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Testing the Home-Site Advantage in Forest Trees on Disturbed and Undisturbed Sites

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Abstract

Restoration of plant populations is often undertaken using seed or plants from local sources because it is assumed they will be best adapted to the prevailing conditions. However, the effect of site disturbance on local adaptation has rarely been examined. We assessed local adaptation in three southwestern Australian forest tree species (*Eucalyptus marginata*, *Corymbia calophylla*, and *Allocasuarina fraseriana*) using reciprocal transplant trials at disturbed and undisturbed sites. Performance of plants within the trials was assessed over 2 years. Planting location accounted for the majority of the variation in most measures of performance, although significant variation of percent emergence among source populations was also detected. In all species, percent emergence and survival of plants sourced from Darling Range populations was significantly higher than that of plants from the Swan Coastal Plain, regions of contrasting edaphic and climatic environment. Survival of *E. marginata* over the first 18 months and emergence of *C. calophylla* were both higher in local plants, providing at least weak evidence for local adaptation. Where a local advantage was observed, the relative performance of local and nonlocal seed did not vary among disturbed and undisturbed sites. Evidence for enhanced establishment from local seed in at least one species leads us to recommend that where sufficient high-quality seed supplies exist locally, these should be used in restoration. We also recommend longer-term studies to include the possibility of local adaptation becoming evident at later life history stages.

Key words: bauxite mine, genetic variation, home-site advantage, jarrah, local adaptation, Marri, Sheoak.

Introduction

Local adaptation by natural selection can be a potent evolutionary force driving genetic divergence in plant species occupying spatially heterogeneous habitats (Endler 1986; Linhart & Grant 1996). This has been demonstrated experimentally for many species in the form of a "home site advantage," where plants grown at their site of origin perform better than those translocated to or from more distant sites (e.g., Waser & Price 1985; Galen et al. 1991; Nagy & Rice 1997; Montalvo & Ellstrand 2000; Joshi et al. 2001; McKay et al. 2001; Hufford & Mazer 2003). Adaptive differentiation within species has important consequences for ecological restoration because the introduction of maladapted source seed or plants may compromise the success of the restored population. Furthermore, interbreeding among individuals from genetically divergent source populations may result in genetic swamping or outbreeding depression, causing population decline in subsequent generations (e.g., Fenster & Galloway 2000; Sackville Hamilton 2001; Hufford & Mazer 2003; Potts et al. 2003). In an effort to maintain locally adaptive genotypes and conserve intraspecific genetic diversity, the use of local provenance seed or plants for restoration is commonly advocated (e.g., Coates & van Leeuwen 1997; Mortlock 2000; Sackville Hamilton 2001; Krauss & Koch 2004).

However, strict adherence to such a strategy has been criticized on the grounds that an assumption of local adaptation may not always be valid (e.g., Lesica & Allendorf 1999; Wilkinson 2001). Sites targeted for restoration are often highly disturbed and may have undergone particularly rapid environmental change due to activities such as mining, land clearing, or pollution. Consequently, current selection pressures are likely to differ from those operating historically, and local genotypes may no longer have an advantage (Lesica & Allendorf 1999). It has therefore been argued that the creation of self-sustaining populations on such sites will be better achieved by collecting from a large number of sources to maximize the genetic variation available to selection (Lesica & Allendorf 1999; Wilkinson 2001).

From a genetic perspective, the maintenance of locally adapted genotypes in restored populations must be balanced against the need to ensure that the population harbors sufficient genetic variation to facilitate adaptive evolution and long-term persistence (Montalvo & Ellstrand

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2000). However, balancing these objectives is complicated by a poor understanding of the relative importance of local adaptation and genetic diversity as determinants of population success and how this is likely to vary at different levels of site disturbance. Studies assessing the relative benefit of sourcing seed locally versus sourcing broadly, at sites of varying disturbance level, are needed to elucidate the contribution of these different factors.

In the jarrah (*Eucalyptus marginata* Donn ex Smith) forest of southwest Western Australia, bauxite mining operations clear and rehabilitate approximately 700 ha each year, generating a substantial demand for seed of native plant species (Gardner 2001). Where possible, seed for rehabilitation is collected within a 20 km radius (Gardner 2001). However, this distance is somewhat arbitrary because the scale of adaptive genetic differentiation within species is generally not known.

We used reciprocal transplant trials to investigate the relative performance of local and nonlocal seed sources of three common southwestern Australian forest trees (*E. marginata*, Marri [*Corymbia calophylla* Lindley], and Sheoak [*Allocasuarina fraseriana* Lodhi]) on sites of varying disturbance level. Our objectives were to evaluate the effect of seed source, planting location, and site disturbance on the performance of plants in restoration and, more specifically, to determine whether deploying local seed resulted in greater restoration success than was achieved using seed from more distant sources on (1) undisturbed and (2) highly disturbed (mined) sites.

Methods

Study Species

Eucalyptus marginata, *Corymbia calophylla*, and *Allocasuarina fraseriana* are all endemic to the southwest of Western Australia. These species represent a significant proportion of the dominant tree component of the jarrah forest on the lateritic gravels of the Darling Range. They also occur to the west of this region and on sandy soils of the Swan Coastal Plain. Mean annual rainfall in areas occupied by these species is between 600 and 1400 mm and appears to be a major factor preventing their expansion into adjacent, drier regions (Churchill 1968; Dell & Havel 1989).

Eucalyptus marginata and *Corymbia calophylla* both have mixed mating systems, although realized outcrossing rates are high (0.81) in *E. marginata* populations (Millar et al. 2000). Outcrossing rates in *C. calophylla* are not known but are likely to be similarly high, based on outcrossing estimates for other multiseeded, mass-flowering eucalypt species (Griffin et al. 1987; James & Kennington 1993; Millar et al. 2000). Most eucalypts are bird pollinated and/or insect pollinated, and it is likely that both of these vectors contribute to pollination in *E. marginata* and *C. calophylla*. Seeds are primarily gravity dispersed, with previous studies of eucalypts suggesting that the vast majority of seeds fall within a radius twice the height of the maternal tree (Potts & Reid 1988).

Allocasuarina fraseriana is dioecious and therefore entirely outcrossing. The winged morphology of *A. fraseriana* seeds facilitates dispersal by wind. Flowers are not specialized to attract birds or insects; therefore, it is likely that wind is also the main pollination vector in this species, as for most species within the Casuarinaceae.

Source Populations

Seeds of the three species were collected from six natural, open-pollinated populations: Bold Park, Baldivis, Huntly, Willowdale, Wells Block, and Boddington (Table 1). Populations were chosen to represent variation of substrate and climate. Bold Park and Baldivis are located on the Swan Coastal Plain and the remaining populations within the Darling Range. Substrate varies considerably between these regions, the Swan Coastal Plain being dominated by sandy soils and the Darling Range by lateritic gravels overlying sandy clay subsoils (Churchward & McArthur 1980; McArthur 1991). Within the Darling Range, there is a gradient of mean annual rainfall, declining from west to east (Australian Bureau of Meteorology: http://www.bom.gov.au). Source populations were chosen to sample the extremes of this variation; Huntly and Willowdale fall within the high-rainfall zone at the western edge of the jarrah forest, with mean annual rainfall of approximately 1200 mm. Wells Block and Boddington are located within the eastern jarrah forest, where mean annual rainfall is

Table 1. Characteristics of source populations included in the reciprocal transplant trial.

Region	Source Population	Latitude	Longitude	Mean Annual Rainfall (mm)
Swan Coastal Plain	Bold Park	31°56′S	115°46′E	850
	Baldivis	32°19′S	115°48′E	850
Western Darling Range	Huntly	32°42′S	116°03′E	1,200
	Willowdale	32°50′S	116°05′E	1,200
Eastern Darling Range	Wells Block	32°46′S	116°26′E	700
	Boddington	32°55′S	116°28′E	700

Rainfall data are from the Australian Bureau of Meteorology Web site (http://www.bom.gov.au).

approximately 700 mm. Rainfall on the Swan Coastal Plain is intermediate, between 750 and 950 mm/yr (Australian Bureau of Meteorology: www.bom.gov.au). Across the area sampled in this study, the climate is characterized by hot, dry summers and cool, wet winters. Rainfall is highly seasonal, with approximately 80% falling between May and October.

Within each population, seed was collected from 10 maternal trees of each species, spaced at intervals of at least 100 m to avoid sampling from close relatives. Seeds were bulked to give a single seedlot for each population of each species, comprising approximately equal numbers of seed from each maternal plant. Mean seed weight for each seedlot was calculated from the weight of 100 randomly chosen seeds. Percent viability was estimated using a cut test on a random sample of 100 seeds from each source population. These data are presented in Table 2.

Trial Establishment

Seeds were sown in April to May 2004 to mimic the timing of natural seed rain in these species. Due to site availability, the transplant design was not entirely reciprocal, with trials established at only four of the six locations where seed was sourced: Bold Park, Huntly, Willowdale, and Boddington.

Huntly, Willowdale, and Boddington are active bauxite mines, where mine rehabilitation pits lie immediately adjacent to undisturbed jarrah forest stands. At these locations, trials were established on both mined and unmined sites to assess whether the relative performance of seed from local and nonlocal source populations varies with the level of site disturbance. Unmined sites were largely cleared of vegetation but the soil left intact. The mining process involves clearing vegetation, removing topsoil, blasting of the caprock, and extraction of the bauxite layer, which lies 4–8 m below the surface. Prior to rehabilitation, topsoil is returned, and the site is ripped to prevent erosion (Gardner 2001). Therefore, soil structure was the major physical difference between disturbed and undisturbed sites examined in this study.

Severe weed infestation at the Bold Park site made it necessary to undertake weeding. Weeds were removed by hand and sprayed with herbicide. At remaining trial sites, existing vegetation was removed by hand prior to sowing. Each site was fenced to prevent grazing by vertebrate her-bivores (rabbits and kangaroos), which has been shown to be a major cause of seedling mortality in these species (Abbott 1984).

With the exception of Bold Park, sites were divided into 36 plots, arranged as 6 rows × 6 columns. Seeds from a single source population of each species were sown in each plot, such that there were six replicate plots of each population within each site, with each population represented exactly once in each row and column. At Bold Park, limited space meant that only 30 plots could be established. These were positioned randomly across the site, divided into five replicate blocks of six plots each. Within each block, source populations were randomly assigned to plots.

Within plots, 25 seeds of each species were sown, arranged as five rows of five seeds. Plots, rows within plots, and seeds within rows were separated by 0.5 m. Seeds of mixed provenance were sown around the perimeter of the trial, spaced at the same interval, to avoid edge effects. Each seed was buried to a depth of 10 mm to prevent displacement by wind or rain. Seeds were marked using plastic tags, allowing individual plants to be identified during trial assessment.

Trial Assessment

Due to the broad geographic distribution and the size of the trials, it was not possible to assess timing of emergence accurately. Hence, emergence at all sites was assessed in November 2004, 6 months after sowing. Assessing emergence at this time was considered likely to yield an accurate measure of total emergence because few seeds germinate after the end of the winter (June to August) rains and, being prior to the onset of the hot summer, mortality of emergent seedlings was expected to be low. Plants that emerged and died prior to this census were often still visible. These individuals were recorded as emerged. Emergence rates were corrected for expected emergence based on seed viability by dividing observed percent emergence by percent viability.

Trials were assessed on three subsequent occasions: in April 2005, November 2005, and April 2006, respectively, 12, 18, and 24 months after sowing. At each census, survival and height of all seedlings were recorded, giving the following measures of performance: percent emergence, percentage of emergent seedlings surviving 12, 18, and 24 months after sowing, height growth between 12 and 18

Table 2. Percent viability of seed of each species from each source population determined using a cut test on a sample of 100 seeds.

			Source Population			
Species	Baldivis	Bold Park	Boddington	Huntly	Wells Block	Willowdale
Eucalyptus marginata	77	69	52	83	62	92
Corymbia calophylla	85	78	96	83	95	94
Allocasuarina fraseriana	69	69	69	32	69	32

months (winter 2005), and height growth between 18 and 24 months (summer 2005–2006). Height growth rather than height was used because the timing of germination, and therefore the exact age of each plant, was not known.

Data Analysis

Effect of Seed Weight. Seed weight has been shown to have a significant influence on survival and growth in several plant species (e.g., Mazer 1987; Ladd & Cappuccino 2005; Shankar 2006); therefore, it was necessary to account for this potentially confounding factor. Regression analyses were used to investigate whether mean seed weight of each seedlot could explain a significant amount of variation of each performance measure.

Variation Among Seed Sources and Trial Locations. We first analyzed variation due to seed source, planting location, site disturbance, and all interactions, using a general linear model. Row was included as a random factor to account for variation within each planting site. This was done for each measure of performance for each species.

Assessing Home-Site Advantage on Disturbed and Undisturbed Sites. A second series of analyses was performed to determine whether locally sourced seed performed better, on average, than nonlocal seed and whether the relative performance of local and nonlocal seed varied with disturbance level at each planting location. These analyses were also performed using a general linear model, with factors local (two levels: local and nonlocal), disturbance (disturbed or undisturbed), and planting location. The main effects of each of these factors and all interactions were assessed. Once again, row was included as a random factor.

A home-site advantage was recognized by significantly better performance of local seed (seed sourced from the population at the planting location) than nonlocal seed (seed from other source populations).

A significant effect of the local × disturbance interaction suggested that the strength of the home-site advantage varied with the level of disturbance. In these cases, the data were examined to determine whether the performance of local seed, relative to nonlocal seed, was poorer on disturbed sites than on undisturbed sites.

All analyses were conducted using the statistical software package CoStat version 6.311. For emergence and survival at each census, the plot was the unit of analysis, with each measure expressed as a percentage of trees per plot emergent or surviving. For height growth, individual tree measurements were used. Tukey's post hoc tests determined the source of significant variation due to main effects. Analyses were performed separately for each of the three study species.

Power Analysis. The power to detect variation where it exists is a critical consideration of this type of study, where

there may be highly detrimental consequences of management practices based on erroneous conclusions that no variation exists among local and nonlocal seed sources. The power to detect variation of each of the performance measures assessed in this experiment was dependent upon the number of plants surviving at each census. Therefore, we used power analyses to determine the magnitude of variation that could be detected with the sample size at each stage of the experiment.

Power analyses were conducted using G*Power 3 for Macintosh (available at http://www.psycho.uni-duesseldorf. de/abteilungen/aap/gpower3/). For each performance measure for each species, we used the post hoc option in G*Power to determine our power to detect a difference between local and nonlocal seed sources at the observed effect size, given the sample size available. We also used the sensitivity option to calculate the effect size required to detect a difference between local and nonlocal seed sources, with power of 0.80.

Results

Effect of Seed Weight

Seed weight did not explain significant variation of any of the performance measures in any of the three species; therefore, we did not adjust for this variable in subsequent analyses.

Variation of Performance

Planting location was associated with significant variation of all performance measures in all three species and in most cases accounted for the largest proportion of the variation (Table 3). In all species, variation of emergence and survival among locations was largely explained by very poor performance at Bold Park, with complete mortality of all species at this site prior to the final census. Patterns of height growth were more variable among species and measurement periods. For *Eucalyptus marginata* and *Corymbia calophylla*, mean height growth was greatest at Huntly and lowest at Boddington, whereas for *Allocasuarina fraseriana*, height growth was lowest at Huntly over both measurement periods, highest at Boddington over winter and at Willowdale over summer.

Disturbance was also an important source of variation, explaining significant variation of most performance measures in all three species (Table 3). It was the most important source of variation of survival at each census date and height growth over summer in *A. fraseriana* and of emergence of *C. calophylla* (Table 3).

For all species, overall mean percent emergence varied significantly with source population (Table 3). In all cases, this was because seed from the two Swan Coastal Plain populations (Bold Park and Baldivis) had lower overall mean percent emergence than those from Darling Range populations (Fig. 1). There was no statistically significant

Table 3. Variation of six performance measures due to seed source, planting location, and disturbance for (a) *Eucalyptus marginata*, (b) *Corymbia calophylla*, and (c) *Allocasuarina fraseriana* from six source populations sown at four locations, with disturbed and undisturbed sites at three of these locations.

Source of Variation	% Emergence df	MS	p	% Survival to 1 yr df	MS	p	% Survival to 1.5 yrs df	MS	p	% Survival to 2 yrs df	MS	p	Height Growth Winter 2005 df	MS	p	Height Growth Summer 2005–2006 df	MS	p
(a) *Eucalyptus marginata*																		
Row	5	0.10	0.07	5	0.03	0.59	5	0.05	0.26	5	0.07	0.12	5	411.7	**<0.01**	5	107.0	**0.03**
Main effects																		
Source	5	0.47	**<0.01**	5	0.02	0.73	5	0.03	0.65	5	0.10	**0.04**	5	94.4	**0.03**	5	54.9	0.27
Location	3	0.55	**<0.01**	3	4.77	**<0.01**	3	5.09	**<0.01**	3	5.19	**<0.01**	3	3674.6	**<0.01**	2	6145.2	**<0.01**
Disturbance	1	0.05	0.32	1	3.57	**<0.01**	1	3.64	**<0.01**	1	3.87	**<0.01**	1	7.3	0.74	1	2316.0	**<0.01**
Interactions																		
Source × location	15	0.04	0.58	15	0.07	**0.04**	15	0.07	0.07	15	0.06	0.14	15	101.6	**<0.01**	10	49.3	0.32
Source × disturbance	5	0.01	0.95	5	0.05	0.22	5	0.04	0.41	5	0.05	0.29	5	73.5	0.09	5	86.1	0.07
Location × disturbance	2	0.39	**<0.01**	2	0.91	**<0.01**	2	0.98	**<0.01**	2	0.78	**<0.01**	2	3317.5	**<0.01**	2	2901.0	**<0.01**
Source × location × disturbance	10	0.02	0.96	10	0.02	0.93	10	0.02	0.90	10	0.03	0.65	10	176.3	**<0.01**	10	40.8	0.48
Error	199	0.04		199	0.04		199	0.04		199	0.04		1,287	38.1		1,200	42.7	
(b) *Corymbia calophylla*																		
Row	5	0.10	0.09	5	0.13	**<0.01**	5	0.08	0.07	5	0.09	0.03	5	754.6	**<0.01**	5	86.6	0.18
Main effects																		
Source	5	0.89	**<0.01**	5	0.05	0.28	5	0.03	0.65	5	0.05	0.26	5	567.6	**<0.01**	5	311.1	**<0.01**
Location	3	0.60	**<0.01**	3	3.83	**<0.01**	3	4.59	**<0.01**	3	6.69	**<0.01**	3	9173.3	**<0.01**	2	3717.5	**<0.01**
Disturbance	1	4.10	**<0.01**	1	0.55	**<0.01**	1	0.43	**<0.01**	1	0.63	**<0.01**	1	5407.4	**<0.01**	1	669.1	**<0.01**
Interactions																		
Source × location	15	0.05	0.05	15	0.03	0.82	15	0.02	0.98	15	0.01	0.99	15	209.5	**0.03**	10	152.1	**<0.01**
Source × disturbance	5	0.12	**<0.01**	5	0.08	0.07	5	0.07	0.15	5	0.07	0.08	5	557.9	**<0.01**	5	67.0	0.31
Location × disturbance	2	0.01	0.90	2	0.43	**<0.01**	2	0.43	**<0.01**	2	0.44	**<0.01**	2	13183.0	**<0.01**	2	4091.2	**<0.01**
Source × location × disturbance	10	0.03	0.48	10	0.04	0.35	10	0.04	0.51	10	0.05	0.19	10	156.7	0.19	10	164.5	**<0.01**
Error	199	0.03		199	0.04		199	0.04		199	0.04		1,794	115.0		1,735	55.9	
(c) *Allocasuarina fraseriana*																		
Row	5	0.04	0.53	5	0.05	0.47	5	0.05	0.39	5	0.02	0.91	5	37.0	0.06	5	148.2	**<0.01**
Main effects																		
Source	5	1.50	**<0.01**	5	0.05	0.47	5	0.04	0.50	5	0.06	0.27	5	33.4	0.09	5	14.4	0.60
Location	3	1.53	**<0.01**	3	5.32	**<0.01**	3	5.16	**<0.01**	3	5.62	**<0.01**	3	396.3	**<0.01**	2	602.0	**<0.01**
Disturbance	1	0.87	**<0.01**	1	9.12	**<0.01**	1	9.45	**<0.01**	1	10.65	**<0.01**	1	72.8	**0.04**	1	1076.7	**<0.01**
Interactions																		
Source × location	15	0.07	0.02	15	0.03	0.89	15	0.03	0.81	15	0.04	0.73	10	29.7	0.07	10	36.5	0.05
Source × disturbance	5	0.04	0.38	5	0.06	0.33	5	0.05	0.43	5	0.12	**0.04**	5	43.9	**0.03**	5	37.0	0.09
Location × disturbance	2	0.02	0.60	2	3.61	**<0.01**	2	3.63	**<0.01**	2	3.92	**<0.01**	2	130.3	**<0.01**	2	478.8	**<0.01**
Source × location × disturbance	10	0.05	0.12	10	0.05	0.54	10	0.05	0.49	10	0.06	0.28	10	39.6	**0.01**	9	37.7	**0.04**
Error	199	0.03		199	0.05		199	0.05		199	0.05		888	17.2		863	19.5	

The remaining location had only an undisturbed site. Cases where a statistically significant ($p < 0.05$) difference was detected are highlighted in bold type. Due to complete mortality at the Bold Park site prior to the final census, the measure of height growth over summer 2005–2006 could only be made at three planting locations.
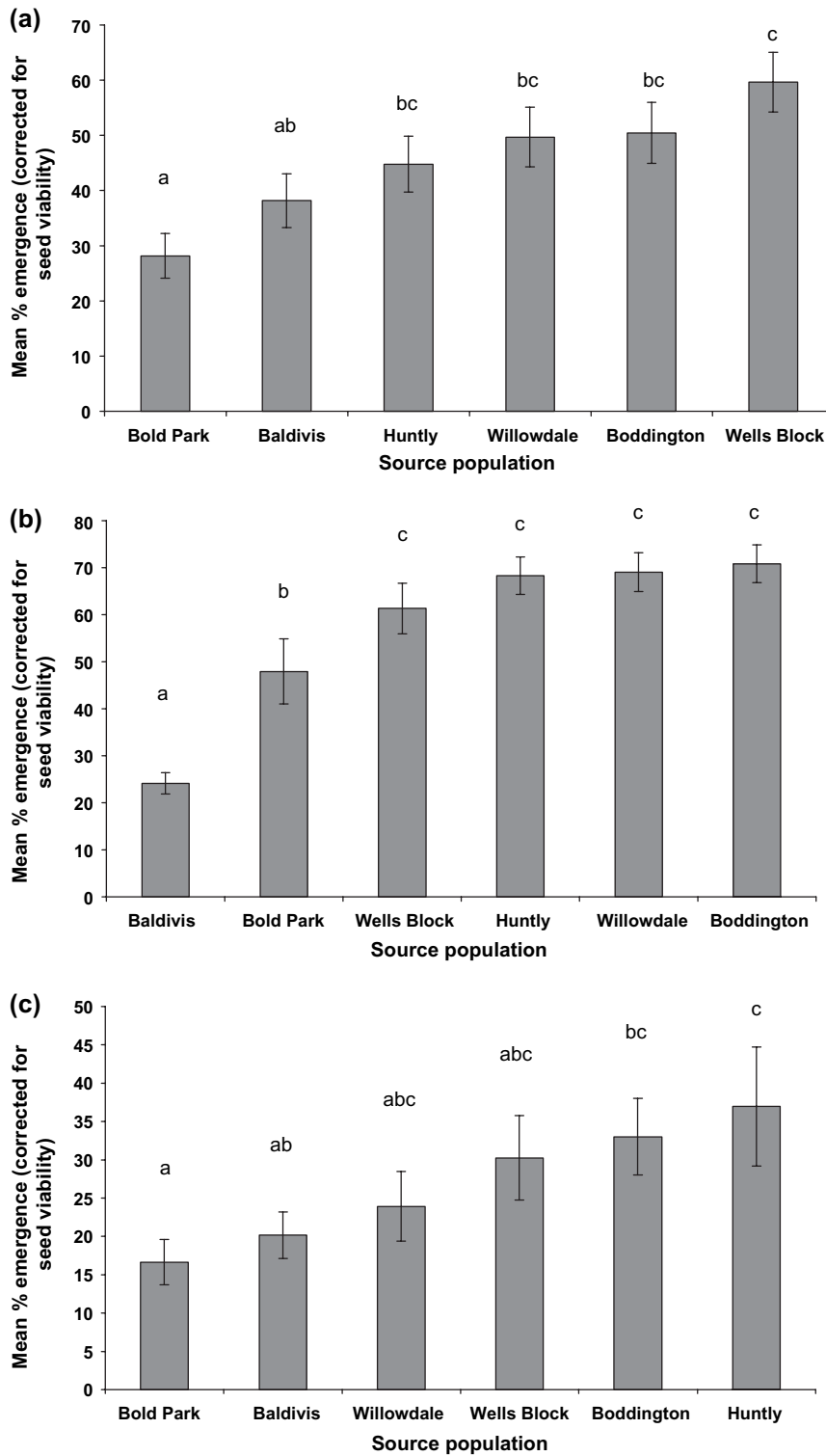
Figure 1. Overall mean percent emergence of seed from each source population across all trial locations for (a) *Eucalyptus marginata*, (b) *Corymbia calophylla*, and (c) *Allocasuarina fraseriana*. Different letters indicate statistically significant differences ($p < 0.05$).

variation in overall percent emergence among the four Darling Range source populations for any of the species (Fig. 1). Source population also accounted for significant variation of survival to 2 years and height growth over winter in *E. marginata* and height growth over both winter and summer in *C. calophylla* (Table 3).

Assessing Home-Site Advantage

The planting location × source population interaction accounted for significant variation of survival to 1 year and height growth over winter in *E. marginata*, height growth over both winter and summer in *C. calophylla*, and emergence and height growth over summer in *A. fraseriana* (Table 3). However, explicit comparisons of local and nonlocal seed sources for each performance measure in each species revealed that they differed significantly in only one of these cases: height growth over winter in *C. calophylla*, where height growth of plants grown from nonlocal seed exceeded that of plants from the local source population (Table 4; Fig. 2).

Despite failure to detect a significant site × source interaction, there were several other performance measures for which a difference between local and nonlocal seed was detected (Table 4). Survival of locally sourced *E. marginata* to 1.5 years was significantly higher than that of plants from nonlocal sources (Fig. 2), although this effect was no longer evident at 2 years (Table 4). Emergence of locally sourced *C. calophylla* was 17% higher than that of seed from nonlocal source populations (Fig. 2), whereas height growth over winter of *A. fraseriana* was greater in plants from local source populations (Fig. 2).

A significant effect of the local × planting location interaction, indicating that the relative performance of local and nonlocal seed sources varies among planting locations, was observed for height growth over winter in *E. marginata* and height growth over both winter and summer in *C. calophylla* (Table 4; Fig. 3).

Home-Site Advantage on Disturbed Sites

The source population × planting location × disturbance interaction effect, which indicates variation in the relative performance of source populations at disturbed and undisturbed sites at each trial location, explained significant variation of height growth over winter in *E. marginata*, height growth over summer in *C. calophylla*, and height growth over both measurement periods in *A. fraseriana* (Table 3). To determine whether the home-site advantage was reduced on highly disturbed sites, we examined the effect of the local × disturbance interaction in these cases (Table 4). This interaction did account for significant variation of height growth over summer in *C. calophylla* and *A. fraseriana*; however, the direction of this effect was not consistent. In *C. calophylla*, plants grown from local seed exhibited comparatively greater (relative to nonlocal sources) growth over summer on disturbed sites than on undisturbed sites, whereas the reverse was true in *A. fraseriana* (Fig. 4).

Power Analysis

The magnitude of the difference between local and nonlocal plants that could be detected with the sample size available is presented in Table 5 for each performance measure of each species. The sample sizes available in this study offered good power (0.8) to detect small to moderate levels of variation of emergence and survival among local and nonlocal seed sources for each species (effect size 0.18). With the same level of power, very small levels of variation of height growth among local and nonlocal plants could be detected (effect sizes of 0.08, 0.07, and 0.09 for *E. marginata*, *C. calophylla*, and *A. fraseriana*, respectively). Failure to detect a significant difference between local and nonlocal seed sources therefore implies that performance differences, if they exist, are very small. For comparison, the effect sizes we observed for each performance measure in each species are also presented in Table 5. In most cases, these were very small (effect size <0.10).

Discussion

Arguments for using locally sourced seed or plant material for restoration rest primarily on an assumption that natural selection drives local adaptation in plant populations, and therefore, local genotypes will be better adapted to conditions at the restoration site than nonlocal genotypes. Although we detected some evidence for local adaptation in three common, long-lived forest trees widely used in ecological restoration in southwestern Australia, other factors were found to have a much more significant impact on plant performance.

Trial location and disturbance accounted for most of the variation of the performance measures examined in *Eucalyptus marginata*, *Corymbia calophylla*, and *Allocasuarina fraseriana*. This finding corroborates those of many other reciprocal transplant studies (e.g., Clark 1980; Cheplick 1988; Joshi et al. 2001; for review, see van Andel 1998), suggesting that site characteristics have a much greater bearing on the success of restoration than do adaptive differences among potential source populations. In particular, the emergence and survival of all populations of all species at the Bold Park trial location was significantly worse than at all other trial locations, culminating in complete mortality by the end of the study period.

Source populations also varied significantly, particularly in emergence rates. A key result was the low emergence rate of seeds from Swan Coastal Plain populations at all trial sites. Overall, emergence of seed from this region was 65, 58, and 59% that of seed from Darling Range populations for *E. marginata*, *C. calophylla*, and *A. fraseriana*, respectively. These two regions have had a long history of isolation and exhibit substantially different environments, particularly substrate (Churchward & McArthur 1980; McArthur 1991). It is therefore likely that restricted gene flow and subsequent selection have produced regional genetic divergence, and indeed, this has already been demonstrated for *E. marginata* (Wheeler & Byrne 2006).

Table 4. Analyses of variance to compare local and nonlocal seed sources on disturbed (mined) and undisturbed sites at each planting location for (a) *Eucalyptus marginata*, (b) *Corymbia calophylla*, and (c) *Allocasuarina fraseriana*.

Source of Variation	% Emergence			% Survival to 1 yr			% Survival to 1.5 yrs			% Survival to 2 yrs			Height Growth Winter 2005			Height Growth Summer 2005–2006		
	df	MS	p	df	MS	p	df	MS	p	df	MS	p	df	MS	p	df	MS	p
(a) *Eucalyptus marginata*																		
Row	5	0.10	0.07	5	0.03	0.59	5	0.05	0.26	5	0.08	0.12	5	411.72	**<0.01**	5	106.97	**0.03**
Main effects																		
Local	1	0.03	0.42	1	0.13	0.07	1	0.23	**0.02**	1	0.08	0.16	1	11.12	0.60	1	12.25	0.59
Location	3	0.55	**<0.01**	3	4.78	**<0.01**	3	5.10	**<0.01**	3	5.20	**<0.01**	3	3718.31	**<0.01**	3	6191.67	**<0.01**
Disturbance	1	0.05	0.32	1	3.55	**<0.01**	1	3.61	**<0.01**	1	3.88	**<0.01**	1	4.44	0.74	1	2293.33	**<0.01**
Interaction																		
Local × location	3	0.05	0.36	3	0.07	0.15	3	0.10	0.07	3	0.05	0.34	3	266.71	**<0.01**	3	35.56	0.44
Local × disturbance	1	0.02	0.57	1	0.01	0.57	1	0.01	0.56	1	0.01	0.66	1	31.46	0.37	1	34.91	0.37
Location × disturbance	2	0.39	**<0.01**	2	0.91	**<0.01**	2	0.98	**<0.01**	2	0.78	**<0.01**	2	3406.44	**<0.01**	2	2848.59	**<0.01**
Local × location × disturbance	2	0.02	0.70	2	0.02	0.55	2	0.03	0.50	2	0.01	0.80	2	91.75	0.10	2	42.76	0.37
Error	227	0.05		227	0.04		227	0.04		227	0.04		1,315	39.40		1,224	43.07	
(b) *Corymbia calophylla*																		
Row	5	0.10	0.09	5	0.13	**<0.01**	5	0.08	0.07	5	0.09	**0.03**	5	754.63	**<0.01**	5	86.57	0.18
Main effects																		
Local	1	0.20	**0.05**	1	0.05	0.28	1	0.04	0.29	1	0.07	0.17	1	1036.46	**<0.01**	1	15.03	0.61
Location	3	0.60	**<0.01**	3	3.83	**<0.01**	3	4.59	**<0.01**	3	6.69	**<0.01**	3	8865.99	**<0.01**	3	3725.07	**<0.01**
Disturbance	1	4.10	**<0.01**	1	0.55	**<0.01**	1	0.43	**<0.01**	1	0.63	**<0.01**	1	5288.37	**<0.01**	1	671.36	**<0.01**
Interaction																		
Local × location	3	0.11	0.09	3	0.03	0.55	3	0.03	0.58	3	0.01	0.80	3	539.44	**<0.01**	3	400.19	**<0.01**
Local × disturbance	1	0.01	0.68	1	0.03	0.42	1	0.02	0.47	1	0.01	0.54	1	168.86	0.23	1	345.09	**0.01**
Location × disturbance	2	0.01	0.90	2	0.43	**<0.01**	2	0.43	**<0.01**	2	0.44	**<0.01**	2	13159.20	**<0.01**	2	4401.06	**<0.01**
Local × location × disturbance	2	0.01	0.83	2	<0.01	0.89	2	<0.01	0.79	2	0.02	0.55	2	963.53	**<0.01**	2	63.03	0.33
Error	227	0.05		227	0.89		227	0.04		227	0.04		1,822	116.91		1,759	56.94	
(c) *Allocasuarina fraseriana*																		
Row	5	0.04	0.53	5	0.05	0.47	5	0.05	0.39	5	0.02	0.91	5	36.98	0.06	5	148.24	**<0.01**
Main effects																		
Local	1	0.07	0.21	1	0.03	0.42	1	0.02	0.53	1	<0.01	0.78	1	212.56	**<0.01**	1	54.11	0.10
Location	3	1.53	**<0.01**	3	5.32	**<0.01**	3	5.16	**<0.01**	3	5.62	**<0.01**	3	365.29	**<0.01**	2	619.50	**<0.01**
Disturbance	1	0.87	**<0.01**	1	9.12	**<0.01**	1	9.45	**<0.01**	1	10.65	**<0.01**	1	72.05	**0.04**	1	1055.13	**<0.01**
Interaction																		
Local × location	3	<0.01	0.91	3	0.04	0.52	3	0.06	0.30	3	0.06	0.36	2	50.54	0.06	2	58.65	**0.05**
Local × disturbance	1	0.05	0.32	1	0.05	0.33	1	0.07	0.23	1	0.05	0.33	1	30.03	0.19	1	77.63	**0.05**
Location × disturbance	2	0.02	0.60	2	3.61	**<0.01**	2	3.63	**<0.01**	2	3.92	**<0.01**	2	96.65	**<0.01**	2	499.34	**<0.01**
Local × location × disturbance	2	0.11	0.10	2	0.04	0.49	2	0.06	0.29	2	0.06	0.34	2	58.12	**0.04**	2	31.40	0.20
Error	227	0.05		227	0.05		227	0.05		227	0.05		912	17.61		886	19.65	

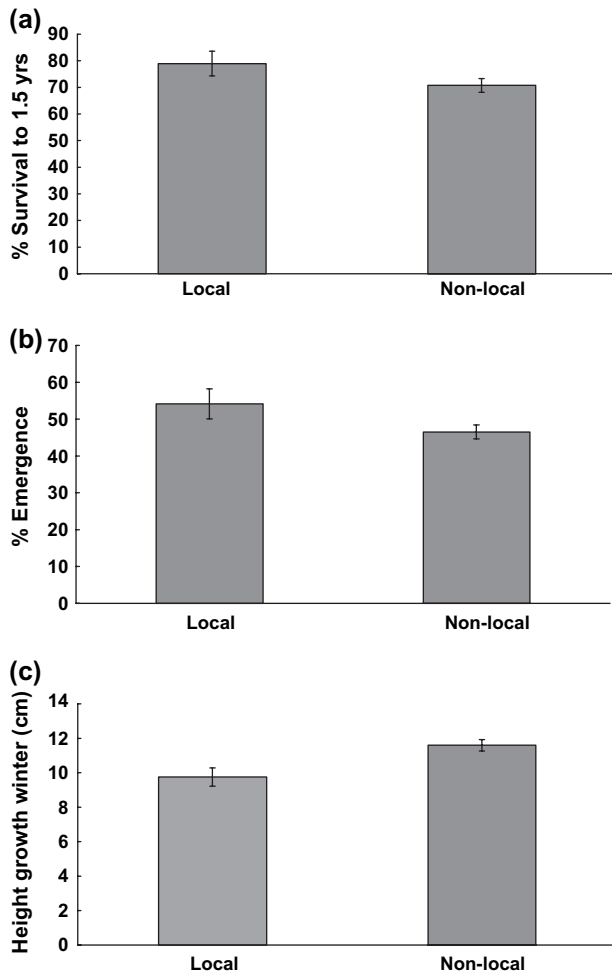Cases where a statistically significant ($p < 0.05$) difference was detected are highlighted in bold type.

Figure 2. Performance of local and nonlocal seed for (a) survival to 1.5 years in *Eucalyptus marginata*, (b) emergence and height growth over winter in *Corymbia calophylla*, and (c) height growth over winter in *Allocasuarina fraseriana*. There was a statistically significant ($p < 0.05$) difference between plants from local and nonlocal seed sources for each of these performance measures.

Another critical difference between these regions is the fragmentation of populations of these species on the Swan Coastal Plain due to clearing for urbanization and agriculture during the last century. This has resulted in reduced size and increased isolation of populations, in contrast with the largely continuous distribution of these species within the Darling Range. A substantial reduction in population size may lead not only to loss of genetic variation but also increased rates of selfing and correlated paternity as a consequence of reduced availability of mating partners (Obayashi et al. 2002). Furthermore, increased isolation is likely to limit gene flow among populations due to restricted movement of pollinators through intervening areas of unsuitable habitat (e.g., Westerbergh & Saura 1994; Townsend & Levey 2005). Consistent with this, several studies demonstrate substantially lower outcrossing rates in populations that have undergone a recent reduc-

tion in size, compared with conspecific populations that have remained undisturbed (e.g., Raijmann et al. 1994; Millar et al. 2000; Obayashi et al. 2002).

Reduced offspring fitness following inbreeding (inbreeding depression) has been documented for numerous species (e.g., Eldridge & Griffin 1983; Potts et al. 1987; Tibbits 1988; Oostermeijer et al. 1994) and is likely to be particularly pronounced in species, such as those examined here, that have high rates of outcrossing under natural conditions (Obayashi et al. 2002). It therefore seems likely that the detrimental genetic effects of reduced size and increased isolation of populations on the Swan Coastal Plain may at least partly account for the consistent poor performance of plants from this region.

Several previous studies have reported among-population variation of germination traits, which appears to have a genetic basis (e.g., Schütz & Milberg 1997; Keller & Kollmann 1999; Shimono & Kudo 2003; Bischoff et al. 2006). At least one study has uncovered the presence of such population differentiation in the absence of a home-site advantage, suggesting the contribution of processes other than local adaptation (Bischoff et al. 2006). This highlights the need to consider factors affecting seed quality that have the potential to influence performance of plants at a site.

Despite the dominant effects of site and source, local adaptation did have a significant, albeit small, impact on the performance of plants in our trials. *Corymbia calophylla* seeds sourced locally had significantly higher emergence rates than those sourced from other populations. Given that survival of emergent seedlings was generally high and relatively uniform among source populations, emergence was the most important determinant of establishment, at least over the first 2 years. This result therefore implies that establishment success of *C. calophylla* in restored populations may be maximized by deploying seed sourced from the local population. A similar trend was observed in *A. fraseriana* (although the difference was not statistically significant), providing some evidence that this may apply more generally.

Height growth over winter also varied between plants from local and nonlocal sources in *C. calophylla* and *A. fraseriana*, being greater in nonlocal *C. calophylla* plants and local *A. fraseriana* plants. Height growth is a complex trait to interpret in the context of local adaptation because different growth rates may be adaptive under different conditions. For example, in a previous study in which we measured 15-year-old *E. marginata* trees grown in a provenance trial, we found slower growth of trees from low-rainfall sites compared with trees from higher rainfall sites, when grown at a site of intermediate mean annual rainfall (O'Brien et al. 2007). It was concluded that maintenance of growth rate variation among different source populations grown in a common environment represents adaptive divergence. It may therefore be more valuable to consider cases where the relative height growth of local and nonlocal plants varied among locations.
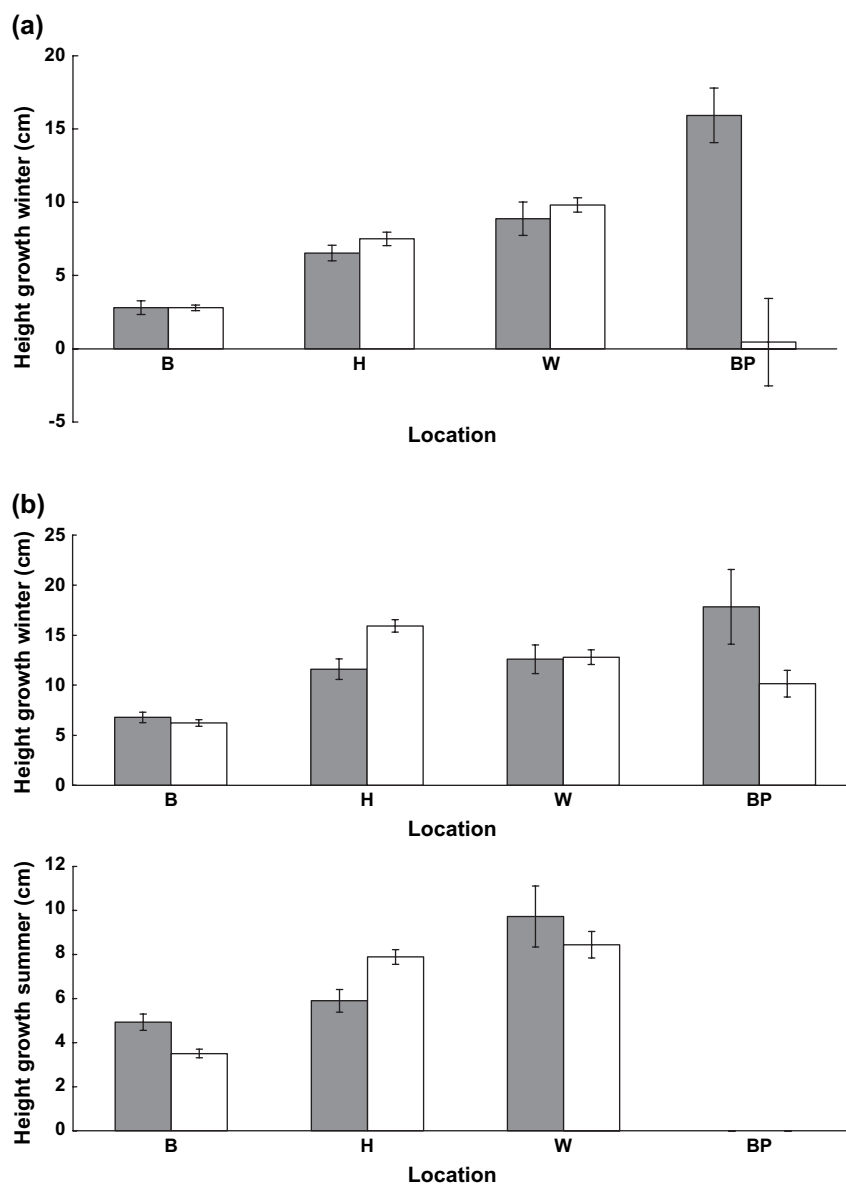
Figure 3. (a) Mean (+SE) height growth over winter in *Eucalyptus marginata* and (b) Mean (+SE) height growth over winter and summer in *Corymbia calophylla* for plants grown from local (gray bars) and nonlocal (white bars) seed at each location. In each case, there was a significant interaction effect of local × location. Summer height growth was not measured at the Bold Park trial location due to complete mortality prior to the final census. B = Boddington, H = Huntly, W = Willowdale, and BP = Bold Park.

Winter height growth of local and nonlocal *C. calophylla* and *E. marginata* plants varied among trial locations, as did summer height growth in *C. calophylla*. In both species, variation of winter growth among local and nonlocal plants across trial locations could be attributed to superior growth of nonlocal plants at Huntly and of local plants at Bold Park. Height growth over summer could not be observed at Bold Park due to complete mortality during this period; however, superior growth of nonlocal *C. calophylla* at Huntly was maintained over the summer. In addition, growth of local *C. calophylla* at Boddington exceeded that of nonlocals over this measurement period. Boddington has the lowest rainfall of any location examined in this study; therefore, this result may indicate superior capacity of local plants to cope with drought, particularly over the driest period of the year. Over both measurement periods, overall growth of *E. marginata* and *C. calophylla* was lowest at Boddington and highest at Willowdale and Huntly, where mean annual rainfall is up to 500 mm greater. This provides further evidence that rainfall is a significant factor limiting growth in these species and may drive selection for variable growth rate among locations.
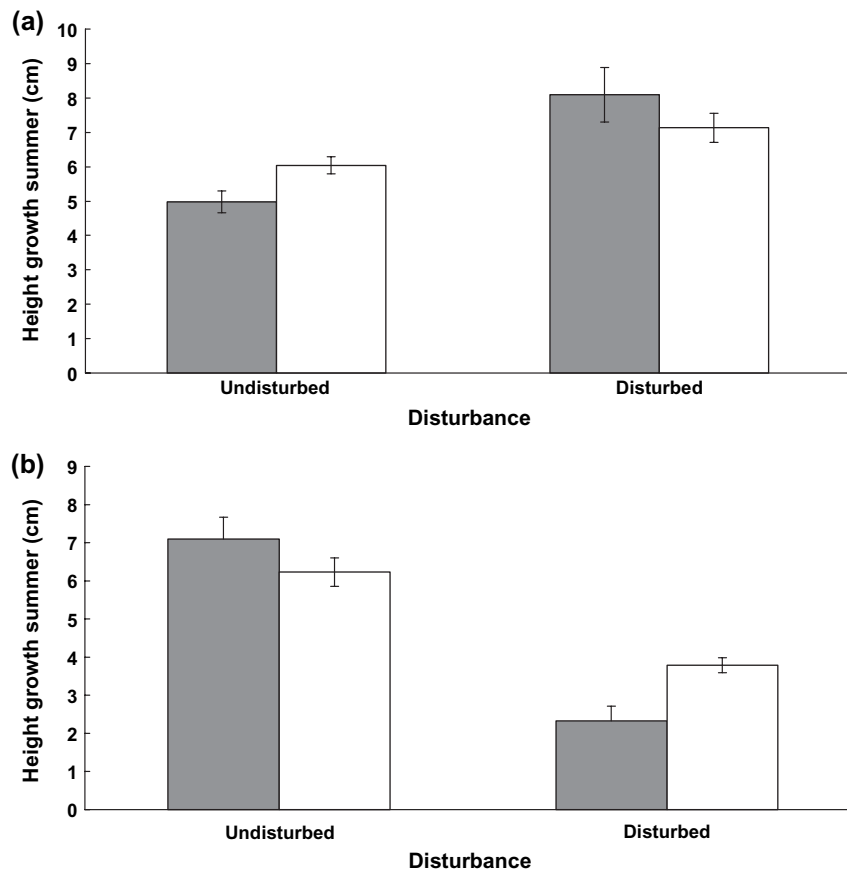
Figure 4. Mean (+SE) height growth over summer (cm) of local (gray bars) and nonlocal (white bars) seed on undisturbed and disturbed sites for (a) *Corymbia calophylla* and (b) *Allocasuarina fraseriana*.

The species included in our reciprocal transplant trials are all long lived and highly (or obligately in the case of *A. fraseriana*) outcrossing. Furthermore, the relatively contiguous distributions of these species, particularly within the Darling Range, is likely to facilitate extensive gene flow that may homogenize the effects of divergent selection. This combination of factors may help to explain why we failed to detect strong local adaptation within the scale of our study. In long-lived species, environmental variation throughout the lifespan of individuals is often considerable and may prevent the evolution of adaptive divergence among populations (Charlesworth 1994; Wilkinson 2001; Hamrick 2004; Kawecki & Ebert 2004). Instead, temporal variation of selection pressures results in high levels of genetic variation within populations and individuals tolerant of a broad range of environmental conditions (Charlesworth 1994; Hamrick 2004; Fang et al. 2006). Consequently, it has been argued that for such species, local adaptation may not be an important determinant of the success of seed or plants deployed in restoration (Wilkinson 2001). However, we did detect at least weak evidence for local adaptation in these southwestern Australian forest tree species, suggesting that deployment of local seed may still be beneficial.

Performance of Local and Nonlocal Seed at Different Levels of Disturbance

Lack of variation in the relative emergence or survival of local and nonlocal seed sources on sites of varying disturbance level for any of the species included in this study implies that establishment success achieved using locally sourced seed is unlikely to decline on highly disturbed sites. This contradicts the hypothesis posited by Lesica and Allendorf (1999) that restoration success on highly disturbed sites may be maximized by deploying seed sourced from a broad geographic range to provide a large pool of genetic diversity on which selection can act. Although limited adaptive divergence among populations of our study species may contribute to this result, there were at least two cases where performance of locally sourced seed exceeded that of nonlocal seed for these measures: survival at 1.5 years in *E. marginata* and emergence in *C. calophylla*. In these cases at least, it seems likely that the conditions favoring local individuals do not differ sufficiently between the two levels of site disturbance examined here to result in a reduction of local advantage on highly disturbed sites.

The relative summer height growth of plants from local and nonlocal sources on disturbed and undisturbed sites

Table 5. Power to detect a local advantage for each trait of each species, given the sample size and the observed effect size.

Species	Trait	Total Sample Size	Observed Effect Size	Power	Required Effect Size With Power of 0.80
Eucalyptus marginata	Emergence	246	0.05	0.13	0.18
	Survival to 1 yr	246	0.08	0.25	0.18
	Survival to 1.5 yrs	**246**	**0.11**	**0.38**	**0.18**
	Survival to 2 yrs	246	0.09	0.29	0.18
	Height growth winter 2005	1,334	0.02	0.09	0.08
	Height growth summer 2005–2006	1,250	0.03	0.18	0.08
Corymbia calophylla	Emergence	**246**	**0.13**	**0.50**	**0.18**
	Survival to 1 yr	246	0.07	0.20	0.18
	Survival to 1.5 yrs	246	0.07	0.18	0.18
	Survival to 2 yrs	246	0.09	0.27	0.18
	Height growth winter 2005	**1,841**	**0.07**	**0.84**	**0.07**
	Height growth summer 2005–2006	1,776	0.01	0.08	0.07
Allocasuarina fraseriana	Emergence	246	0.08	0.24	0.18
	Survival to 1 yr	246	0.05	0.13	0.18
	Survival to 1.5 yrs	246	0.03	0.07	0.18
	Survival to 2 yrs	246	0.01	0.05	0.18
	Height growth winter 2005	**930**	**0.11**	**0.91**	**0.09**
	Height growth summer 2005–2006	903	0.04	0.22	0.09

The final column indicates the required effect size to detect a significant difference between local and nonlocal plants, given the sample size, with power of 0.95. Traits where a significant difference between local and nonlocal plants was detected are indicated in bold type.

did vary for both *C. calophylla* and *A. fraseriana* but in opposite directions. Summer height growth of *C. calophylla* grown from locally sourced seed was higher, relative to that of non-local plants, on disturbed sites than on undisturbed sites, whereas *A. fraseriana* showed the reverse pattern. Variation of height growth is complex to interpret for reasons already discussed. However, it is interesting to note that overall, summer height growth was greater on disturbed sites in *C. calophylla* and undisturbed sites in *A. fraseriana*, which were the sites at which the local source population performed best. It may be that in both species, plants from the local population are better able to exploit favorable growth conditions, but that these conditions vary among species.

It is important to emphasize that the lack of strong evidence for local adaptation indicates that the current experiment provided only a weak test of reduced home-site advantage on disturbed sites. Future studies should target species that have been shown to exhibit a home-site advantage on "natural" sites to elucidate the effect of site disturbance on the relative performance of different source populations. Clearly, the relative performance of plants from local and nonlocal sources on sites of varying disturbance level will depend upon (1) what conditions drive adaptive divergence and (2) whether these conditions have changed considerably with the "disturbance." Further research to elucidate the conditions that are important for local adaptation in different species and landscapes would assist in predicting the likely performance of seed at different sites and varying levels of disturbance.

Conclusions

Empirical evidence for local adaptation has been found in numerous plant species (e.g., Waser & Price 1985; Galen et al. 1991; Nagy & Rice 1997; Joshi et al. 2001; McKay et al. 2001), and there is little doubt that this is an important evolutionary process shaping patterns of intraspecific genetic variation. Consequently, the sourcing of seed locally for restoration of native plant populations is commonly advocated (e.g., Sackville Hamilton 2001; Krauss & Koch 2004). However, the extent to which populations are locally adapted clearly varies among species and landscapes, and the issue of whether it is better to mix or match seed sources for the restoration of disturbed sites has rarely been addressed. We found some evidence for local adaptation in three long-lived southwestern Australian forest tree species grown in reciprocal transplant experiments and significant variation of emergence and survival of seed sourced from different regions. Of particular interest was the finding that where local adaptation was observed, it was maintained on sites of differing disturbance level.

We concur with previous recommendations that where substantial local seed sources exist, they should be used to augment populations on restoration sites to avoid loss of local adaptation. However, we caution against an uncritical view that seed collection should always be limited to a very local area, arguing that this may be detrimental if there is insufficient genetic variation either within the source population or within the founding population at the restoration site. We also emphasize that adaptive differences may become more pronounced at later life

history stages; therefore, long-term monitoring of trials such as these, as well as plants in restoration programs, is recommended.

Implications for Practice

- Consistent with studies of other species in other landscapes, site characteristics and local factors affecting seed quality were found to have the greatest bearing on plant performance. Efforts should therefore be concentrated on ensuring favorable conditions at restoration sites and deployment of high-quality seed.
- We found evidence in at least one species that establishment rates are maximized by using local seed. Hence, where sufficient high-quality local seed exists, this should be used as the source of seed deployed at restoration sites. Where local seed sources are small or of poor quality, the nearest available high-quality seed sources should be used.
- Where we detected local adaptation, it was maintained on both undisturbed and highly disturbed (mined) sites, suggesting that similar seed sourcing guidelines should be followed for restoration of sites with different levels of disturbance. However, this is likely to depend upon the nature of the disturbance; therefore, we recommend further research in this area.

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