

Shallow-soil endemics: adaptive advantages and constraints of a specialized root-system morphology

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Summary

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- Worldwide, many rare plant species occur in shallow-soil, drought-prone environments. For most of these species, the adaptations required to be successful in their own habitats, as well as their possible consequences for establishment and persistence in others, are unknown.
- Here, two rare *Hakea* (Proteaceae) species confined to shallow-soil communities in mediterranean-climate south-western Australia were compared with four congeners commonly occurring on deeper soils. Seedlings were grown for 7 months in a glasshouse in individual 1.8 × 0.2-m containers, to allow for unconstrained root development. In addition, a reciprocal transplant experiment was carried out.
- The rare *Hakea* species differed consistently from their common congeners in their spatial root placement. They invested more in deep roots and explored the bottom of the containers much more quickly. In the reciprocal transplant experiment they showed increased survival in their own habitat, but not in others.
- This research suggests that shallow-soil endemics have a specialized root system that allows them to explore a large rock surface area, thereby presumably increasing their chance to locate cracks in the underlying rock. However, this root-system morphology may be maladaptive on deeper soils, providing a possible explanation for the restricted distribution of many shallow-soil endemics.

Key words: commonness, ironstone, rarity, root placement, root-system morphology, shallow-soil endemics, specialization, trade-offs.

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Introduction

Plant species vary widely in their geographical distribution and local abundance. As a result of human activities, the number of plant species that are rare is rising sharply. To prevent or slow down the extinction of rare species, a better understanding of the factors involved in causing their restricted distribution is crucial. As autecological studies are not feasible for all rare species, many researchers have searched for generalities by employing rare–common species comparisons. However, no unifying theory explaining plant species commonness or rareness has yet emerged (reviewed by Kruckeberg & Rabinowitz, 1985; Kunin & Gaston, 1997; Murray *et al.*, 2002), leading some authors to suggest that all species are idiosyncratic (Gitzendanner & Soltis, 2000). In this study, we

attempt to understand the restricted distribution of rare species that are confined to one particular habitat: shallow-soil environments. By focusing on rare species from a single habitat type that have evolved under similar selection pressures, we believe it is more likely to find traits that are associated with a species' rarity.

Worldwide, a disproportionate number of rare species occur in relatively open, shallow, rocky and drought-prone environments (Kruckeberg & Rabinowitz, 1985; Baskin & Baskin, 1988; Pate & Hopper, 1993; Medail & Verlaque, 1997). Why do many species that occur in these habitats tend to be confined to them? We believe this is related to the extreme droughts that communities on these shallow habitats experience, and the resulting strong selection pressures on establishing seedlings. Indeed, drought-related mortality is known to be a

major factor in seedling demography in these environments (Frazer & Davis, 1988; Enright & Lamont, 1989; Richards *et al.*, 1997 for Mediterranean environments). The extremity of these habitats would have favoured the development of local specialized phenotypes (Van Tienderen, 1997), but at the expense of a reduction of fitness in deeper-soiled habitats. However, for most shallow-soil endemics we do not know what the specific adaptations are that enable them to persist in their own adverse environments, nor can we evaluate how these adaptations hinder establishment or survival in neighbouring communities. There is some evidence suggesting that there are costs of adaptation or specialization, as several rare edaphic endemics have been shown to be relatively poor competitors when grown in other environments (Hart, 1980; Prober, 1992; Walck *et al.*, 1999; Lloyd *et al.*, 2002; but cf. Gottlieb & Bennett, 1983; Snyder *et al.*, 1994). None of these studies, however, provides a mechanistic explanation for these trade-offs.

In this study we examine the local adaptations, and their consequences for survival, of two rare *Hakea* (Proteaceae) species, confined to shallow-soil ironstone communities in Mediterranean south-western Australia. Ironstone communities are seasonally wet, shallow-soil shrublands that contain many endemic species as well as species that have their distribution centred on them (Gibson *et al.*, 2000). Field observations suggest that neither ironstone *Hakea* species suffers from reproductive constraints, as populations contain numerous, easily germinable seeds. In previous work we demonstrated that both *Hakea* species differ from five of their common congeners in their root-system morphology (Poot & Lambers, 2003a). In the early seedling stages the ironstone endemics had higher root mass ratios and a higher specific root length (length of root per unit root mass), while in later stages of growth they invested more in deep roots. We argued that the specific root-system morphology of the ironstone species reflects adaptations that maximize their chances of finding crevices in the underlying ironstone rock, thereby increasing their chances of obtaining water before the onset of summer drought. Although we found consistent differences between rare and common species in root-system morphology, we could not examine the implications for root exploration due to the constraints of the pot dimensions. Therefore, for the present study we developed 1.8-m-long custom-made containers with transparent bottoms. These enabled us to study the spatial, temporal and functional root-system development of the rare and common *Hakea* species in much greater detail and under more natural and less restrictive conditions. In a second experiment, we examined the possible consequences of differences in root-system morphology for survival in the natural habitats through a fully reciprocal transplant experiment. Therefore the aims of this study were twofold: to investigate which specific root traits of the ironstone *Hakea* species distinguish them from their common congeners; and to investigate the possible consequences of these traits for survival in their own as well as in surrounding habitats.

Materials and Methods

Experimental species

Hakea species are woody perennials from the southern hemisphere family Proteaceae, which range in size from shrubs to small trees. Two rare south-western Australian *Hakea* species with their distribution centred on winter-wet, shallow-soil ironstone communities (*H. oldfieldii* Benth, *H. tuberculata* R. Br.) were compared with four of their common congeners originating from nearby winter-wet (*H. ceratophylla* Smith R.Br., *H. varia* R.Br.) or nonwetland habitats on deeper soils (*H. lissocarpha* R. Br., *H. cyclocarpa* Lindl.). Both ironstone endemics are relatively common within their own highly localized habitat, but rarely occur outside it, whereas all four common species are more widespread and occur over a much greater geographical range.

Ironstone communities are winter-wet shrublands that occur on very shallow, reddish loamy sands (0–0.2 m deep) over massive ironstone rock. They occur as scattered remnants either on the coastal plain or on the foot slopes of the nearby and geologically much older lateritic scarps and plateaus (Gibson *et al.*, 2000). The underlying ironstone rock is believed to have been formed by the precipitation of ferric iron from the groundwater in the zone of water-table fluctuation, and is thought to be still actively forming ('bog iron' formation; Johnstone *et al.*, 1973; Gibson *et al.*, 2000). Although iron-rich impeding layers are common on south-western Australian coastal plains, they generally occur at much greater depth, and most soils are composed of deep layers of Quaternary sand deposits. By contrast, the shallow sandy loam soils of the ironstone communities (0–0.2 m deep) are derived mainly from weathering of the underlying ironstone rock, and have a distinct red-brown coloration. For a further description of the floristics, climate and soils of the ironstone communities, see Gibson *et al.* (2000) and Supplementary Material.

The common winter-wetland *Hakea* species occur on a variety of damplands and sumplands on poorly drained sandy soils on the coastal plain, as well as on poorly drained valleys of the nearby lateritic hills. In normal winters, *Hakea* species from both 'winter-wet' habitats (ironstone as well as nonironstone) would experience variable periods of soil saturation and shallow soil inundation in their natural habitats. By contrast, the common nonwetland *Hakea* species occur in the understorey of eucalypt woodlands on well drained soils higher in the landscape, and would never experience soil inundation. For further species and distribution information, see Supplementary Material.

Root foraging experiment

For each of the *Hakea* species, woody follicles containing the seeds were sampled in the field during March and April 2002 (for approximate locations see Supplementary Material).

Follicles of at least five plants per species were collected. Within 2 wk at room temperature, all woody follicles had dehisced naturally. The average seed mass of the ironstone species was significantly lower than that of the other species (mean \pm SE for ironstone species *H. oldfieldii* and *H. tuberculata*, respectively: 11.5 ± 0.5 and 12.1 ± 1.1 mg; winter-wet common species *H. ceratophylla* and *H. varia*, respectively: 32.7 ± 1.7 and 18.5 ± 1.2 mg; nonwetland common species *H. lissocarpa* and *H. cyclocarpa*, respectively: 24.8 ± 2.3 and 87.4 ± 7.1 mg; $P < 0.05$, Tukey test after one-way ANOVA). On 21 August 2002, 20 seeds per species were placed on moistened paper in a temperature-controlled room (day/night 15°C) for germination. Germination percentages were high (80–100%), and did not differ among species. Except for seeds of *H. cyclocarpa*, which germinated on average 3 d later, seeds of all species germinated between 8 and 11 d.

After germination, seedlings were transferred to individual custom-made containers that were 1.8 m long, 0.2 m wide and 0.15 m deep, and filled to a depth of 0.11 m with washed river sand. To ensure proper drainage, 10 evenly spaced holes were drilled in the bottom of each container. Initially, two seedlings were planted in the middle of each container. After 10 d growth, the smallest seedling was removed, leaving five seedlings for each species. The containers were constructed from untreated pinewood sides and transparent polycarbonate bottoms to enable measurements of root growth along the bottom. To shield the developing root systems from light while still allowing access to the transparent bottoms, a 1.8-m long, 0.5-m wide, black plastic film was stapled to one side of each container, and was attached to the other side by an elastic guiding line glued to the plastic and held by nails. The U-shaped plastic film collected the drainage water after each watering event, and kept the air under the container moist. The containers were positioned on adjacent frames in a temperature-controlled glasshouse (20 : 15°C, day : night, light intensities 65% of ambient), in five blocks with one individual of each species randomly placed within each block. Plants were watered with tap water every 2–3 d, and pots were flushed once a week with approx. 500 ml of a diluted nutrient solution (200 μ M Ca(NO₃)₂, 100 μ M K₂SO₄, 4 μ M KH₂PO₄, 54 μ M MgSO₄, 0.24 μ M MnSO₄, 0.10 μ M ZnSO₄, 0.018 μ M CuSO₄, 2.4 μ M H₃BO₃, 0.030 μ M Na₂MoO₄, 40 μ M Fe-EDTA).

Lateral spread of roots was determined visually every 7–12 d on the transparent bottom of the containers. Two weeks after root systems of the first plants had reached the far sides of the containers (approx. 7 months after germination), plants were harvested. Stems were cut at the root–shoot junction, and fresh mass and dry mass (after 48 h at 70°C) of stems and leaves were determined. To ascertain spatial root placement, root systems were harvested separately for seven horizontal (0–0.15, 0.15–0.45, 0.45–0.75, 0.75–1.05, 1.05–1.35, 1.35–1.65, 1.65–1.80 m) and two vertical (0–0.10, 0.10–0.11 m deep) sections. This was achieved by pushing sharpened, stainless steel plates into the sand and

flushing out each of the 14 sections separately. After rinsing the roots to remove all sand, they were separated into cluster and noncluster roots. Cluster roots of *Hakea* species and many other members of the Proteaceae are bottle brush-like structures that are involved in nutrient mobilization and uptake (Shane & Lambers, 2005). The noncluster roots were then computer scanned and analysed for total root length, volume and average root diameter (WINRHIZO ver. 3.9 software, Regent Instruments, Quebec, Canada). Fresh and dry mass (after 48 h at 70°C) were determined for both types of root.

Field transplant experiment

In May 2002, 320 seeds per species were placed on trays with moistened paper in a temperature-controlled room (15°C) for germination. After germination, seedlings were planted into trays filled with washed river sand. Approximately 4–5 wk after germination (first and second week of June 2002, winter) the young seedlings were transplanted into six field sites. At this stage, most seedlings had only just formed their first pair of leaves. Field sites coincided with the six locations where seeds of the six species had been collected. Therefore, at each location one of the *Hakea* species was the ‘home-playing’ species. All species were transplanted in two winter-wet ironstone communities, two winter-wet communities on deeper soils, and two nonwetland habitats in the undergrowth of eucalypt woodlands. At each site, four plots were chosen in areas where the ‘home-playing’ species was most numerous. In each plot, 60 seedlings (10 per species) were planted randomly in a rectangular area (0.9 \times 0.5 m) situated in the middle of a chicken-wire enclosure (1.30 \times 0.9 m), with seedlings placed at 100-mm distance from each other. The enclosure was necessary to prevent any interference by wildlife (e.g. kangaroos or rabbits). Before the seedlings were transplanted, the area inside the enclosure as well as a border area of 0.3 m outside the enclosure were cleared of vegetation by pulling out plants. This was done to create a situation as close as possible to a ‘natural’ recruitment (usually after fire) with enhanced light and nutrient levels. Four weeks after transplanting the seedlings, we removed the larger weeds to facilitate further seedling establishment. Thereafter, no further interference with naturally emerging plants inside the plots took place. In the following years we regularly monitored plant survival and growth. Here we report the survival data of this field experiment until April 2005.

Statistical analyses

To test for differences among species in their relative root-distribution patterns, we used nonmetric multidimensional scaling (MDS) of the multivariate statistical package PRIMER (ver. 6; Clarke & Warwick, 2001; see Supplementary Material). Other variables were analysed with the ‘General Analysis of Variance’ procedure of the statistical package

Table 1 General characteristics of rare and common *Hakea* species after 7 months' growth in a glasshouse on individual 1.80-m-long containers

Variable	Rare ironstone			Common		Common	
	Unit	winter-wet		winter-wet		nonwetland	
		HO	HT	HCE	HV	HLS	HC
Biomass allocation (dry mass)							
Shoot	g	4.3 ± 1.1	3.6 ± 0.7	3.8 ± 0.5	5.8 ± 0.6	3.9 ± 0.5	5.0 ± 0.7
Root	g	2.8 ± 0.6	2.6 ± 0.4	2.2 ± 0.3	3.4 ± 0.5	2.4 ± 0.2	2.3 ± 0.2
Total	g	7.1 ± 1.6	6.2 ± 1.1	6.0 ± 0.8	9.2 ± 1.0	6.3 ± 0.7	7.3 ± 0.8
Root mass ratio	g g ⁻¹	0.40 ± 0.03	0.43 ± 0.02	0.37 ± 0.01	0.37 ± 0.04	0.38 ± 0.02	0.33 ± 0.02
Root characteristics							
Total root length	m	89 ^b ± 15	84 ^b ± 24	36 ^a ± 5	77 ^b ± 10	72 ^b ± 12	49 ^{ab} ± 10
Root diameter	mm	0.74 ± 0.04	0.73 ± 0.01	0.71 ± 0.05	0.60 ± 0.02	0.63 ± 0.04	0.63 ± 0.03
Specific root length	m g ⁻¹	44 ^b ± 3	44 ^b ± 5	34 ^a ± 5	43 ^{ab} ± 4	54 ^b ± 8	42 ^{ab} ± 5
Root dry mass percentage		12.4 ^a ± 0.4	12.6 ^a ± 0.4	17.2 ^b ± 0.7	15.7 ^b ± 1.1	15.4 ^b ± 0.8	16.9 ^b ± 0.4
Percentage cluster roots		22 ^a ± 3	30 ^a ± 3	48 ^b ± 5	49 ^b ± 5	44 ^b ± 4	56 ^b ± 3

Values are means ± SE. Letters indicate significant differences among means ($n = 5$, $P < 0.05$, Student–Newman–Keuls pairwise comparison test after one-way ANOVA). All variables were log-transformed before testing.

HO, *H. oldfieldii*; HT, *H. tuberculata*; HCE, *H. ceratophylla*; HV, *H. varia*; HLS, *H. lissocarpha*; HC, *H. cyclocarpa*.

GENSTAT (ver. 4.2, VSN International, Oxford, UK). Species-specific differences were evaluated statistically using the Student–Newman–Keuls pairwise comparison test after ANOVA (experiment-wise error rate $\alpha = 0.05$). Most variables were log-transformed to ensure homogeneity of variances and normality.

Results

Whole-plant characteristics

After 7 months' growth in 1.8-m-long containers under glasshouse conditions, we could not detect any significant differences in total root or shoot biomass among the six *Hakea* species (Table 1). Similarly, there were no habitat-related differences in general root characteristics such as total root length, average root diameter, specific root length or root mass ratio (Table 1). However, the rare ironstone species produced roots with a lower dry mass percentage, and with a lower relative amount of cluster roots than species from the other habitat groups (Table 1).

Spatial root placement

Despite the overall similarity in whole-plant characteristics, a spatial analysis of root-system placement revealed major habitat-related differences among the species. The ironstone endemics showed a much more uniform horizontal root distribution than all other species (Figs 1, 2). The middle section, where the seedlings had been planted (300 mm wide), contained as much as 42–65% total root fresh mass in the

common species, whereas it only contained 21 (HO) to 27% (HT) in the rare ironstone endemics (sections 4 and 11, Figs 1, 2, respectively; $P < 0.05$). Conversely, the ironstone species allocated considerably more root biomass to the outer sections of the containers (Figs 1, 2). This was especially so in *H. oldfieldii*, which had a remarkable 17% of its total root system in these outer sections (sections 1, 7, 8, 14).

In addition to differences in horizontal root placement, the ironstone species also allocated more roots to the bottom 10 mm of the containers ($P < 0.01$), except for *H. ceratophylla*, which did not differ significantly from the ironstone species (Figs 1, 2). Overall, the ironstone species invested 35 (HO) and 26% (HT) of their root system in the bottom layer, compared with 22 (HCE) and 13% (HV) for the winter-wetland species, and only 6 (HC) and 3% (HLS) for the nonwetland species. A multivariate analysis of the root-system distribution also showed a clear separation of the rare ironstone species compared with their common congeners (for further details see Supplementary Material).

As observed earlier for the whole root system (Table 1), the ironstone endemics invested relatively less root mass in cluster roots (shaded areas in Figs 1, 2). This was especially so in the bottom layer, where the ironstone species produced hardly any clusters (Fig. 2). In most species, root-system distribution was somewhat asymmetrical, with a tendency for more roots to be produced towards one side of the container.

Temporal root placement

By monitoring the horizontal extension of root systems over the transparent bottoms of the containers, we were able to

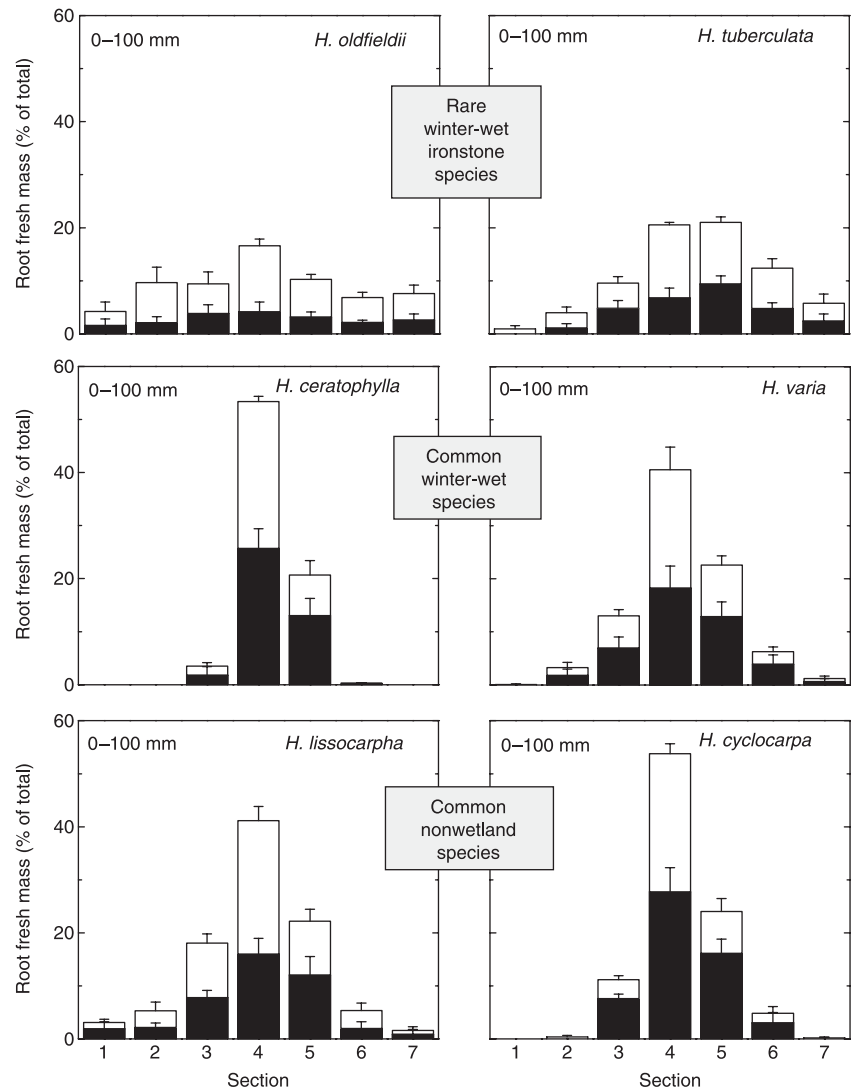


Fig. 1 Relative distribution of root fresh mass (percentage of total plant root mass) in the top seven sections (0–100 mm depth) of 1.8-m-long pots for six *Hakea* species originating from three different habitats. The contribution of cluster (black bars) and noncluster root mass (white bars) is indicated separately. Seedlings were planted in the middle of each pot (section 4); all sections were 0.3 m wide except for the outer sections (1 and 7), which were 0.15 m wide. Bars represent means \pm SE ($n = 5$).

determine when the differences in spatial root placement appeared. Seedlings of one of the ironstone species, *H. oldfieldii*, started showing a significantly wider horizontal root system extension 63 d after germination (Fig. 3). At this stage the other ironstone species, *H. tuberculata*, did not differ from its common congeners. However, almost 3 months later (day 155), this ironstone endemic had also spread its roots over a significantly larger area of the bottom of the containers than its widespread congeners. At the end of the experiment, both ironstone species had explored a 1.5- to 3.5-fold wider area of the bottom of the containers than any of the other species.

Seedling survival in the field

Overall, 3-yr-old seedling survival was much lower in the winter-wet ironstone habitats (7, 22%) than in the winter-wet

habitats on deeper soils (59, 53%), and the nonwetland woodland sites (64, 55%; Fig. 4). Especially the more northerly community, which has a drier and warmer habitat (community 1), had very high mortality rates, which differed greatly among the species. All the species nonnative to this site died, except for one small individual of *H. varia*, whereas there were still 17 out of 40 seedlings of the ‘home-playing’ *H. oldfieldii* alive. The vast majority of the seedling deaths in this community occurred during the first summer (Fig. 4).

The more southerly ironstone community (community 2) showed less, but still substantial, mortality (Fig. 4). At this site, early winter waterlogging caused the death of all seedlings of the nonwetland species. Similarly to the other ironstone community, the first summer was largely responsible for the mortality in the remaining species. Surprisingly, *H. oldfieldii*, which does not occur on this site, showed the highest survival

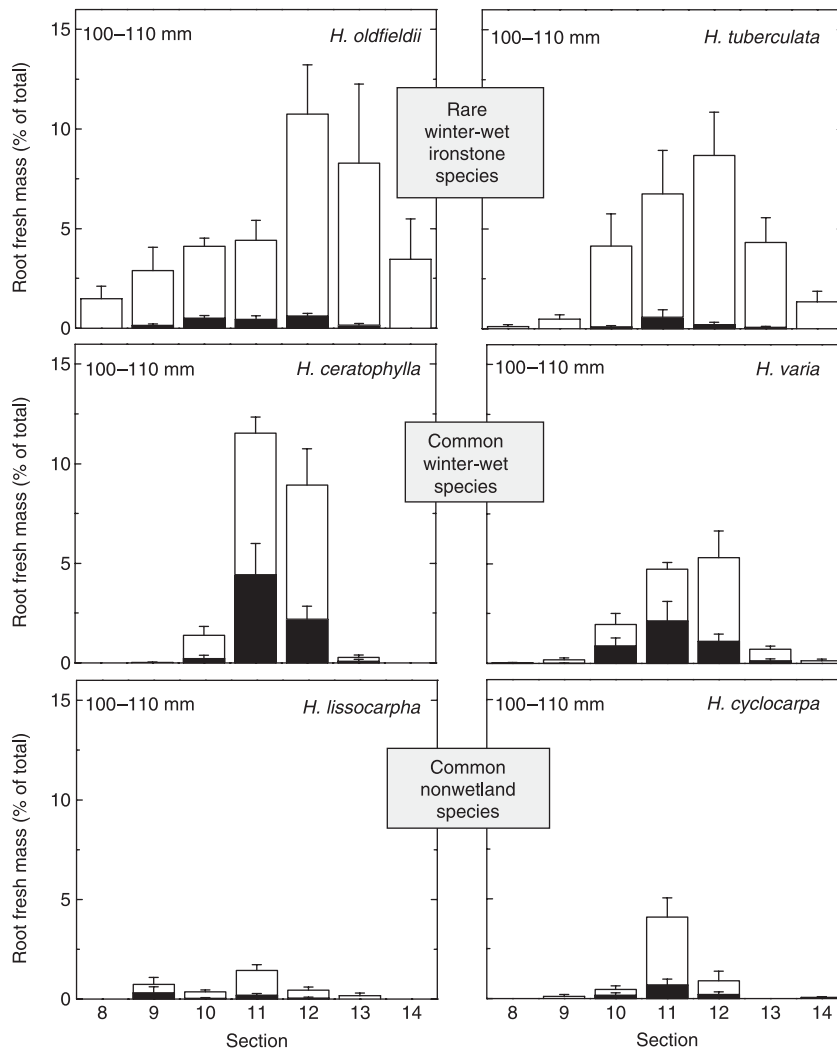


Fig. 2 Relative distribution of root fresh mass (percentage of total plant root mass) in the bottom seven sections (100–110 mm depth) of 1.8-m-long pots for six *Hakea* species originating from six different habitats. The contribution of cluster (black bars) and noncluster root mass (white bars) is indicated separately. Seedlings were planted in the middle of each pot (section 11); all sections were 0.3 m wide except for the outer sections (8 and 14), which were 0.15 m wide. Bars represent means \pm SE ($n = 5$).

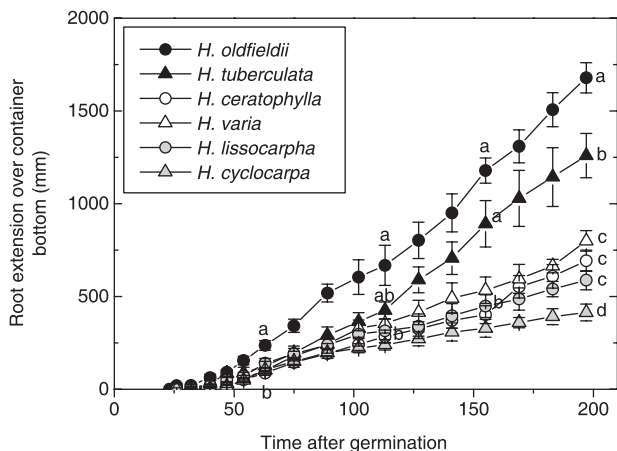


Fig. 3 Time course of the one-dimensional horizontal extension of root systems over the bottom of 1.8-m-long containers for six *Hakea* species originating from different habitats. Bars represent means \pm SE ($n = 5$). Letters indicate significant differences among means at each point in time ($P < 0.05$, Student–Newman–Keuls pairwise comparison test after one-way ANOVA). Note that only changes in significance over time are indicated.

rate (70%). The ‘home-playing’ species *H. tuberculata* had the second-highest survival (38%), but did not differ significantly from *H. oldfieldii* or from both common winter-wet species, which on average had much lower survival rates (17.5, 10%). Possible differences were obscured by the large variation among the four plots, with the most extreme plot having only six *H. oldfieldii* and one *H. tuberculata* seedlings surviving.

On the winter-wet sites on deeper soils and on the nonwetland sites, species-specific differences in seedling survival were much less clear-cut. Although the trend at ‘winter-wet site 1’ was similar to that at site 2, only at site 2 were there significant differences in survival, with both nonwetland species having higher mortality rates than all other species. This was not related to waterlogging events in winter, as most mortality occurred during dry summer months. In the nonwetland woodland sites, species survival was very similar among species, with most mortality occurring during the summer periods.

When comparing seedling survival on the basis of individual species instead of sites, some interesting patterns emerged

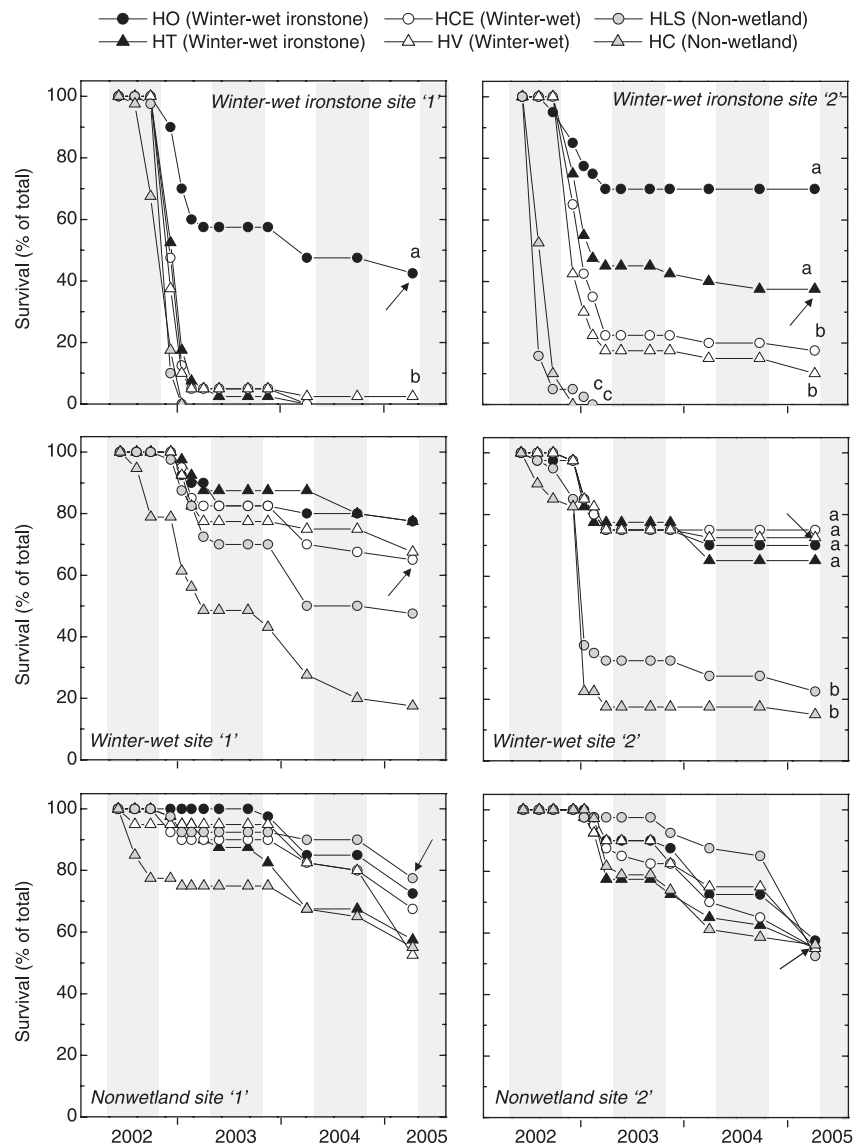


Fig. 4 Three-year survival (percentage of total) of 1-month-old seedlings of six *Hakea* species transplanted into six different field sites. At each field site, the 'home-playing' species is indicated with an arrow. Grey-shaded areas represent the 'wet season'. Symbols indicate mean values of four plots within each site ($n = 10$ per plot for each species). Standard errors were omitted for clarity. Letters indicate significant differences among means at the last time point ($P < 0.05$, Student–Newman–Keuls pairwise comparison test after one-way ANOVA). For further details see Materials and Methods. HO, *H. oldfieldii*; HT, *H. tuberculata*; HCE, *H. ceratophylla*; HV, *H. varia*; HLS, *H. lissocarpha*; HC, *H. cyclocarpa*.

(results not shown explicitly, but they can easily be deduced from Fig. 4). *Hakea oldfieldii* was the only species that did not show a differential survival among the six sites, but it tended to do worst at its own site. *Hakea tuberculata* did not survive in the northern ironstone community, but did not differ in survival among the other five sites. Again, among these other five sites it tended to do worst at its own site. By contrast, the survival rate of the common winter-wet species was significantly less at the ironstone sites compared with the other four sites, and they tended to do quite well in their own sites. Similarly, the nonwetland species showed lower survival rates in the ironstone sites, and tended to do best (*H. lissocarpha*), or did best (*H. cyclocarpa*) in their own nonwetland sites.

Discussion

Adaptations to shallow-soil habitats

Many shallow-soil habitats in seasonally dry climates support plant communities that include perennial woody species that are confined to them. However, their thin soils have only a limited water-holding capacity, and there is increasing evidence that, during the dry season, water held within the underlying bedrock is essential for meeting the transpiration demands of shrubs and trees (e.g. Rose *et al.*, 2003 and references therein). Therefore obtaining root or mycorrhizal (Bornyasz *et al.*, 2005) access to the water stored in the weathered bedrock via cracks, fissures and micropores is

probably essential for the establishment and survival of many species. Indeed, growth of roots into rock fissures and crevices has commonly been observed (Zwieniecki & Newton, 1995 and references therein). However, despite the potential importance of root-system morphology for survival in these shallow-soil communities, it has seldom been studied. Here we provide the first evidence for the significance of root-system morphology for the survival of species confined to shallow-soil ironstone communities.

The ironstone endemics differed consistently from their common congeners in their spatial and temporal root placement: after having reached the bottom of the container (cf. a hardpan), they invested predominantly in long laterals. These laterals explored the bottom surface of the container much more quickly than did the root systems of their common congeners. In their natural, shallow-soil habitats, this root-foraging strategy would lead to the exploration of a much larger rock surface area, and thus presumably greatly enhance the chance of accessing water through cracks and crevices in the underlying rock. Indeed, the field transplant experiment confirmed that in the ironstone environment, seedlings of the ironstone endemics had substantially higher summer survival rates than their common congeners. These results strongly suggest that the root allocation pattern of these species is adaptive, contributing to their relative success in their own habitat. As, worldwide, many rare and endemic plant species occur in similar shallow-soil, drought-prone environments (see references in Introduction), the present results are probably of much wider significance.

To our knowledge, this is the first detailed study designed to compare the root allocation pattern of rare and common plant species (cf. Poot & Lambers, 2003a). In a review on rare–common species comparisons, Murray *et al.* (2002) documented 94 plant traits in a total of 54 studies. However, apart from root mass ratio (Walck *et al.*, 1999), none of these studies included any other root-related traits (cf. Pohlman *et al.*, 2005). Root traits are obviously difficult to measure in the field, and for some critically endangered species, root-system excavations or even the collection of seeds or other plant material for glasshouse experimentation may not always be feasible. Even when studies are conducted in the glasshouse, space considerations often restrict researchers to relatively small pot sizes (e.g. our earlier study in Poot & Lambers, 2003a). Apart from possible species-specific effects of root confinement on nutrient and water uptake and biomass allocation (McConaughay & Bazzaz, 1991), these studies are less likely to reveal relevant differences in root-system morphology. We believe that our approach of providing individual plants with adequate rooting space, and analysing their root-system development in space and time, has strong merits. In this study, apart from revealing the large differences in root placement between shallow-soil endemics and their common congeners, we show that all species had near-distinct rooting patterns (see also the multivariate analysis in Supplementary Material).

This suggests an important role for root-system morphology in local adaptation, providing new insights into its adaptive and evolutionary significance.

How did the ironstone species achieve their faster horizontal root exploration? Earlier work with the same set of species suggests they have a quicker start by allocating more biomass to roots at the early seedling stage (higher root mass ratio 62 d after germination; Poot & Lambers, 2003a, 2003b). However, at later stages of growth these differences disappear (Poot & Lambers, 2003a, 2003b; Table 1). Within the root system, the ironstone species invest more biomass in the main root axis and in long, spreading laterals, whereas the common species invest more in shorter laterals and cluster roots close to the base of the plant. This could be due to inherent differences in root-system architecture (e.g. differences in initiation of lateral- and cluster-root primordia), or it could be the result of a differential response to encountering a hardpan or obstruction. In the latter case, the response of the common species could be explained by the typical loss in apical dominance and a subsequent outgrowth of lateral primordia, thus circumventing the obstruction (Goss, 1977; Misra & Gibbons, 1996; Thaler & Pages, 1999). On a homogeneous shallow soil, this strategy is unlikely to be successful in terms of exploring a large surface area in order to secure alternative water sources. The decreased investment of ironstone species in cluster roots is probably functional. Although the relatively small lateral rootlets of the clusters are very important for nutrient acquisition (Shane & Lambers, 2005), their small diameters, placement and short life span make them very inefficient for water uptake. Therefore the ironstone species' predominant allocation to long laterals, as opposed to cluster roots, may reflect an evolutionary trade-off between nutrient- and water-acquisition functions.

Although the two ironstone endemics have disjunct distributions, their performance in each other's ironstone habitat differed markedly. The species native to the northern ironstone habitat (*H. oldfieldii*) did extremely well at the southern sites, whereas the species adapted to the southern sites (*H. tuberculata*) did not survive its first summer in the northern ironstone habitat. This is probably associated with adaptations of these species to differences in local climate, as earlier glasshouse experiments showed that the specific chemistry of the northern ironstone soil does not hinder growth and development of *H. tuberculata* (unpublished results). During the summer months with highest mortality (generally December–February), the northern ironstone site experienced average daily temperatures that were 5°C higher and average amounts of rainfall that were 40% less than the southern site (data from nearest climate stations obtained from the Australian Bureau of Meteorology). Therefore the onset of drought is earlier, and the impact of drought greater, in the northern ironstone sites. Of the two ironstone endemics, the species adapted to the drier sites (*H. oldfieldii*) proliferates its roots much more quickly over the bottom of the container. Although the above may explain the failure of *H. tuberculata*

to establish on the more extreme northern sites, it does not explain the success of *H. oldfieldii* on a site that is > 80 km south of its nearest occurrence. However, winter rainfall has decreased steadily in the southwest of Australia, by 10–20% since the mid-1970s, and the years since transplantation have all been moderately to extremely dry (Indian Ocean Climate Initiative, 2002; Australian Bureau of Meteorology). Therefore the success of *H. oldfieldii* in the southern ironstone communities may be related to its competitive strength in consecutive dry years, and thus to climate change, rather than to stochastic or historical causes.

Confinement to shallow-soil habitats

Although it has been suggested for several edaphic endemics that they are poor competitors when grown in other environments (see references in Introduction), no mechanistic explanation has been put forward. Lavergne *et al.* (2004), in a comparison of 20 rare–common species pairs from the French Mediterranean region, suggested that the rare species are poor competitors, and that this explains their confinement to rocky habitats with low aboveground competition. However, this was based mainly on their smaller stature. As they measured plant traits in the field, and rare species were mostly confined to marginal habitats on shallow soils, size or stature differences could easily have been due to habitat constraints. The results of our study provide a more mechanistic explanation. It is commonly believed that adaptation to a specific environment is coupled to reduced fitness in certain other environments (Futuyma & Moreno, 1988; Van Tienderen, 1997). However, these ‘costs of specialization’ in other environments have seldom been demonstrated, and studies on the costs of specialized root systems are particularly rare (Jansen *et al.*, 2005). The costs of the ‘ironstone root-system morphology’ may lie in the inability to produce prolific surface roots where nutrients are located in the topsoil. In an evolutionary sense, the extreme environment of the shallow-soil habitats may not have allowed for the development of plastic phenotypes, but favoured local, specialized genotypes (Reboud & Bell, 1997; Van Tienderen, 1997; DeWitt *et al.*, 1998; Sultan & Spencer, 2002). Assuming that water availability is a major constraint in these shallow-soil habitats, both a high early investment in roots (Walck *et al.*, 1999; Poot & Lambers, 2003a) and a particular root-system morphology (this study) could critically increase an individual’s chances of accessing water sources before the onset of summer drought. However, on deeper soils this ‘strategy’ is unlikely to be competitive. Too much early investment in roots would come at the expense of a lower initial above-ground competitive ability. Similarly, allocating too few roots to the topsoil, where most nutrients occur, would decrease nutrient-uptake capacity (e.g. Lynch & Brown, 2001 for P acquisition). This may be especially relevant in the context of the severely nutrient-impooverished soils of south-western Australia (Foulds, 1993).

Here, a low allocation of resources to shallow roots may limit nutrient-uptake capacity to such an extent as to seriously compromise both above- and belowground competitiveness. Therefore the restricted distribution of the ironstone endemics, and possibly of many other rare shallow-soil endemics, may be a consequence of an extreme root-system specialization to shallow-soil and seasonally water-limited environments.

Unexpectedly, during the first 3 yr after transplantation, seedlings of the ironstone endemics did not show a greater mortality than those of their common congeners in the deeper-soiled environments. Also, the heights they attained after 3 yr, although highly habitat-dependent (much larger in the open winter-wet habitats than in the more shady nonwetland woodland environments), were similar to those of their common congeners (results not shown). There are several plausible reasons for this apparent discrepancy. Possibly, in these severely nutrient-impooverished soils where growth is slow, above-ground competitive displacement takes longer than 3 yr. The initial survival of the ironstone seedlings would thus be due to reduced competition as a result of vegetation removal and slow growth rates. Alternatively, the ‘unnatural’ start of the experiment, with seedlings transplanted from glasshouse conditions into an artificially disturbed environment, as opposed to a more natural germination event after a fire, may have favoured the rare species. Common species, with their preferred allocation to superficial roots, would benefit more than their rare congeners from enhanced nutrient availability in ash beds. A third reason for the unexpected success of the ironstone endemics on deeper soils may be the low average rainfall during the experimental period. During years of below-average rainfall, a larger allocation to deep roots might actually be beneficial, and offset, or at least delay, possible costs in terms of a decrease in nutrient-uptake capacity.

Search for generalities in rare–common species comparisons

The characteristic root-system morphology of the ironstone endemics can potentially explain their limited distribution. We expect that other shallow-soil endemics have similar adaptations, provided their habitats also have soil water at depth. Rare species from other habitats, however, are expected to have adaptations to the restrictions imposed by their own specific environments. We propose that highly specialized, habitat-specific morphological and physiological adaptations explain success in the rare species’ habitat as well as failure in surrounding habitats. Ecophysiological trade-offs associated with their adaptations, and/or reduced phenotypic plasticity in traits essential to their own habitat, would decrease their fitness in others.

Several comparative studies provide support for limited phenotypic plasticity in species with narrow ecological amplitudes (leaf mass per area, Walters & Field, 1987; photosynthetic capacity, Chazdon, 1992; spatial root deployment,

Bell & Sultan, 1999). Therefore future rare–common comparisons would benefit greatly from an approach that is more habitat-oriented, and that incorporates measurements of phenotypic plasticity of ecophysiological traits particularly relevant to the habitat under consideration.

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Supplementary Material

The following supplementary material is available for this article online:

Appendix S1 Further species and distribution info.

Appendix S2 Experimental setup and field site photographs.

Appendix S3 Multivariate analysis of root distribution patterns.

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