Genetic Determination of Erect and Prostrate Growth Habit in Five Shrubs from Windswept Headlands in the Sydney Region

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Abstract

In the Sydney region, many plants from populations on windswept headlands have a more prostrate growth habit compared with plants from populations of the same species occurring away from the coast. To determine whether these different growth habits are genetically determined, plants from four populations of each of five species (*Acacia myrtifolia, Acacia suaveolens, Banksia ericifolia, Casuarina distyla, Hakea teretifolia*) were grown under uniform glasshouse conditions. Multivariate analyses of six morphological characteristics indicate that, for four of these species, the offspring are similar to their maternal parent; we thus conclude that the habit differences are genetically fixed in these populations. The same trend is apparent for *C. distyla*, although significant variation occurs in the offspring. Univariate analyses indicate that different characteristics reflect the habit differences in different species. For conservation biology, the implications of this intra-specific variation are that attempts should be made to conserve viable populations of all genetically isolated taxa within a species.

Introduction

Taxonomists delineate species on a range of morphological and anatomical attributes while often ignoring such ecological considerations as survival, fecundity, reproductive biology or biotic interactions. However, to the ecologist it is often important to determine what might be called 'ecological' rather than taxonomic species, i.e. populations of organisms which behave as distinct entities while still possessing morphological characteristics that would group them together into the one taxon. Nevertheless, species are not uniform entities, either morphologically or ecologically, and intra-specific variation in many species is high, with populations differentiated spatially as ecotypes (see the reviews of Heslop-Harrison 1964; Kruckeberg 1969; Langlet 1971; Grant 1981).

Consequently, it is important to know something of the level of variations among populations of the same taxonomic species; in particular, whether observed phenotypic differences among populations are genetically fixed or not. Phenotypic differences that are genetically fixed may influence the reliability of species-wide generalisations (Grubb 1985). In conservation biology, ecological differences within a species are usually ignored in favour of species lists and distribution patterns, e.g. rare or threatened plant listings (Briggs and Leigh 1988). Significant genetic within-species variation is also worthy of attention by organisations whose aim is the conservation of biodiversity.

In this paper we examine the genecological question of whether the differences between two distinct growth forms of the same taxonomic species are genetically determined. We do this by growing, under uniform environmental conditions, five species with two distinct growth forms, a prostrate or low-growing form from windswept headlands and a more widespread upright form. If the habit differences are genetically determined in these species then the offspring should be similar to the maternal parent for this characteristic.

Exposed rocky headlands are a conspicuous feature of the New South Wales coastline, but their vegetation has been little studied (Adam *et al.* 1989). Plants growing in these exposed habitats commonly have prostrate habits, or else they grow erect and become deformed (Beadle 1981). Parsons and Gill (1968) have presented evidence that the latter habit is probably a phenotypic response to chloride toxicity, while the prostrate habit is usually considered to be a response to high wind velocity and duration (Hamilton 1917; Pidgeon 1937, 1938; Beadle 1981) which increase transpiration and therefore desiccation and which may have direct mechanical effects on plant growth.

Floristically, there are two main groups of plants on these headlands (Adam *et al.* 1989): (*a*) those widespread in other coastal habitats, such as saltmarsh, sand dunes or strandline; and (*b*) those widespread in other habitats further inland in the same area. It is the second group in which we are interested, as these plants are relatively common on the headlands of the Sydney region (Hamilton 1917; Beadle 1981). Adam *et al.* (1989) consider it likely that many of these widely distributed species have prostrate genotypes restricted to the headlands, but there have been no genecological studies to test this hypothesis in Australia.

Plants with a prostrate habit were formerly more widespread prior to the urbanisation of the Sydney coastline (cf. Hamilton 1917), while the upright growth habit is still widespread throughout the Sydney region, often in close proximity to the headlands. The consequences of distinct, genetically isolated forms of a species in relation to the conservation of these taxa is therefore also briefly discussed.

Materials and Methods

Field Sampling

Five species were chosen for this study: *Acacia myrtifolia* (Smith) Willd. and *Acacia suaveolens* (Smith) Willd. (Fabaceae); *Banksia ericifolia* L.f. and *Hakea teretifolia* (Salisb.) Britten (Proteaceae); and *Casuarina distyla* Vent. (Casuarinaceae). These species are common components of many of the shrubland and heathland communities recognised by Adam *et al.* (1989) for N.S.W. coastal headlands. Most of our headland samples were taken from their *Banksia ericifolia–Westringia fruticosa* heathland community type. All samples were taken within 10 km of each other.

Each of the five study species was sampled at two separate sites for each of the erect and prostrate forms (Table 1). At each site, two fruiting plants were randomly chosen and the following variables measured on each plant:

(i) plant height (cm);

(ii) two orthogonal canopy diameters (cm). This variable and plant height were then combined into a shape variable (see analysis below);

(iii) the vertical height of the edge of the canopy, measured perpendicular to the leading edge, hereafter referred to as edge height (cm);

(iv) the height to the first branch (cm);

(v) the length and width of 10 randomly selected leaves (or phyllodes in *Acacia* spp.) (mm). Care was taken to avoid leaves near the growing tips that may not have been fully grown, leaves damaged

Table 1. Description of field sampling sites

Growth form	Site	Species sampled	Location and description
Erect	1	All	Red Hill, Dee Why West. Open heath with occasional emergents
	2	All	Manly Dam Reserve. Open heath with occasional emergents
Prostrate	3	All	McKillop Park, South Curl Curl. Low heath
	4	All, except *A. myrtifolia*	Dee Why Head, North Curl Curl. Low heath
	5	*A. myrtifolia*	Turimetta Headland, Warriewood. Low heath

in any way, and basal, potentially juvenile leaves. For *C. distyla*, only the width of the cladode was measured;

(vi) the length of 10 randomly selected internodes (mm).

Additionally, as field sampling coincided with fruit maturation in the *Acacia* spp., a collection of ripe fruits was harvested from each plant. For *B. ericifolia*, *C. distyla* and *H. teretifolia*, all of which have serotinous fruits, care was taken to select fruits that were obviously mature. Fruits were kept separate on an individual plant basis and stored in seed envelopes in the laboratory.

Laboratory / Glasshouse Sampling

In the laboratory, seeds were extracted from the fruits collected in the field. The fruits of all species, except *B. ericifolia*, readily dehisced after being harvested. For *B. ericifolia*, the fruits were heated with a small blowtorch to promote the opening of follicles prior to seed extraction.

In the glasshouse, two seeds from each adult/site/growth form were placed in a pot (15 cm diameter × 15 cm deep) filled with coarse sand. This was then replicated for a second pot per adult/site/growth form. Prior to placement, seeds from the two *Acacia* spp. were scarified by rubbing on sandpaper in order to break the seed-coat dormancy. No pretreatment was necessary for the other study species. The pots were watered with tap water and placed on a central bench in the glasshouse in a randomised block design.

Once germination had occurred, seedlings were thinned, if necessary, to 1 per pot, thus giving two separate pots/adult/site/growth form. Unfortunately, for *H. teretifolia*, only one seedling could be successfully grown from one of the upright growth form sites (Site 1). Seedlings were watered with Aquasol (Hortico [Aust.] Pty Ltd) once per week for a period of several months, after which measurements of variables (i), (ii), (iii), (v) and (vi) as per adults were made on the seedlings. As most of the erect growth form plants had not branched when sampled, it was decided to drop variable (iv), height to first branch, for seedlings.

Analysis

Plant height (Ht) and the two orthogonal diameter measurements (O1 and O2) were combined to give an estimate of plant shape, viz. shape = $Ht/[(O1 + O2)/2]$. In this way, comparisons between plant shapes were possible. In all the analyses performed this shape variable was used in preference to HT, O1 and O2.

For the length and width of leaves and internode lengths for adults and seedlings, 3-factor nested ANOVAs (A, growth form; B(A), site; C(B(A)), individual) were used to compare individuals from different sites and with different growth forms (Wilkinson 1989). For the comparisons of differences in adult plant shape, edge height and height to first branch, 2-factor nested ANOVAs were used, there being no individual replication for these variables. Similarly, 2-factor nested ANOVAs were used for comparisons of all variables in the *H. teretifolia* seedling data because of the missing seedling replicate at Site 1. Adult and seedling data were not pooled in the one analysis because of the different growing conditions for each, i.e. field *v.* glasshouse. Cochran's test was used to test for homogeneous variances (Underwood 1981). Where Cochran's test was significant at $P = 0.05$ or $P = 0.01$, data were transformed using either natural logs or square roots. If, after data transformations, Cochran's test was still significant, a conservative approach was taken to acceptance of *F*-ratios in the ANOVA.

In addition, a hierarchical agglomerative classification and non-metric multidimensional scaling (MDS) ordination were used to compare growth forms for adults and seedlings, separately (Belbin 1989). These techniques used all measured variables in the one analysis. The GOWER coefficient was used to calculate the dissimilarity between variables, with data range standardised for each variable. An unweighted pair-group method using arithmetic averaging (UPGMA) clustering strategy was used to derive the hierarchical classification.

Results

For four species (*A. myrtifolia*, *A. suaveolens*, *B. ericifolia* and *H. teretifolia*), the seedlings produced by the plants of the erect and prostrate growth forms were clearly different, being recognisably similar to their maternal parents (Fig. 1). This same pattern occurs in only some *C. distyla* seedlings (Fig. 1).

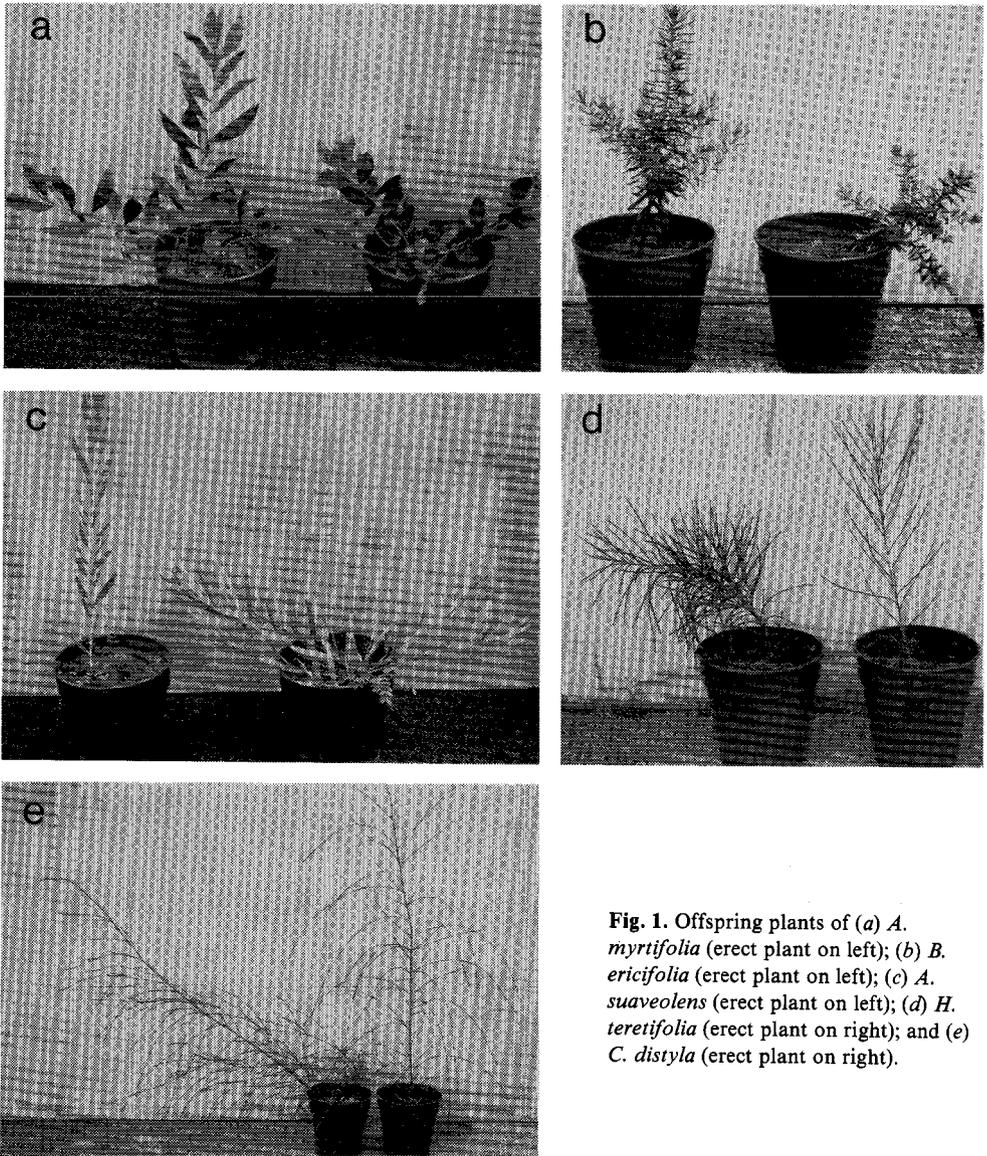When the information from the sampled variables is combined in the one analysis

Fig. 1. Offspring plants of (*a*) *A. myrtifolia* (erect plant on left); (*b*) *B. ericifolia* (erect plant on left); (*c*) *A. suaveolens* (erect plant on left); (*d*) *H. teretifolia* (erect plant on right); and (*e*) *C. distyla* (erect plant on right).

differences between erect and prostrate forms are found for both adults and seedlings. Plants from the two growth forms are clearly separated on the ordination axes and in the corresponding classifications for *A. myrtifolia* (Fig. 2*a*), *A. suaveolens* (Fig. 2*b*) and *H. teretifolia* (Fig. 2*c*). For *B. ericifolia* (Fig. 2*d*) the same pattern occurs, except that the seedling classification distinguishes the two seedlings from individual 1 at Site 4 from the remaining prostrate seedlings. The main point, that the two growth forms are distinguished, is still supported. Only *C. distyla* does not readily follow this pattern (Fig. 2*e*). While prostrate and erect forms are clearly distinguished in the adult data the seedling data are more confounded. One seedling from individual 1, Site 1 erect form is an outlier. Two prostrate seedlings, Site 3, individual 1 and Site 4 individual 1, are more similar to the erect seedlings than to the other prostrate seedlings. Similarly,

one erect seedling, Site 2 individual 1, is more similar to the prostrate seedlings than to the other erect seedlings.

Significant differences between growth forms were found for all species for only some of the measured variables (Table 2). For adults, prostrate plants had a significantly smaller shape variable than erect plants in all species, except *A. myrtifolia*. In this species, variation between the two erect sites outweighed the trend for prostrate plants to have smaller shapes. Only seedlings of *C. distyla* and *H. teretifolia* showed the same trend. For *A. suaveolens* and *B. ericifolia*, variation in the offspring from the erect sites swamped the expected trend, while in *A. myrtifolia* no trend was apparent.

Similarly, the edge height of all prostrate adult plants, except *H. teretifolia*, was significantly lower than for erect plants, although *H. teretifolia* did show the same trend. Again only the seedlings of *C. distyla* and *H. teretifolia* also significantly showed this trend, although it was apparent in *A. suaveolens*. *Acacia myrtifolia* and *B. ericifolia* showed no differences for seedlings and more time may have been needed for an effect to be apparent.

The height to the first branch was lower in prostrate adults for *B. ericifolia* and *H. teretifolia*. No such comparison could be made for the seedlings as most erect seedlings had not branched by the end of this study.

Leaf length was significantly longer in erect plants in *A. suaveolens*, a feature also found in the seedlings of this species. While the same pattern was present in *A. myrtifolia* (Table 2), significant adult site and individual effects at the prostrate sites reduced the likelihood of a significant growth form effect. No significant growth form effects for leaf length were found in either adults or seedlings of *B. ericifolia* and *H. teretifolia*.

Leaves were significantly wider in the prostrate adults of *A. suaveolens* and *H. teretifolia*. For *H. teretifolia* this trend was matched in the seedlings, while for *A. suaveolens* the offspring of erect plants had larger leaf widths, matching those of the offspring of prostrate plants. Both *A. myrtifolia* and *B. ericifolia* showed no differences between growth forms for either adult or seedling leaf widths. The significant growth form effect for cladode width in seedlings of *C. distyla* was biologically meaningless and was caused by the lack of errors in the data.

The average internode length was significantly greater in erect plants for adults of *A. myrtifolia* and *H. teretifolia*. A similar trend was present in *A. suaveolens*, although significant individual effects at Site 1 (erect plants) reduced the likelihood of a growth form effect. Seedlings of these three species also showed significantly longer internode lengths in erect plants. No growth form differences were found for internode length for either adults or seedlings in *B. ericifolia* and *C. distyla*.

Discussion

By using all measured variables in a multivariate analysis, a clear difference between erect and prostrate forms was evident in both adults and seedlings. Only in *C. distyla* seedlings was this picture slightly variable. The conclusion from this analysis is that distinct forms of the five study species exist in the field, with the prostrate form being confined to windswept headlands and the erect form being widespread elsewhere. When grown under uniform conditions in a glasshouse the two growth forms maintain their distinct identities; hence the more restricted prostrate form is not simply different because of the environmental variables found in its habitat, e.g. high salt and wind levels. The differences in growth form are therefore genetically controlled and passed on to the offspring.

Looking at the individual variables in isolation, different variables appear to reflect the difference between growth forms in different species (Table 2). The variables are significantly different between growth forms for both adult and seedlings are for *A. myrtifolia*, internode length; for *A. suaveolens*, leaf length; for *C. distyla*, plant shape;
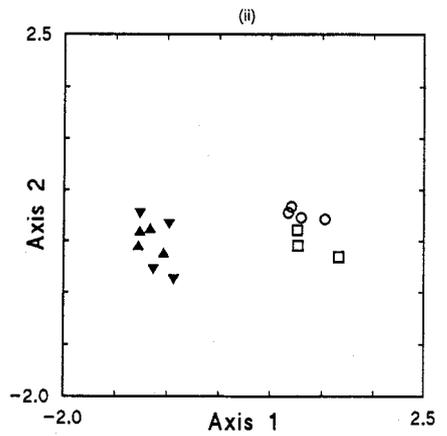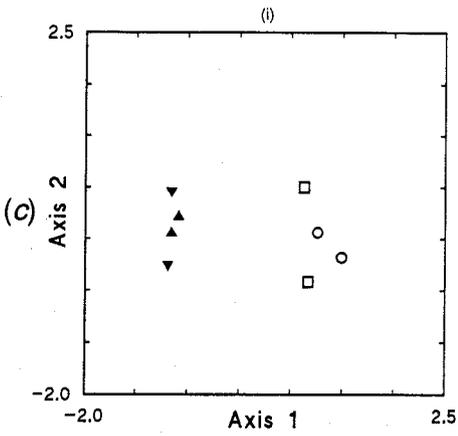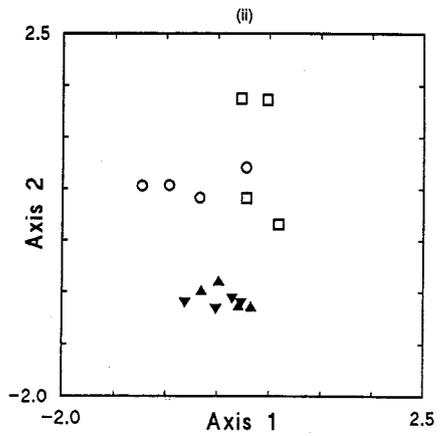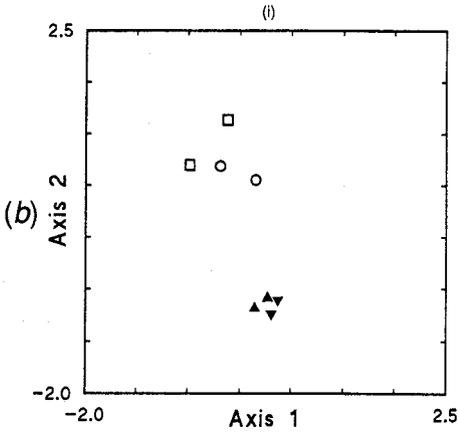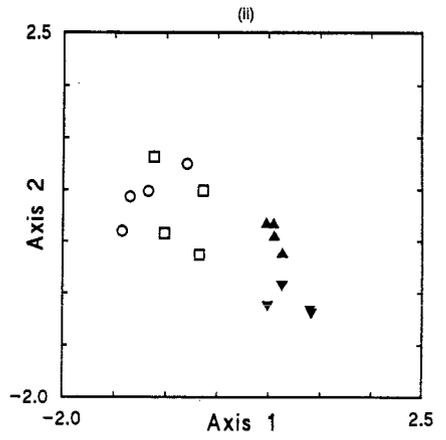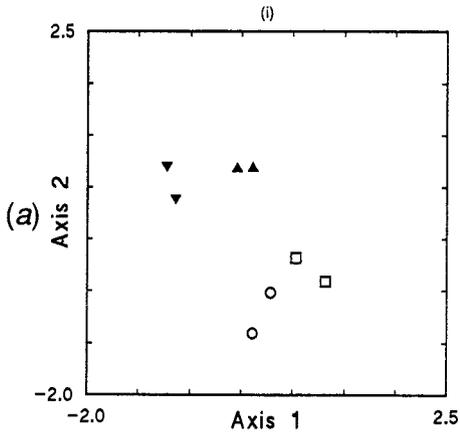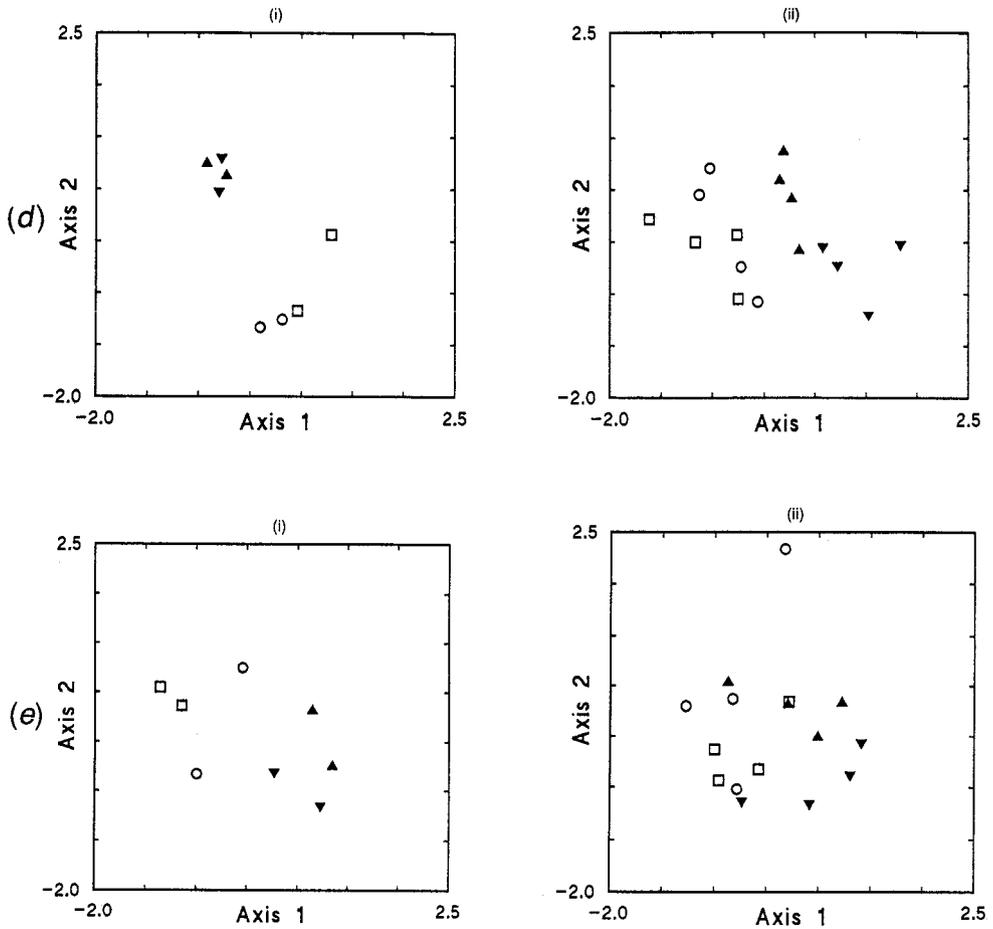
Fig. 2. Multidimensional scaling ordination of individual (i) adults and (ii) seedlings of (*a*) *A. myrtifolia*; (*b*) *A. suaveolens*; (*c*) *H. teretifolia*; (*d*) *B. ericifolia*; and (*e*) *C. distyla*. Site 1 (○), Site 2 (□), Site 3 (▲) and Site 4 (Site 5 for *A. myrtifolia*) (▼).

for *H. teretifolia*, plant shape, leaf width and internode length; while for *B. ericifolia*, no individual variable was significant at the growth form level for both adults and seedlings. Consequently, it is difficult to suggest particular attributes that clearly distinguish the two forms, even though the trends in plant shape, for instance, are clear (See Fig. 1). Of course, the types of variables measured are potentially flexible and greater sample size may be needed to clarify the patterns found in this study. For example, in *H. teretifolia*, leaf length in adult plants was some three times shorter than in seedling plants (Table 2); hence, this variable may be strongly influenced by environmental growth conditions. Internode length gave more consistent results between field and glasshouse samples (Table 2).

The trends in difference between erect and prostrate plants are generally maintained in their seedlings, even though the absolute values may vary. This indicates that, while the measured variables are influenced by environmental conditions, the limitations on variable size under a given set of environmental conditions varies between the growth forms. Hence, environmental conditions are important but do not override inherent genetic limitations as expressed in the phenotypic characters measured.

Table 2. Summary of ANOVA results

Data are means (± s.e.). * Significant F ratio; NA, not applicable

Variable	Growth form		Analysis F ratio		
	Erect	Prostrate	Form	Site	Individual
Adults					
A. myrtifolia					
Shape	2·8 (0·7)	0·5 (0·1)	4·49	7·96	NA
Edge height (cm)	89·5 (18·0)	8·3 (2·5)	30·31*	0·57	NA
1st branch ht (cm)	28·3 (4·3)	9·5 (5·5)	4·86	1·96	NA
Leaf length (mm)	53·4 (1·2)	31·1 (1·2)	6·54	8·12*	9·02*
Leaf width (mm)	16·5 (0·4)	12·9 (0·7)	0·91	20·46*	4·89*
Internode length (mm)	17·6 (0·7)	6·3 (0·4)	33·95*	3·13	3·57*
A. suaveolens					
Shape	4·4 (0·4)	0·5 (0·1)	814·95*	0·10	NA
Edge height	196·8 (16·8)	14·0 (3·4)	135·17*	2·08	NA
1st branch ht	79·5 (14·0)	3·3 (1·9)	15·97	3·11	NA
Leaf length	86·9 (2·3)	51·9 (1·5)	60·57*	0·66	5·80*
Leaf width	5·3 (0·2)	7·4 (0·2)	32·51*	3·24	0·65
Internode length	14·7 (0·7)	8·2 (0·4)	8·41	2·41	6·05*
B. ericifolia					
Shape	1·6 (0·1)	0·3 (0·0)	1273·78*	0·30	NA
Edge height	88·8 (6·2)	38·3 (4·1)	187·17*	0·18	NA
1st branch ht	57·8 (4·9)	19·8 (3·7)	27·18*	1·74	NA
Leaf length	12·3 (0·2)	10·8 (0·2)	2·47	2·34	4·84*
Leaf width	1·1 (0·1)	1·0 (0)	3·94	2·00	0·52
Internode length	1·3 (0·1)	1·0 (0)	35·50	0·40	1·14
C. distyla					
Shape	3·0 (0·4)	0·5 (0·0)	160·90*	0·48	NA
Edge height	159·5 (22·3)	30·5 (3·3)	28·88*	1·22	NA
1st branch ht	52·5 (6·9)	22·5 (7·8)	7·81	1·10	NA
Cladode width	1·3 (0·1)	1·8 (0·1)	2·98	1·13	11·20*
Internode length	14·2 (0·5)	14·5 (0·6)	0·02	2·15	10·38*
H. teretifolia					
Shape	1·7 (0·2)	0·5 (0·1)	104·94*	0·22	NA
Edge height	120·5 (25·0)	48·3 (9·0)	4·79	2·11	NA
1st branch ht	93·8 (14·8)	13·8 (3·5)	57·31*	0·70	NA
Leaf length	35·3 (1·1)	35·6 (1·3)	0·16	0·06	7·04*
Leaf width	1·8 (0·1)	2·4 (0·1)	57·60*	5·00	0·11
Internode length	9·6 (0·3)	4·6 (0·2)	21·74*	8·92*	0·95
Seedlings					
A. myrtifolia					
Shape	1·0 (0·0)	0·5 (0·1)	17·21	6·93	1·63
Edge height	13·6 (1·6)	6·6 (1·0)	14·39	1·91	0·42
Leaf length	74·8 (0·9)	49·3 (0·6)	33·41*	3·66	0·66
Leaf width	23·3 (0·3)	20·3 (0·4)	1·15	3·79	7·35*
Internode length	14·8 (0·4)	8·8 (0·2)	24·98*	3·05	1·29
A. suaveolens					
Shape	4·1 (0·5)	0·6 (0·1)	10·98	4·67	2·88
Edge height	47·1 (11·3)	8·9 (1·3)	4·69	2·14	4·01*
Leaf length	113·9 (1·8)	65·0 (0·7)	43·46*	1·00	11·56*
Leaf width	7·6 (0·1)	7·4 (0·1)	0·52	0·24	3·33
Internode length	12·7 (0·4)	7·9 (0·2)	183·06*	0·04	16·26*

Table 2. (*continued*)

Variable	Growth form		Analysis *F* ratio		
	Erect	Prostrate	Form	Site	Individual
		B. ericifolia			
Shape	1·5 (0·3)	0·8 (0·1)	9·58	1·47	0·80
Edge height	16·0 (1·8)	16·0 (2·2)	0·00	0·40	0·06
Leaf length	25·0 (0·4)	21·9 (0·5)	0·01	3·98	1·06
Leaf width	3·2 (0·1)	3·0 (0·1)	0·01	6·28	2·89
Internode length	3·9 (0·2)	1·8 (0·1)	34·38	1·57	3·07
		C. distyla			
Shape	1·9 (0·3)	0·8 (0·1)	150·21*	0·06	2·28
Edge height	38·6 (9·5)	29·0 (5·2)	0·54	2·03	0·72
Cladode width	1·0 (0)	1·1 (0)	72·00*	0·04	1·03
Internode length	14·1 (0·3)	13·0 (0·2)	0·20	9·46*	0·45
		H. teretifolia			
Shape	3·9 (0·3)	1·4 (0·2)	28·91*	1·37	NA
Edge height	46·9 (4·3)	18·7 (2·3)	9621·04*	0·00	NA
Leaf length	127·7 (1·5)	101·7 (1·6)	30·83	0·55	18·46*
Leaf width	1·0 (0)	1·7 (0)	3015·33*	0·46	0·36
Internode length	8·8 (0·2)	3·4 (0·1)	79·30*	4·77*	1·53

Our results therefore suggest that the localised prostrate forms may largely be genetically isolated from the populations of the erect forms. If a species occupies several different habitats it can do so by possessing (*a*) a suitable degree of phenotypic plasticity and/or (*b*) a sufficient degree of genetic variability. The first characteristic allows the species to occupy these habitats without any genetic change, while the latter requires the differentiation of distinct populations. Differentiation of localised populations is dependent on the interplay between natural selection and gene flow; the more highly localised the differentiation is, the higher and more directional the selection pressures need to be to counteract the effects of gene flow (Grant 1981). The prostrate growth habit in the five study species appears to be genetically fixed in the localised headland populations, and may therefore be maintained by high directional selection due to the effects of wind and/or poor gene flow due to reproductive isolation mechanisms.

Genetically fixed intra-specific variation in plants has been noted in response to many habitat factors, including soil moisture, soil fertility, serpentine soils, heavy metal contamination, use of fertilisers, date of snowmelt, photoperiod and temperature (Turkington and Aarssen 1984), as well as to degree of wind exposure (e.g. Aston and Bradshaw 1966). Genecological differentiation of habit has also been demonstrated in several other *Acacia* species (e.g. Coaldrake 1971; Hannon and McMillan 1972; McMillan 1973; Farrell and Ashton 1978), so it is possible that this characteristic may be quite widespread in this cosmopolitan genus. Genecological differentiation of habit has not been reported in the other three genera, although some species of *Banksia* and *Hakea* do show phenotypic habit differentiation in the Sydney region (e.g. plants of both *Banksia marginata*, and *H. teretifolia* produce lignotubers in some populations but not others; D. Keith, R. Bradstock, personal communication).

What do our results mean in terms of conservation biology? If it is accepted that the two growth forms are distinct for all five study species then the acceptance of taxonomic groupings into species limits the potential conservation of distinct forms. Such forms may be ecologically distinct and thus, warrant conservation at a level now accepted for species. In the Sydney region, the five species examined are all widespread and adequately conserved in existing reserves such as Ku-ring-gai Chase, Royal and Blue Mountains National Parks. However, this only represents adequate conservation

of the more widespread erect forms of these species. Some of the restricted prostrate forms, should they be given species status, would probably be listed in the Rare or Threatened Plant List (Briggs and Leigh 1988) since much of their former habitat has been cleared and their present habitat is restricted and poorly conserved. The same may apply to distinct growth forms of other widespread species.

In conservation biology, a key question is what is the level of difference between organisms which is acceptable to delineate a taxon? Is the current level of taxonomic species, a higher level, or a level below the species level adequate? By what criteria can such a conservation taxon level be decided? Clearly, the more a taxonomic species is divided into subgroups and subgroups of subgroups, the more unworkable the conservation of distinct taxa becomes. Perhaps at present it is best, in plants at least, to use taxonomic species for conservation purposes, given that information on delineation of species is readily available in the form of keys and that information below the species level is usually lacking. However, should such information become available some attention should be paid to it, either in terms of planning for future work to determine the variation in genotype across populations of a species, e.g. via electrophoresis, or by considering forms which are distinct as candidates for active conservation efforts, should such forms be threatened. Clearly, a greater understanding of ecological variation within species is required in Australian conservation biology.

Acknowledgments

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