C at night to over 30 °C on clear days).

The above initial set of gas exchange and chlorophyll fluorescence parameters were measured when all plants had been watered according to the regular water regime (high water treatment plants watered twice a day and low water treatment plants watered as needed to prevent wilting). Measurements were timed to occur on low water plants the morning after an evening watering. This led to a conservative estimate of the differences between water treatments.

To further investigate the differences between water treatments, both high- and low-water plants were subjected to a short-term water stress trial during weeks 14 and 15. This trial was imposed to determine whether widespread and restricted species respond differently to sudden, severe environmental

stress. All plants in the experiment were left to dry for 4 days without watering, at which point most plants had begun to wilt. On the morning of the fourth day, the gas exchange measurements were repeated. The dark fluorescence measurements were repeated on the evening of the fourth day and the light fluorescence measurements on the following afternoon. Most of the plants had to be watered again before the final set of light fluorescence measurements were taken, to prevent mass mortality, although it took most plants several days to visibly recover from the drought condition treatment.

Statistical analysis

Seedling growth and allocation

Results were analysed using a general linear mixed model in which the fixed effects were range size (restricted or widespread), soil water availability treatment (low or high) and all interaction

terms, whilst the random effects were block (species pair), seedling provenance, replicate plant and all interaction terms. The two fundamental levels of replication in this experiment were at the level of block (species pair) and seedling provenance within each block. For this reason, statistical inferences were not drawn at the level of provenance within species or at the level of species within species pair, but rather on general patterns across all species pairs. All biomass measurements were ln-transformed before analysis to approximate normality. As the RGR measurements were taken from the averaged values for the high water treatment of each seedling provenance, the fixed term treatment and the random term of plant replicate were not included in the model for this parameter. For all parameters other than RGR, the focus of the statistical analysis was on the effects of range size, soil water treatment and their interaction. A significant range size by soil water treatment interaction term would indicate a difference in the plasticity of restricted and widespread species in response to water availability.

Leaf-level physiology

Results were analysed using a general linear mixed model in which the fixed effects were range size category, soil water treatment, drought condition (drought or watered) and their interactions, whilst the random effects were block (species pair), seedling provenance and their interactions. Plant replicates were included as random effects for the analysis of the fluorescence measurements. Inferences about these results were drawn in a similar manner to that described for the seedling growth measurements.

As species were paired geographically rather than phylogenetically, it is possible that the results obtained may have differed if species had been paired in a different way. To examine the effect of species pairing, we randomly altered the species pairing and analysed the data again, ten times, for a single parameter. We chose A_{\max} because of the significant

differences between restricted and widespread species observed in this parameter (see Results).

RESULTS

Seedling growth measurements

Relative growth rate did not differ significantly between seedlings of narrowly distributed and widespread species (Table 3). The random term block (species pair) by range size interaction term was significant, indicating that the RGRs of widespread species were neither consistently higher nor consistently lower than those of narrowly distributed species. This suggests that RGR is more likely to be related to the biology of the individual species than to range size.

None of the biomass measures differed between widespread and narrowly distributed species (Table 3). However, across all species, plants grown at high soil water availability were larger than plants grown at low water availability (Table 3). Likewise, plants grown at high soil water availability had greater foliage biomass, stem biomass and root biomass, as well as greater leaflet area and greater total foliage (leaflets plus phyllodes) area (Table 3). Root to shoot ratio did not differ with either soil water treatment or range size. There was a significant effect of soil water treatment on foliage mass ratio (Table 3) with plants grown at low water availability having higher values than plants grown at high water availability. The range size by treatment interaction term was not significant for any of the above parameters. Thus, the plasticity of these traits in response to soil water availability was not greater for widespread species than for narrowly distributed species.

The plasticity of the specific leaf area of leaflets (cm^2 total leaflet area/g total leaflet mass = SLA) in response to soil water availability was greater for widespread species than narrowly distributed species (Fig. 2), although this difference was not statistically significant at $P \leq 0.05$ [Wald statistic = 3.61,

Table 3 Biomass and allocational traits for all widespread vs. restricted and all low versus high soil water treatments

Parameter	Distribution					Water treatment					d.f.
	Widespread	Restricted	Wald statistic	Lsd	P-value	Low	High	Wald statistic	Lsd	P-value	
Relative growth rate	4.678	3.921	1.2	1.373	ns	NA	NA	NA	NA	NA	45
Total biomass (g)	1.939	1.628	0.5	0.920	ns	1.684	1.883	6.2	0.160	< 0.05	276
Foliage biomass (g)	1.190	0.931	0.3	0.886	ns	0.979	1.142	4.2	0.160	< 0.05	277
Stem biomass (g)	0.437	0.037	0.4	1.219	ns	0.119	0.355	7.0	0.179	< 0.01	277
Root biomass (g)	0.676	0.272	1.0	0.816	ns	0.370	0.578	6.2	0.166	< 0.05	277
Root/shoot ratio	0.407	0.429	0.24	0.089	ns	0.412	0.424	0.48	0.033	ns	272
Foliage mass ratio	0.477	0.501	1.59	0.038	ns	0.498	0.480	7.53	0.013	0.006	272
Total leaflet area (cm^2)	422.5	486.8	2.9	75.68	ns	403.1	506.2	7.39	65.60	0.007	278
Total foliage area (cm^2)	484.3	503.5	0.26	75.58	ns	432.0	555.8	10.85	75.50	< 0.001	278
SFA ($\text{cm}^2 \text{g}^{-1}$)	125.5	143.5	10.71	10.94	0.001	132.3	136.7	0.73	10.92	ns	271

Means predicted from linear model. Lsd at the 0.05 significance level represents 2 times the standard error of the difference for each parameter; d.f. refers to both range size and water treatment. The first column of P-values is for differences between range sizes, while the second column of P-values is for differences between soil water treatments. RGR was not subject to water treatment. Total, foliage, stem and root biomass were ln-transformed prior to analysis.

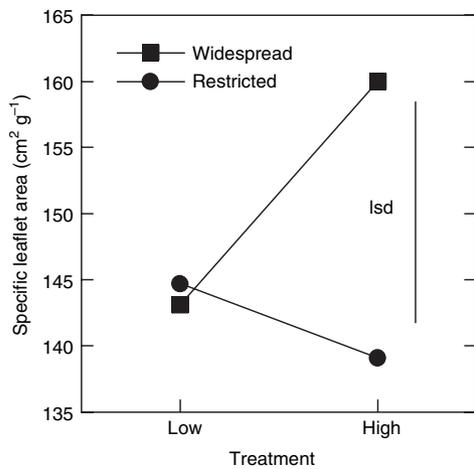


Figure 2 Leaflet SLA as a function of soil water availability. Although only marginally statistically significant, this interaction displays the predicted result, with geographically widespread species having greater plasticity than restricted species in response to soil water availability. Predicted means and least significant difference (Lsd) at the 5% level are shown.

$P(\chi^2_{271} > 3.61) = 0.058$]. In addition, widespread species had significantly lower overall SFA [(cm² leaflet area + cm² phyllode area)/(g leaflet mass + g phyllode mass) = SFA] than narrowly distributed species (Table 3).

For the statistical analysis of these data, the full model (all random terms) was fitted first. Non-significant random terms were then dropped, leaving only block (species pair) effect, block by seedling provenance interaction and block by range size interaction as random terms in the models. There was no significant effect of seedling provenance, suggesting that these growth parameters do not differ greatly within the environmental range of these species.

Leaf-level physiology

Widespread species had a significantly higher photosynthetic capacity (A_{\max}) than narrowly distributed species (Fig. 3a). A_{\max} remained greater for widespread species when calculated on a dry mass basis [Wald = 5.70, $P(\chi^2_{177} > 5.70) = 0.017$, widespread 1176 $\mu\text{mol g}^{-1} \text{s}^{-1}$, narrowly distributed 983 $\mu\text{mol g}^{-1} \text{s}^{-1}$, lsd 162.42 $\mu\text{mol g}^{-1} \text{s}^{-1}$]. Further, A_{\max} was significantly higher for geographically widespread species, regardless of the way in which species were paired. Similarly, the potential quantum yield (Fv/Fm) of widespread species was significantly higher than that of narrowly distributed species [Wald statistic = 8.05, $P(\chi^2_{535} > 8.05) = 0.04$, widespread 0.8126, narrowly distributed 0.8060, lsd 0.004676]. As would be expected given their higher photosynthetic capacity, electron transport rate (ETR) of widespread species was significantly higher than that of narrowly distributed species [Wald statistic = 8.11, $P(\chi^2_{541} > 8.11) = 0.03$, widespread 81.63, restricted 75.56, lsd 4.266]. Thus, values for all the parameters describing aspects of the photosynthetic capability of leaflets were higher for widespread species than narrowly distributed species.

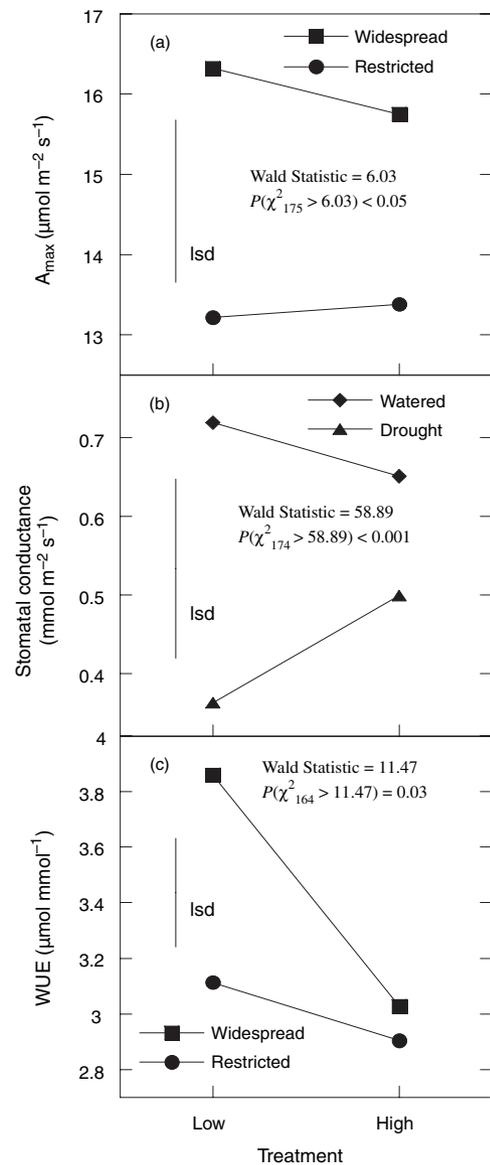


Figure 3 (a) photosynthetic capacity (A_{\max}), (b) stomatal conductance and (c) water use efficiency, as a function of soil water availability and either range size (a and c) or drought condition (b). Predicted means and least significant differences (Lsd) at the 5% level are shown.

Only one of the parameters related to photosynthetic traits responded significantly to soil water availability. Plants from the low soil water treatment had a higher Fv/Fm than plants from the high soil water treatment [Wald statistic = 10.89, $P(\chi^2_{535} > 10.89) = 0.02$, high water 0.8062, low water 0.8123, lsd 0.003716].

Stomatal responses did not differ between narrowly distributed and widespread species, but did vary with soil water availability. Stomatal conductance was affected by both soil water treatment and drought condition (drought or watered), which was reflected in the significant interaction term

(Fig. 3b). Transpiration rate responded to watering condition [Wald statistic = 172.26, $P(\chi^2_{174} > 172.26) < 0.001$, drought 1.45 mmol m⁻² s⁻¹, watered 6.43 mmol m⁻² s⁻¹, lsd 0.7586 mmol m⁻² s⁻¹] but not soil water treatment [Wald statistic = 0.39, $P(\chi^2_{174} > 0.39) = 0.53$, low water 4.075 mmol m⁻² s⁻¹, high water 3.801 mmol m⁻² s⁻¹, lsd 0.6380 mmol m⁻² s⁻¹]. C_i/C_a mirrored the response of stomatal conductance in the drought condition by soil water treatment interaction [Wald statistic = 4.81, $P(\chi^2_{174} > 4.81) = 0.03$].

Because widespread species had a greater photosynthetic capacity but equivalent transpiration rates to narrowly distributed ones, and because transpiration rates varied with growth water treatment, we find that the plasticity of the WUE of widespread species was greater than that of the narrowly distributed species under the low water treatment. As such, we can conclude that the widespread species had greater plasticity in WUE, supported by the significant soil water treatment by range size interaction term (Fig. 3c). The drought condition by soil water treatment interaction term was also significant [Wald statistic = 12.21, $P(\chi^2_{164} > 12.21) = 0.02$].

Of the random effects included in the statistical model, only the block (species pair) effect and block by condition (drought or watered) interaction term were significant for the gas exchange and fluorescence parameters measured. As was the case for the growth traits, there was no significant effect of seedling provenance.

DISCUSSION

We predicted that widespread species would display greater plasticity than narrowly distributed congeners in key seedling establishment traits, and asked whether these species would differ in mean values of these traits. Across growth and allocational traits, there were no differences in either mean or plasticity, but among the physiological traits we found both mean and plasticity differences. These results support the conclusion that differences between widespread and narrowly distributed species will be taxon and context dependent.

We examined variation in RGR because it is a fundamental trait of plant species. Interspecific variation in RGR is high and has been associated with variation in the seedling establishment strategies of plants adapted for habitats of differing productivity (Biere 1996, Westoby 1998, Atkin *et al.*, 1999; Rees *et al.*, 2001), different successional niches (Rees *et al.*, 2001) and different competitive abilities (Westoby 1998, Rees *et al.*, 2001). Our study species were chosen from a variety of different habitats at different latitudes along the east coast of Australia and our results indicate that no one single RGR strategy consistently differentiates between widespread and narrowly distributed *Acacia* species within this region. Although Robson & Maze (1995) found that the growth rate of one rare species was lower than two of its widespread congeners, no consistent relationship between geographic

range size and growth rate has yet emerged (Murray *et al.*, 2002a).

Likewise, neither of our measures of biomass allocation (root to shoot ratio or foliage mass ratio) differed consistently between geographically widespread and narrowly distributed *Acacia* species. Only one study to date has found a difference in the biomass allocation patterns between rare and widespread species. Poot & Lambers (2003) found that within the genus *Hakea*, rare species restricted to ironstone communities in south western Australia allocate a greater proportion of biomass to roots during early development than widespread species, however, the authors related the differences between these *Hakea* species to the specific edaphic habitats occupied by the rare and common species, rather than to range size itself (Poot & Lambers, 2003).

Widespread and narrowly distributed *Acacia* species did, however, display different patterns in SFA; and SFA was significantly higher for narrowly distributed species than for widespread species. As the specific leaf area of leaflets (SLA) did not differ between widespread and restricted species, the difference in SFA must have been generated by the production of phyllodes. As only three of our 10 study species produced phyllodes (and two of these were widespread species) we suggest that further research is required to draw any general conclusions about the influence of phyllodes or SFA on geographic range size. As different seedling growth strategies are favoured in different environments (Westoby 1998, Leishman, 1999), there may not be any single strategy that allows species to become widespread in all habitats (Edwards & Westoby, 2000).

We did, however, predict differences in plasticity of growth traits, and yet found only weak support for our hypothesis: the SLA of geographically widespread *Acacia* species tended to display greater plasticity in response to soil water availability than the SLA of restricted *Acacia* species. Widespread species increased SLA at high soil water availability whereas there was not a significant change in SLA of narrowly distributed species. We note that SLA is well correlated with gas exchange traits (Reich *et al.*, 1997), and that we found both differences in mean and plasticity of physiological traits among the *Acacia* species.

Geographically widespread *Acacia* species had significantly higher photosynthetic capacities than narrowly distributed *Acacia* species. This result was not altered by changes to the way in which species were paired with each other or by method in which photosynthetic traits were measured (infra-red gas analysis vs. fluorescence). The lack of response in A_{max} and ETR to either the long-term soil water availability treatment or the short-term drought treatment suggests that there may be a considerable degree of adaptive flexibility in the parameters which influence and maintain photosynthetic capacity in response to both long-term growth conditions and short-term drought stress.

Consistent with our second hypothesis, the plasticity of instantaneous photosynthetic WUE in response to soil water availability was greater for widespread than for narrowly distributed *Acacia* species. Widespread species showed a

greater increase in WUE with decreased soil water availability than restricted species. The higher photosynthetic capacity (A_{\max}) and higher WUE at low soil water availability of widespread *Acacia* species suggest that they may be adapted for drier conditions and have a higher leaf nitrogen content than the restricted *Acacia* species (Ball *et al.*, 1995; Wright *et al.*, 2001). It may also be the case that widely distributed species are more resilient through time as a result of greater ability to tolerate variation in water availability over years. As such, narrowly distributed species may be lost from more variable sites, thus explaining their narrower distributions.

The physiological differences found in our study were measured on leaflets only and so are independent of the difference in SFA between our study species. However, as *Acacia* phyllodes have a higher A_{\max} (on both a mass and an area basis) and WUE (Brodribb & Hill, 1993) and a lower unit foliage area per unit foliage mass (Atkin *et al.*, 1998) than bipinnate *Acacia* leaves, the physiological differences between the leaflets of widespread and restricted species would most likely be increased by the contribution of phyllodes to the overall physiology of our study species. Brodribb & Hill (1993) suggested that the leaves that *Acacia* seedlings initially produce may be adapted to maximize the growth rates of seedlings. Thus, the increase in the SLA of widespread species at high water availability may indicate a shift from the low-SLA, high-WUE, lower-growth rate morphology of dry-adapted plants towards the high-SLA, low-WUE, higher-growth rate morphology of plants in moister environments (Wright *et al.*, 2001). In our study, provenances were paired to maximize similarity between habitats of widespread and narrowly distributed species, however, the realized ranges of the widespread species are likely to encompass a greater range of soil water availability. If so, the greater plasticity in SLA and WUE of widespread *Acacia* species may thus allow these species to utilize efficiently both moist and dry habitats, whereas the rare *Acacia* species may be limited to comparatively moister environments than their widespread partners.

Such a restriction of the rare *Acacia* species to moister habitats may be a result of temporal environmental variability. Climatic fluctuations associated with the El Niño Southern Oscillation (ENSO) increase the range of environmental conditions plants must endure, even within the mesic zone, and the effects of ENSO are particularly severe for eastern Australia (Markgraf & Diaz, 2000). Markgraf & Diaz (2000) report that, since the onset of ENSO conditions in the late Holocene (5 ka BP to the present), pollen records have shown an increase in the distribution of vegetation tolerant of greater climatic extremes. It is not inconceivable that species with seedlings able to establish under a broader range of conditions would be able to maintain a larger geographical range than those able to establish only under wetter conditions, in a region subject to extreme, ENSO-related droughts. As such, a seedling trait that may show adaptive plasticity is the actual germination and establishment success under varied water availability.

Habitat specialization is associated with smaller range sizes in small mammals (Glazier & Eckert, 2002), primates (Harcourt *et al.*, 2002) and in some plant genera (e.g. Lloyd *et al.* 2002, Murray *et al.*, 2002a; Poot & Lambers, 2003), but it has yet to be demonstrated that lower environmental tolerance (or greater habitat specialization) is a universal trait of taxa with smaller range sizes (Coates & Kirkpatrick, 1999; Murray *et al.*, 2002a). As biogeographical histories and the most limiting climatic factors differ between regions (Edwards & Westoby, 2000) and specific responses to these selective pressures may be phylogenetically constrained (Edwards & Westoby, 2000), it is likely that there will be no consistent patterns of variation within any individual trait that universally differentiate between geographically widespread and restricted species. Overall, our results are consistent with the hypothesis that relationships between rarity and species traits are both context and taxon specific (Edwards & Westoby, 2000; Murray *et al.*, 2002b).

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BIOSKETCHES

Catherine Pohlman is interested in seedling ecology and ecophysiology. She currently studies edge effects of natural and artificial linear canopy openings as they relate to the understorey microclimate and seedling dynamics of rain forest in northeast Queensland, Australia.

Adrienne Nicotra's research examines relationships among and plasticity in leaf- and whole-plant level traits from an evolutionary perspective.

Brad Murray has research interests in biodiversity conservation, evolutionary ecology and macroecology.

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