

## Patterns of Morphological Variation within *Acacia suaveolens* (Mimosaceae)

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### ABSTRACT

*Acacia suaveolens* shows a considerable degree of morphological variability throughout its range in eastern Australia. Multivariate morphometric analyses of data from 375 herbarium specimens suggest that there are five polythetically distinct forms within this species. The morphological boundaries between these forms are somewhat arbitrary but are closely related to a number of environmental variables. Discrimination between these forms is possible only on the basis of a combination of attributes. In all cases, the distinctions between the forms are maintained in offspring plants grown under controlled environmental conditions, indicating that these morphological differences are genetically fixed. These forms are taxonomically treated as new subspecies. Apart from the typical form (subsp. *suaveolens*), which is widespread, the following morphological forms have been identified: a form with narrower phyllodes, restricted to the Holocene sand dunes in the Myall Lakes region (subsp. *myallensis* D. Morrison & A.J. Rupp); a form with wider phyllodes and longer pulvinus, and longer and thicker seeds, occurring in areas with an altitude above 300 m (subsp. *montana* D. Morrison & A.J. Rupp); a form with wider phyllodes, more flower heads per raceme, thicker seeds, and a small rootstock, restricted to the Grampians region (subsp. *grampianensis* D. Morrison & A.J. Rupp); and a form with shorter phyllodes, shorter internodes, shorter fruits, thicker seeds and a prostrate habit, occurring on windswept coastal headlands (subsp. *prostrata* D. Morrison & A.J. Rupp).

### Introduction

*Acacia suaveolens* Sm. (Willd.) (Mimosaceae) is a small semi-woody shrub that is endemic to eastern temperate Australia, from coastal Queensland and New South Wales to Victoria and Tasmania, including many of the off-shore islands (Morrison 1987). It is generally restricted to sandy soils within a few kilometres of the coast, and below an altitude of 300 m; however, it does occur inland and at higher altitudes, notably in the McPherson Range, the Blue Mountains, the Budawang Range, the Grampians, and at the South Australia–Victoria border (Morrison 1987). Within this broad geographical range, the plants show considerable morphological variation. For example, Armitage (1977) recorded populations in the Myall Lakes region with very narrow phyllodes, Auld and Morrison (1992) examined a prostrate form on coastal headlands of the Sydney region, and Morrison (1987) reported a form in the Grampians with a small rootstock. Apart from these

documented variants, there is further apparent variation in phyllode size and shape, in the number of flowers per inflorescence, and in fruit and seed size. Elliot and Jones (1982) even noted a cultivated form with a cream band on each side of the phyllode midvein.

It is important to know something about the level of inter-population variation within widespread taxonomic species, and especially whether the observed phenotypic differences among populations are genetically fixed or not (Quicke 1993). For example, the potential for evolutionary change within a species is dependent on the existence of genetic variation (Hamrick and Godt 1989); genetically-fixed differences may affect the reliability of species-wide generalisations (Grubb 1985), and significant genetic within-species variation may be worthy of attention in the conservation of biodiversity (Auld and Morrison 1992).

Therefore, our study seeks to answer three general questions:

- (1) What is the precise nature of the morphological variation within *A. suaveolens*?
- (2) Are the morphometric variants related to any environmental or geographic factors?
- (3) Is the morphological variation genetically fixed within the species?

*Acacia suaveolens* is morphologically very similar to *A. subcaerulea* Lindley, which occurs along the south coast of Western Australia from Albany to Israelite Bay, sharing with it the combination of conspicuous imbricate bracts and distinctive broad fruits. However, *A. subcaerulea* forms a more spreading shrub that generally has phyllodes that are both shorter (average c. 70 mm) and wider (c. 7 mm) than those of any of the forms of *A. suaveolens* (see Table 1), the phyllode gland is usually much closer (c. 2 mm) to the pulvinus, there are almost always more flowers per head (c. 13) and more heads per raceme (c. 12), although the raceme axis is usually shorter (2–3.5 cm), and the mature fruits are usually slightly longer (c. 37 mm). This taxon is thus easily distinguished morphologically as well as being geographically isolated from *A. suaveolens*, and it is thus best treated as a separate species.

## Materials and Methods

### MORPHOMETRIC ANALYSES

In total, 384 dried herbarium specimens from the National Herbarium of New South Wales (NSW) and the John Ray Herbarium (SYD) were examined under a binocular dissecting microscope. The phyllodes, flowers and fruits were examined without further treatment. These specimens include those collected during extensive field trips, covering the full geographic range of the species; these collections were usually deposited at SYD. Thus, our sample includes at least one specimen from each  $0.5^\circ \times 0.5^\circ$  cell of the national grid within the known range of *A. suaveolens*.

In total, 13 morphological attributes of the phyllodes, flowers, fruits and seeds were scored for the 375 most complete specimens, and five ratios were calculated (Table 1). These attributes include all of those previously noted to vary within the species (Morrison 1987). Five representative phyllodes were scored from each specimen, and three representative inflorescences, fruits or seeds were scored for those specimens that possessed them, with mean values per specimen being used for analysis. Care was taken to avoid organs that were immature or damaged.

Principal components analysis (PCA) of the range-standardised data (ter Braak 1988), was used to analyse the pattern of variation among the morphological samples. This ordination technique is often inferior to multidimensional scaling for taxonomic data (e.g. Hartman 1988; Crisp and Weston 1993), but no available computer program will handle this large data set. Four separate analyses were run:

- (1) the phyllode data, using all 375 specimens;
- (2) the phyllode and flower data for the 159 flowering specimens;
- (3) the phyllode and fruit data for the 159 fruiting specimens; and
- (4) the phyllode and seed data for the 79 specimens with seeds.

All ratio data were  $\log_e$  transformed prior to analysis (Atchley and Anderson 1978).

In order to evaluate the spatial pattern of morphological variation, the specimens were assigned to 11 geographical and ecological groups:

- (1) Queensland (23 specimens);
- (2) NSW north coast (as defined by Anderson 1961) (69 specimens);
- (3) NSW central coast (approximately as defined by Anderson 1961) (100 specimens);
- (4) NSW south coast (as defined by Anderson 1961) (31 specimens);
- (5) eastern Victoria (29 specimens);
- (6) Grampians (17 specimens);

- (7) South Australia–Victoria border (five specimens);
- (8) Tasmania (21 specimens);
- (9) mountain area (above 300 m altitude) (36 specimens);
- (10) headland area (windswept coasts) (24 specimens); and
- (11) Myall Lakes (see below for definition) (20 specimens).

The *a priori* recognition of these geographical–ecological groups was straightforward in all cases except for the definition of the Myall Lakes group, as there was considerable morphological variation apparent within this region. To examine this region in more detail, extensive surveys were carried out, covering both the Pleistocene and Holocene sand areas (see Myerscough and Carolin 1986). A separate PCA ordination was then carried out on the vegetative attributes of the 56 specimens available from this region, to assist in the recognition of any morphological variants occurring in this region. Two morphological variants were thus recognised from this analysis (see Results), with 20 of the specimens being assigned to the Myall Lakes group and the rest to the NSW north coast group.

#### CULTIVATION EXPERIMENT

Thirty-seven samples, covering the full morphological variation, were collected and cultivated under standard conditions in a glasshouse. Replicate samples were collected from most of the geographical–ecological groupings: Queensland (three samples), NSW north coast (three samples), NSW central coast (three samples), NSW south coast (three samples), eastern Victoria (three samples), Grampians (three samples), South Australia–Victoria border (one sample), Tasmania (three samples), mountain area (three samples), headland area (three samples), and Myall Lakes (five Holocene dune samples and four Pleistocene dune samples).

For each sample plant in the field, a shoot was collected and then pressed and dried for incorporation into the herbarium (usually SYD), and a collection of ripe fruits was harvested. Fruits were stored in paper envelopes in the laboratory.

In the glasshouse, the seeds were scarified by rubbing on sandpaper in order to break the seed-coat dormancy. Two seeds from each sample were placed in each of two replicate pots (15 cm diameter × 15 cm deep) filled with washed river sand. The pots were placed on a central bench in the glasshouse in a randomised block design (two blocks). Eight weeks after germination, the seedlings were thinned, if necessary, to one per pot. The seedlings were watered daily, and were fertilised with Aquasol (Hortico (Aust.) Pty Ltd) once per fortnight. The plants were harvested at 8 months, and then pressed and dried.

The five original phyllode attributes (see Table 1) were scored for two groups of three representative phyllodes from the parent specimen and for three representative phyllodes from each of the offspring specimens. Each attribute was analysed by a separate two-factor (morphological form, parent–offspring) analysis of variance (Wilkinson 1987). Homogeneity of the variances was tested by Bartlett's test (Wilkinson 1987), and where this was significant at  $P = 0.05$  the data were  $\log_e$  transformed.

## Results

#### MORPHOMETRIC ANALYSES

The ordination analysis of the vegetative (phyllode) data (Fig. 1a) does not indicate the existence of any discrete morphological forms within *A. suaveolens*, as would be expected for within-species variation such as we are dealing with here, but there is nevertheless considerable differentiation among the specimens.

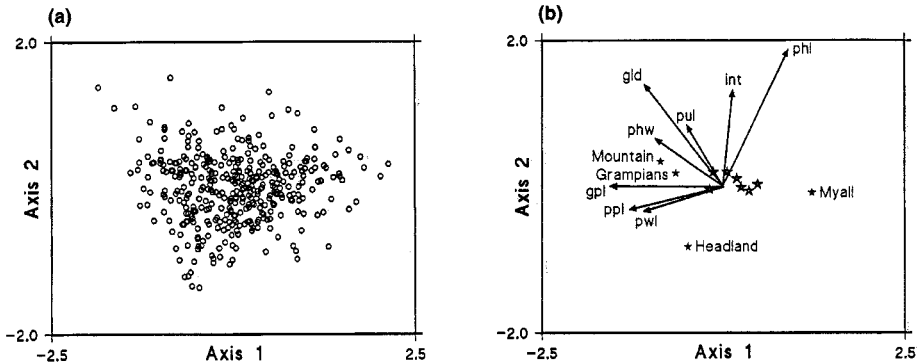
Four of the geographical–ecological groups are morphologically differentiated from the other seven based on the phyllode data (Fig. 1b): (1) the headland form differs from the other forms by having shorter phyllodes (and consequently a larger phyllode width : length ratio and a larger pulvinus : phyllode length ratio) and shorter internodes; (2) the Myall Lakes form differs in having narrower phyllodes (and consequently a smaller phyllode width : length ratio) and a shorter distance of the gland from the pulvinus (and consequently a smaller gland distance : phyllode length ratio); (3) the mountain form differs by having wider phyllodes (and consequently a larger phyllode width : length ratio), a longer pulvinus (and consequently a larger pulvinus : phyllode length ratio) and a longer distance of the gland from the pulvinus (and consequently a larger gland distance : phyllode length ratio); (4) the Grampians form differs in having wider phyllodes (and consequently a larger phyllode width : length ratio) and a longer distance of the gland from the pulvinus (and consequently a larger gland distance : phyllode length ratio). However, these five groups (including the

Table 1. Means and ranges of the morphological data from the *Acacia suaveolens* herbarium specimens

Attribute (code)	Typical form	Myall Lakes form	Headland form	Mountain form	Grampians form
<i>Phyllodes</i> (no. specimens examined)	(278)	(20)	(24)	(36)	(17)
1 Phyllode length (mm) (pbl)	94.4 52.8-154.2	108.5 72.8-139.6	59.9 39.0-103.8	91.1 63.2-133.4	88.5 73.6-106.4
2 Phyllode width (mm) (phw)	5.0 2.2-12.7	1.9 1.0-2.9	5.3 3.6-7.9	7.1 3.8-11.7	6.4 3.9-9.4
3 Pulvinus length (mm) (pul)	1.8 1.0-3.3	1.6 1.0-2.1	1.5 1.0-2.1	2.6 1.3-5.7	2.0 1.5-2.5
4 Distance of gland from pulvinus (mm) (gid)	3.5 1.5-6.4	2.5 1.6-3.6	2.8 1.7-5.3	4.9 1.9-8.0	4.9 3.2-6.6
5 Internode length (mm) (int)	13.9 6.8-26.8	12.2 5.8-18.6	9.6 6.0-13.0	13.8 8.0-23.2	12.9 11.2-15.6
6 Phyllode width : length ratio (pwl)	0.052 0.019-0.186	0.017 0.007-0.025	0.088 0.051-0.133	0.076 0.046-0.121	0.071 0.043-0.100
7 Pulvinus length : phyllode length ratio (ppl)	0.019 0.009-0.037	0.015 0.008-0.022	0.024 0.018-0.033	0.028 0.017-0.048	0.022 0.016-0.027
8 Gland distance : phyllode length ratio (gpl)	0.036 0.013-0.086	0.023 0.012-0.038	0.047 0.033-0.059	0.052 0.026-0.086	0.054 0.037-0.074

Table 1. continued

Attribute (code)	Typical form	Myall Lakes form	Headland form	Mountain form	Grampians form
<i>Flowers</i> (no. specimens examined)	(124)	(8)	(7)	(16)	(4)
9 No. flowers / head (flo)	7.9 5.3-10.7	9.5 6.0-11.0	7.0 5.3-8.0	8.2 5.3-10.0	8.9 7.7-10.0
10 No. heads / raceme (hd)	5.3 4.0-8.0	5.4 4.3-6.3	5.2 5.0-6.0	5.3 4.3-6.3	7.0 7.0-7.0
11 Raceme axis length (cm) (ax)	3.7 3.3-4.3 (109)	3.9 3.5-4.2 (11)	3.6 3.3-3.7 (12)	3.8 3.5-4.0 (17)	4.1 4.0-4.3 (10)
<i>Fruits</i> (no. specimens examined)					
12 Fruit length (mm) (fl)	30.8 20.7-41.0	30.0 24.7-34.0	26.6 19.0-37.7	32.9 26.7-43.3	27.0 19.3-32.0
13 Fruit width (mm) (fw)	14.2 10.3-18.0	14.2 7.7-19.3	13.5 12.3-16.0	15.4 12.0-18.7	12.3 10.0-13.3
14 Fruit width : length ratio (fwl)	0.47 0.29-0.68 (54)	0.47 0.27-0.63 (12)	0.52 0.33-0.70 (4)	0.47 0.33-0.63 (6)	0.46 0.37-0.54 (3)
<i>Seeds</i> (no. specimens examined)					
15 Seed length (mm) (sl)	6.3 5.0-7.5	6.1 4.4-7.5	6.3 6.0-6.5	7.1 6.5-7.7	6.7 6.4-6.9
16 Seed width (mm) (sw)	3.1 1.9-3.9	3.0 2.5-3.4	2.9 2.4-3.0	3.6 3.0-4.1	3.4 2.9-3.7
17 Seed thickness (mm) (st)	2.1 0.7-3.3 0.483	2.0 1.3-2.5 0.495	2.5 2.3-2.8 0.452	2.4 1.8-2.7 0.499	2.6 2.4-2.8 0.502
18 Seed width : length ratio (swl)	0.336-0.589	0.407-0.577	0.375-0.502	0.440-0.583	0.423-0.577



**Fig. 1.** Projection of the *A. suaveolens* herbarium specimens onto axes representing the first two components of the principal components analysis of the phyllode data. (a) All 375 specimens. (b) Centroids of the 11 geographical and ecological groups (see text). The arrows indicate the magnitude and direction of change among the specimens of the eight morphological attributes (attribute codes are as in Table 1).

typical form) are not exclusive, as the measurement for any one vegetative characteristic of an individual specimen may overlap with one or more of the other groups (Table 1). Thus, these groups are multivariately differentiated, and no single attribute can be used to discriminate among them or to assign a specimen to a particular group.

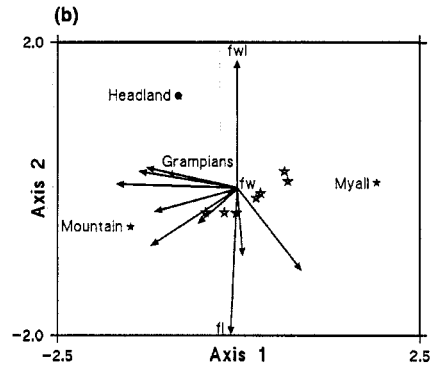
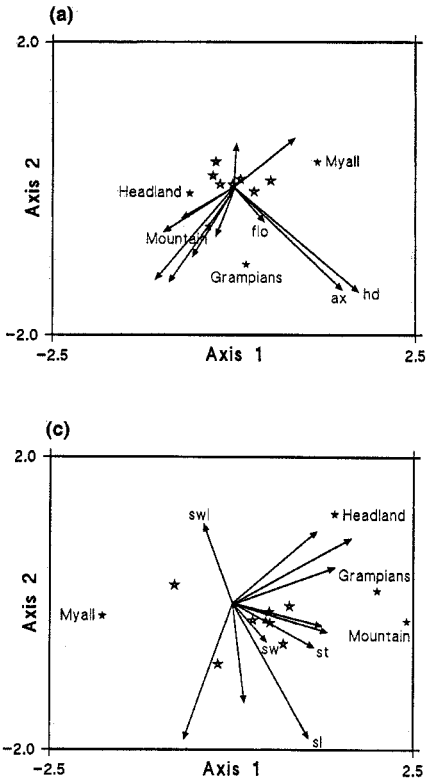
Only a few of the reproductive attributes distinguish any of these five groups. The ordination analysis of the flower data (Fig. 2a) indicates that the Grampians form differs from the others in having more flower heads per raceme (and consequently a longer raceme axis). The ordination analysis of the fruit data (Fig. 2b) indicates that the headland form differs from the others in having shorter fruits (and consequently a larger fruit width : length ratio; note that Table 1 indicates a fairly high mean fruit length for this form, but this is a result of one individual plant producing long fruits). The ordination analysis of the seed data (Fig. 2c) indicates that the mountain form differs from the others in having longer seeds (and consequently a smaller seed width : length ratio) and thicker seeds; and the headland, mountain and Grampians forms differ from the others in having thicker seeds. Once again, these groups are multivariately differentiated (Table 1), and thus no single attribute can be used to discriminate among them or to assign a specimen to a particular group.

The ordination of the phyllode attributes of the specimens from the Myall Lakes region does not reveal any non-overlapping groups (Fig. 3), but it is clear that the 20 specimens occurring in the *Eucalyptus pilularis*-*Angophora costata* forest on the Holocene sand dunes are morphologically distinguishable from those occurring in the woodlands and heaths on the Pleistocene dunes. The Holocene sand form differs in having narrower phyllodes (and consequently a smaller phyllode width : length ratio) and a shorter distance of the gland from the pulvinus. The four apparent exceptions to this generalisation are specimens from the Pleistocene dunes that have normal width phyllodes but a very short distance of the gland from the pulvinus. The within-group variation in these two forms is largely a product of variation in phyllode length and internode length.

It is also apparent from this analysis that the plants growing on the mined Holocene dunes at Bridge Hill only consist of a small part of the range of morphological variation apparent within the Myall Lakes form (which would have been the form existing there prior to mining), and that some of the plants are morphologically indistinguishable from the form occurring on the Pleistocene dunes.

#### CULTIVATION EXPERIMENT

The glasshouse-grown offspring plants differ significantly from their parents for all of the measured phyllode attributes except for phyllode length (Table 2), with the phyllode width



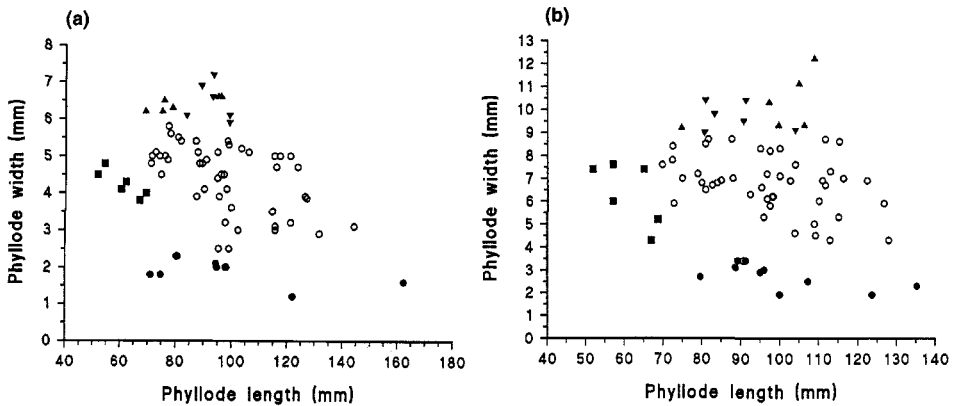
**Fig. 2.** Projection of the *A. suaveolens* herbarium specimens onto axes representing the first two components of the principal components analysis of the (a) flower, (b) fruit and (c) seed data. Only the centroids of the 11 geographical and ecological groups (see text) are shown. The arrows indicate the magnitude and direction of change among the specimens of the morphological attributes (attribute codes are as in Table 1).

**Fig. 3.** Projection of the *A. suaveolens* herbarium specimens from the Myall Lakes region onto axes representing the first two components of the principal components analysis of the phyllode data. The specimens are indicated as coming from the Holocene dunes (●), the Pleistocene dunes (○) or the mined Holocene dune at Bridge Hill (□). The arrows indicate the magnitude and direction of change among the specimens of the eight morphological attributes (attribute codes are as in Table 1).

being on average 41% broader in the offspring than the parents, the pulvinus length 13% shorter, the gland distance 21% longer, and the internode length 25% longer. Thus, four of these attributes are influenced by the environmental conditions in which the plants occur. However, for all five attributes the interaction term is not significant in the analyses of variance (Table 2), indicating that the relationship between parent and offspring does not differ significantly among the five morphological groups. Thus, the multivariate morphological differentiation among the groups is genetically controlled—the offspring maintain the morphological differentiation that is apparent among the parent plants (Fig. 4).

**Table 2.** Analysis of variance results for the comparative cultivation experiment

Source	d.f.	<i>F</i>	<i>P</i>
<i>Phyllode length</i>			
Morphological form	4	7.09	< 0.001
Parent-offspring relationship	1	0.51	0.478
Interaction	4	0.52	0.720
Residual	64		
<i>Phyllode width</i> ( $\log_e$ transformed)			
Morphological form	4	52.39	< 0.001
Parent-offspring relationship	1	28.44	< 0.001
Interaction	4	0.41	0.805
Residual	64		
<i>Pulvinus length</i>			
Morphological form	4	5.76	0.001
Parent-offspring relationship	1	10.18	0.002
Interaction	4	0.99	0.421
Residual	64		
<i>Distance of gland from pulvinus</i>			
Morphological form	4	4.83	0.002
Parent-offspring relationship	1	6.32	0.014
Interaction	4	1.16	0.337
Residual	64		
<i>Internode length</i>			
Morphological form	4	6.72	< 0.001
Parent-offspring relationship	1	19.54	< 0.001
Interaction	4	0.89	0.474
Residual	64		



**Fig. 4.** Relationship between phyllode length and width for the (a) parent and (b) offspring samples of *Acacia suaveolens* from the comparative cultivation experiment. The specimens are indicated as being of the typical (O), Myall Lakes (●), headland (■), mountain (▲) or Grampians (▼) form.

## Discussion

We conclude from our analyses that there are five phenetically differentiated morphometric groups within *Acacia suaveolens*, which can be distinguished based on a range of vegetative and reproductive characters (summarised in Table 3). The ordination analyses suggest that these are coherent polythetic taxa, but the morphological boundaries between them are somewhat arbitrary, and these taxa are thus not mutually exclusive—i.e.



**Table 3. Summary of the distinguishing features of the morphological forms of *Acacia suaveolens***

Attribute	Typical form	Myall Lakes form	Headland form	Mountain form	Grampians form
Phyllode length	average	average	shorter	average	average
Phyllode width	average	narrower	average	wider	wider
Pulvinus length	average	average	average	longer	average
Distance of gland from pulvinus	average	shorter	average	longer	longer
Internode length	average	average	shorter	average	average
No. heads per raceme	average	average	average	average	more
Fruit length	average	average	shorter	average	average
Seed length	average	average	average	longer	average
Seed thickness	average	average	thicker	thicker	thicker

the vast majority of the plants can be assigned unambiguously to one of the five forms, but identifying the occasional plant on purely morphological grounds is more problematic.

Therefore, these groups are multivariately differentiated, and no single attribute can be used to discriminate among them or to assign a specimen to a particular group. A simple dichotomous key, for example, would thus not be easy to construct for these taxa, and this form of identification aid would indeed be inappropriate in this case. However, the non-typical taxa are all distinct geographical and ecological variants of the typical form, occurring within a restricted habitat and/or geographical area. The taxa are here treated as subspecies.

The narrow-phyllode form (*A. suaveolens* subsp. *myallensis*) on the Holocene sand dune land system in the Myall Lakes region occupies a distinct habitat in a restricted geographical area. It is restricted entirely to the Holocene dunes that transgress the older Pleistocene sand, thus occurring on topography of considerable relief, frequently with steep slopes. The soils are freely-draining poorly-developed podzols, and often have a higher nutrient status than the Pleistocene dunes. The vegetation of this land system is mapped by Myerscough and Carolin (1986) as the distinctive *Eucalyptus pilularis*-*Angophora costata* open-forest. This forest type is confined to the lower north and central coast of New South Wales (Myerscough and Carolin 1986), but the narrow-leaved form of *A. suaveolens* has not been recorded anywhere except at Myall Lakes. The typical form of *A. suaveolens* occurs on the surrounding Pleistocene dune land systems, in a variety of woodland and heath vegetation, and the two forms occur within 100 m of each other near the land system boundaries. The *A. suaveolens* plants growing on the mined Holocene dune of Bridge Hill ridge only consist of a restricted set of genotypes compared with the surrounding area, which was apparently the source of seed for the post-mining revegetation, and some of the plants are clearly of the typical form, which would not have been native to the pre-mined vegetation. Thus, although the *A. suaveolens* plants are similar in abundance in the mined and unmined areas (Buckney and Morrison 1992), the full genetic biodiversity has not re-established in the mined area. This may be a common phenomenon among the other species as well, and should be further examined.

The short-phyllode headland form (*A. suaveolens* subsp. *prostrata*) occupies a distinct habitat but is geographically widespread. It occurs only in low heath on windswept coastal headlands, but has been recorded from all along the New South Wales coast and along the north-east coastline of Tasmania. Auld and Morrison (1992) noted that this form also has a distinctly prostrate habit, the plants spreading at about 5 cm above the ground and being

twice as broad as they are high (unlike the typical form, which is four times as high as broad). We could not quantify habit from the herbarium specimens, but our glasshouse-grown plants maintained their prostrate habit (as did those of Auld and Morrison 1992), thus indicating genecological differentiation of this characteristic as well.

The broad-phyllode mountain form (*A. suaveolens* subsp. *montana*) also occupies a distinct habitat but is geographically widespread. It occurs much further inland than the typical form and above about 300 m in altitude, and has been recorded from the Blue Mountains (from Mt Coricudgy to Hill Top) and the Budawang Range. It may also occur in the McPherson Range, but this has not been confirmed. Altitudinal variation in morphology has also been reported in the Sydney region for species in several genera, including *Leptospermum polygalifolium* and *Leptospermum morrisonii* (Myrtaceae; Morrison 1984), and *Banksia marginata*, *Hakea dactyloides* and *Hakea teretifolia* (Proteaceae; D. Keith and R. Bradstock, pers. comm.), so this characteristic may be quite common.

The broad-phyllode Grampians form (*A. suaveolens* subsp. *grampianensis*) is morphologically quite similar to the mountain form, sharing three distinctive attributes with it (Table 3) (but differing in three other attributes). It also occupies a similar inland higher altitude habitat. However, it is restricted to a small geographical area: the deeper sands of the west-facing slopes of the Grampians. This form is thus geographically isolated from all of the other forms. Interestingly, the only other geographically-isolated plants, the inland low-altitude plants at the South Australia–Victoria border, are all of the typical form. Morrison (1987) notes that plants of the Grampians form also have phyllodes with a small axillary angle, and have a small underground rootstock that produces new shoots if the stem is destroyed. We could not quantify these attributes from the herbarium specimens, nor could we confirm them in our glasshouse-grown plants. However, resprouting forms have been reported in a number of other Australian species (e.g. Lee 1984; Pate *et al.* 1991).

The trends in differences between phyllodes among the five morphological forms are maintained in their seedlings, even though the absolute values of the attributes may vary. This indicates that, while the measured attributes are clearly influenced by environmental conditions, the limitations on the size of an attribute under a given set of environmental conditions vary between the morphological forms. Hence, environmental conditions are important but do not over-ride the inherent genetic limitations as expressed in the phenotypic attributes measured. The morphological differentiation among the forms is thus genetically controlled.

Genecological differentiation of morphology has been reported in a number of other geographically-widespread species of *Acacia*, both in Australia (e.g. Coaldrake 1971; Farrell and Ashton 1978; Lamont and Fox 1981; Auld and Morrison 1992) and elsewhere (e.g. Ross 1971; Ross and Morris 1971; Hannon and McMillan 1972; McMillan 1973). It is thus possible that this characteristic may be widespread in this cosmopolitan genus.

The demographic work of Auld and Myerscough (1986), Auld (1986*a*, 1986*b*, 1986*c*, 1987) and Morrison and Myerscough (1989) was all conducted in the Sydney region, and in all cases it was performed on populations of *A. suaveolens* ssp. *suaveolens*. It is not clear how many of the results of these studies can be assumed to apply to the other subspecies, although some of the behaviour discussed (e.g. adult plants being killed by even low-intensity fires) obviously cannot apply to all of the subspecies (since the Grampians form has a rootstock from which it can regenerate new shoots after a fire).

## Nomenclature

*Acacia suaveolens* (Sm.) Willd., Species Plantarum ed. 4, 4: 1050 (1806).

BASIONYM: *Mimosa suaveolens* Sm., Transactions of the Linnean Society of London 1: 253 (1791).

TYPE CITATION: 'Flowered 1790, in Sion Gardens, from seeds brought from New South Wales. *Mr. Hoy*.'

TYPE (here designated): There are no specimens labelled as *Mimosa suaveolens* in the Smith Herbarium at LINN, and any such specimen was presumably disposed of when the Linnean Society auctioned most of its holdings in November 1863. Some of these ex-LINN

specimens are at K, but they are doubtfully types. There is one specimen at LINN (no. 1598-15 of Spencer Savage's *Catalogue of the Smithian Herbarium in the Possession of the Linnean Society of London*, 1963) that would maintain the current usage of the name, and this is chosen as the neotype (n.v., microfiche seen).

*Mimosa ambigua* Salisb., *Prodromus Stirpium in Horto ad Chapel Allerton Vigentium* 325 (1796), nom. superfl.; *Racosperma suaveolens* (Sm.) C. Martius, *Hortus Regius Monacensis Seminifer* 188 (1829), nom. inval., as the combination is not correctly made; *Phyllodoce suaveolens* (Sm.) Link, *Handbuch zur Erkennung* 2: 133 (1831); *Hecatandra suaveolens* (Sm.) Raf., *Sylva Telluriana* 120 (1838).

*Mimosa obliqua* Lam., *Journal d'Histoire Naturelle Paris* 1: 89, t.5 (1792), non Wendl. (1798), non Desf. (1804), non Pers. (1806).

TYPE CITATION: None.

TYPE (here designated): There are no specimens labelled as *Mimosa ambigua* in the Lamarck Herbarium at P, nor are there any specimens of *A. suaveolens*. Therefore, the figure accompanying the protologue, t.5, is designated as the lectotype.

*Acacia suaveolens* var. *platycarpa* DC., *Prodromus* 2: 453 (1825).

TYPE (here designated): De Candolle implies that his name refers to the same taxon as *M. ambigua* Salisb., and may therefore be considered to be based on the same type. There is a specimen at G-DC labelled 'Jard. D'Angle<sup>m</sup>. M. Salisbury' and 'M. ambigua Sal. suaveolens Sm.', and this is selected as the lectotype for De Candolle's name if it is not considered to be based on Salisbury's type (n.v., microfiche seen).

*Mimosa angustifolia* Jacq., *Plantarum Rariorum Horti Caesarei Schoenbrunnensis* 3: 74 t.391 (1798).

TYPE CITATION: 'Crescit ad Port Jackson in New Southwales. Floret in caldario aestate.'

HOLOTYPE: W (n.v.).

*Acacia odorata* var. *angustifolia* (Jacq.) Desv., *Journal de Botanique* 3: 67 (1814), nom. inval.; *Acacia angustifolia* (Jacq.) H.L. Wendl., *Commentatio de Acaciis Aphyllis* 34 (1820); *Phyllodoce angustifolia* (Jacq.) Link, *Handbuch zur Erkennung* 2: 133 (1831).

### 1. *Acacia suaveolens* (Sm.) Willd. **subsp. suaveolens**

Erect shrub; phyllodes c. 9 (5–15) cm long, c. 5 (2–13) mm wide, gland c. 3.5 (1–6) mm from the pulvinus, internodes c. 14 (7–27) mm long; c. 5 (4–8) flower heads per raceme; fruits c. 3 (2–4) cm long; seeds c. 6 (5–7) mm long, c. 2 (1–3.5) mm thick. Common in coastal areas in southern Queensland, New South Wales, eastern Victoria, and northern and eastern Tasmania.

#### SELECTED SPECIMENS

NEW SOUTH WALES: 2 miles S of Narooma, *L.G. Adams* 610, 25.iv.1963 (CANB, NSW); Nanguda Lake, c. 3.5 km S of Narooma, 36°15'S, 150°08'E, *L.G. Adams* 3214, 5.v.1973 (CANB, NSW); Bombah Point, Myall Lakes, 32°30' S, 152°18' E, *R. Coveny s.n.*, 2.ix.1967 (NSW); 1.1 miles S of Frenchs Forest, 33°46'S, 151°14'E, *R. Coveny* 4810, 5.iii.1973 (A, BRI, CANB, K, L, NSW, US); 1.1 miles S of Frenchs Forest, 33°46'S, 151°14'E, *R. Coveny* 4812, 5.iii.1973 (K, NSW, US); 0.5 miles E of Kariiong, 33°26'S, 151°18'E, *R. Coveny* 4878, 9.v.1973 (A, AD, B, BRI, CANB, G, K, L, NSW, PERTH, S, UC, US); NW end of Uloomla track, 34°09'S, 151°01'E, *F.E. Davies* 402 & *T. Mulcahy*, 6.xii.1987 (CBG, NSW); Mullumbimby, 28°33'S, 150°30'E, *S.L. Everist* 2558 & *L.J. Webb*, 5.vi.1951 (BRI, NSW); 2 km N of Hawks Nest along the rd to Myall Lakes NP, *W. Greuter* 20484, 3.ix.1988 (NSW); Pigeon House Rd, S of Burrill Lake, 35°24'S, 150°26'E, *M. Hancock* 141, 4.xii.1989 (CANB, NSW); Rose Bay, *R. Helms* 32, 28.vii.1900 (B, BRI, K, KLU, KW, L, MEL, MO, NSW, P, PE, RSA, UC); Rose Bay, *R. Helms s.n.*, 15.vi.1901 (BRI, CHR, MEL, NSW, TL, US); c. 2 km N of Mt White, 33°25'S, 151°13'E, *P. Hind* 3746, 13.xi.1984 (NSW, PERTH); Hermitage Foreshore Trail, Sydney Harbour NP, 33°51'12''S, 151°15'47''E, *P. Hind* 5993 & *A. Price*, 15.iii.1990 (MO, NSW); Yatteyattah–Lake Conjola rd, *E.J. McBarron* 13021, 3.ix.1966 (MEL, NSW); 1 mile W of

Scarborough, 34°16'S, 150°56'E, *C.W.E. Moore s.n.*, 23 iv.1953 (CANB, NSW); 1.5 miles N of Nowra, *C.W.E. Moore* 3882, 23.viii.1966 (CANB, NSW); 3 miles N of Tuncurry on rd from Taree, *I.V. Newman* 559, 17.vii.1971 (NSW); ridge c. 2 miles NE of Tabletop Mtn, Nadgee Nature Reserve, *J. Pickard* 1081, 1.vi.1970 (NSW)

QUEENSLAND: SW approach to summit of Mt Coolum, 26°33'S, 153°05'E, *S.J. Davies* 35 & *J.M. Powell*, 3.v.1989 (MEL, NSW, PERTH); c. 40 km SSE of Maryborough, 25°51'S, 152°49'E, *L. Pedley* 5377, 15.vii.1987 (BRI, MEL, MO, NSW, PR);

SOUTH AUSTRALIA: Mount Julia, section 453, Hundred of Penola, *D.N. Kraehenbuehl* 3164, 6.i.1965 (AD, NSW); Hundred of Short, 40 km W of Penola, *K.J. Stuckey s.n.*, 22.viii.1987 (AD, SYD);

TASMANIA: Circular Head, *R. Gunn* 372/1842, 17.viii.1837 (BM, NSW); Hobart, *R. Gunn* 372/1842, 3.i.1841 (BM, NSW); Blackman's Bay, 43°00'S, 147°19'E, *S.J. Jarman s.n.*, 16.viii.1979 (HO, NSW); track to The Garden, near St Helens, *M.E. Phillips s.n.*, 30.i.1962 (CBG, NSW); Upper Scamander rd, *M.E. Phillips s.n.*, 7.xii.1965 (CBG, NSW); Eaglehawk Neck, Tasman Peninsula, 43°01'S, 147°55'E, *J.M. Powell* 547, 16.v.1976 (CANB, LE, NSW, Z);

VICTORIA: Brighton, *A. Morrison* 1574, 30.v.1891 (MEL, NSW); heights behind town, Anglesea, *M.E. Phillips* 206, 25.x.1971 (CBG, NSW); 3 km SE Stringer Knob, 37°38'55"S, 148°13'25"E, *H. van Rees* 011, 14.viii.1979 (MEL, NSW); 2.6 km NW Tamboon Inlet mouth, Croajingalong NP, 37°44'55"S, 149°05'25"E, *N.G. Walsh* 50, 29.v.1979 (MEL, NSW).

**2. *Acacia suaveolens* (Sm.) Willd. subsp. *myallensis* D.A. Morrison & A.J. Rupp, subsp. nov.**

Frutex erectus, phyllodiis c. 11 (7–14) cm longis c. 2 (1–3) mm latis, glande ex pulvino c. 2.5 (1–4) mm, internodiis c. 12 (6–19) mm longis.

HOLOTYPE: Myall Lakes National Park, Hawks Nest road, 6.7 km south of Bungwahl–Seal Rocks road, 32°28.5'S, 152°25.5'E, *D. Morrison* 77, 31.v.1983 (SYD).

Erect shrub; phyllodes c. 11 (7–14) cm long, c. 2 (1–3) mm wide, gland c. 2.5 (1–4) mm from the pulvinus, internodes c. 12 (6–19) mm long; c. 5 (4–6) flower heads per raceme; fruits c. 3 (2.5–3.5) cm long; seeds c. 6 (4–7) mm long, c. 2 (1.5–2.5) mm thick. Restricted to the Holocene sand dunes in the Myall Lakes region of NSW.

SELECTED SPECIMENS

NEW SOUTH WALES: Seal Rocks, 32°28'S, 152°20'E, *Fox* 7907018, 7.vii.1979 (NSW); 3 km N along mining rd adjacent to Bridge Hill Ridge, 32°24.5'S, 152°30'E, *D. Morrison* 62, 27.v.1983 (SYD); 1.1 km N along mining rd adjacent to Bridge Hill Ridge, 32°25'S, 152°29.5'E, *D. Morrison* 63, 27.v.1983 (SYD); Hawks Nest rd, 8.7 km S of Bungwahl–Seal Rocks rd, 32°28.5'S, 152°24.5'E, *D. Morrison* 76, 31.v.1983 (SYD); 200 m along tk to Submarine Beach from Hawks Nest rd, 32°28'S, 152°25.5'E, *D. Morrison* 138, 30.x.1983 (SYD); 2.3 km S of Bungwahl–Seal Rocks rd on Hawks Nest rd, 32°27.5'S, 152°26'E, *D. Morrison* 139, 30.x.1983 (SYD); junction of Hawks Nest rd and Bungwahl–Seal Rocks rd, 32°25'S, 152°28'E, *D. Morrison* 140, 30.x.1983 (SYD); Mungo Brush area of Myall Lakes, 32°26'S, 152°20'E, *N. Perry* 18, 15.vii.1977 (NSW).

**3. *Acacia suaveolens* (Sm.) Willd. subsp. *prostrata* D.A. Morrison & A.J. Rupp, subsp. nov.**

Frutex prostratus, phyllodiis c. 6 (4–10) cm longis c. 5 (3–8) mm latis, glande ex pulvino c. 3 (1–6) mm, internodiis c. 10 (6–13) mm longis.

HOLOTYPE: McKillop Park, Harbord, 33°46'S, 151°17'E, *D. Morrison* 80, 26.vi.1983 (SYD).

Prostrate shrub; phyllodes c. 6 (4–10) cm long, c. 5 (3–8) mm wide, gland c. 3 (1–6) mm from the pulvinus, internodes c. 10 (6–13) mm long; c. 5 (5–6) flower heads per raceme; fruits c. 2.5 (1.5–4) cm long; seeds c. 6 (6–6.5) mm long, c. 2.5 (2–3) mm thick. Restricted to windswept coastal headlands of NSW and north-eastern Tasmania.

SELECTED SPECIMENS

NEW SOUTH WALES: Black Head, Nadgee Faunal Reserve, 15 miles ESE of Timbillica, *E.F. Constable* 4384, 18.viii.1963 (NSW); McKillop Park, Harbord, 33°46'S, 151°17'E, *D. Morrison* 79,

26.vi.1983 (SYD); McKillop Park, Harbord, 33°46'S, 151°17'E, *D. Morrison 148*, 6.xi.1983 (SYD); Grants Head Reserve, Bonny Hills, S of Lake Cathie, *D. Morrison 282*, 5.xi.1988 (SYD); Long Bay rifle range, *I.V. Newman 362*, 19.v.1952 (NSW); Gabo Is., *F.A. Rodway 2472*, v.1922 (NSW);

TASMANIA: Circular Head, *R. Gunn 372/1842*, 17.viii.1837 (BM, NSW); 200 m E of Tomahawk, 39°53'S, 147°46'E, *D. Morrison 51 & K. Gallagher*, 10.ii.1983 (SYD); Eaglehawk Neck, *F.A. Rodway 2458*, iv.1916 (NSW).

**4. *Acacia suaveolens* (Sm.) Willd. subsp. *montana* D.A. Morrison & A.J. Rupp, subsp. nov.**

Frutex erectus, phyllodiis c. 9 (6–13) cm longis c. 7 (4–12) mm latis, glande ex pulvino c. 5 (2–8) mm, internodiis c. 14 (8–23) mm longis.

HOLOTYPE: Du Faur's Rocks, Mt Wilson, *L.A.S. Johnson s.n.*, 23.ix.1949 (NSW).

Erect shrub; phyllodes c. 9 (6–13) cm long, c. 7 (4–12) mm wide, gland c. 5 (2–8) mm from the pulvinus, internodes c. 14 (8–23) mm long; c. 5 (4–6) flower heads per raceme; fruits c. 3 (2.5–4.5) cm long; seeds c. 7 (6–8) mm long, c. 2.5 (1.5–3) mm thick. Restricted to areas above 300 m altitude in the Blue Mountains and Budawang Range of NSW and the McPherson Range in southern Queensland.

SELECTED SPECIMENS

NEW SOUTH WALES: 12 km SW of Sassafras, Budawang Ra., 35°11'S, 150°09'E, *M.P. Austin & J. Duggan 27*, 9.xii.1972 (CANB, NSW); Tallong, *C. Burgess B29*, 19.ix.1972 (CBG, NSW); 1 mile S of Queen Victoria Hospital, King's Tableland, *E.F. Constable 6998*, 2.vi.1966 (NSW); Lawson on road to Adelina Falls, 33°44'S, 150°26'E, *R. Coveny 183*, 6.iv.1968 (NSW); 5 miles N of Bilpin on the Mountain Lagoon Rd, *R. Coveny 2994*, 12.viii.1970 (BRI, K, L, NSW, US); 'Little Switzerland', Wentworth Falls, 33°40'30"S, 150°22'30"E, *R. Coveny 12365*, *K.U. Kramer & M.D. Tindale*, 7.x.1986 (NSW); 2.4 km E of Wallaya Geodesic Station, 34°41'S, 150°40'E, *I. Crawford 956*, 2.viii.1988 (CBG, NSW); Leura, *A.A. Hamilton s.n.*, iv.1914 (NSW); Comleroy Rd, 2–3 km S of Wheeny Ck crossing, Wollemi NP, 33°27'S, 150°44'E, *P. Hind 4635*, 20.xi.1986 (NSW); Picton Lakes, 5 miles SW of Picton, *I. Keats & R. Coveny 3428*, 14.xii.1970 (CANB, K, NSW); Hill Top near Mittagong, *E.J. McBarron 10938*, 28.viii.1965 (NSW); plateau edge above Jamberoo Pass, *R. Pullen 4053*, 14.iv.1964 (CANB, NSW); Old Budderoo Track, near Dhruwalgha Mtn, *H. Salasoo 6771*, 29.vi.1971 (NSW).

**5. *Acacia suaveolens* (Sm.) Willd. subsp. *grampianensis* D.A. Morrison & A.J. Rupp, subsp. nov.**

Frutex erectus, phyllodiis c. 9 (7–11) cm longis c. 7 (4–10) mm latis, glande ex pulvino c. 5 (3–7) mm, internodiis c. 13 (11–16) mm longis.

HOLOTYPE: Grampians, 6.5 km north along Harrop's Tk from Victoria Valley Rd, 37°19'S, 142°14'E, *D. Morrison 102 and K. Gallagher*, 9.viii.1983 (SYD).

Erect shrub, often with a rootstock; phyllodes c. 9 (7–11) cm long, c. 7 (4–10) mm wide, gland c. 5 (3–7) mm from the pulvinus, internodes c. 13 (11–16) mm long; c. 7 flower heads per raceme; fruits c. 3 (2–3.5) cm long; seeds c. 6.5 (6–7) mm long, c. 2.5 (2–3) mm thick. Restricted to the west-facing slopes in the Grampians region of Victoria.

SELECTED SPECIMENS

VICTORIA: 3.6 km N along Harrop's Tk from Victoria Valley Rd, 37°21'S, 142°12'E, *J. Jacobs B*, 8.xi.1983 (SYD); 3.6 km N along Harrop's Tk from Victoria Valley Rd, 37°21'S, 142°12'E, *J. Jacobs G*, 8.xi.1983 (SYD); junction of Rose Creek Rd and Phillips Island Tk, 37°09'S, 142°22'E, *D. Morrison 90 and K. Gallagher*, 8.viii.1983 (SYD); 3.6 km north along Harrop's Tk from Victoria Valley Rd, 37°21'S, 142°12'E, *D. Morrison 97 and K. Gallagher*, 8.viii.1983 (SYD); 3.6 km north along Harrop's Tk from Victoria Valley Rd, 37°21'S, 142°12'E, *D. Morrison 98 and K. Gallagher*, 8.viii.1983 (SYD); 6.5 km north along Harrop's Tk from Victoria Valley Rd, 37°19'S, 142°14'E, *D. Morrison 101 and K. Gallagher*, 9.viii.1983 (SYD); 6.5 km north along Harrop's Tk from Victoria Valley Rd, 37°19'S, 142°14'E, *D. Morrison 160*, 29.i.1984 (SYD); Harrop's Tk, 31 km NE of Cavendish, Grampians, *H. Streimann 3208*, 17.xii.1975 (A, CBG, L, NSW).

## Acknowledgments

Thanks to the Director of the National Herbarium of New South Wales and the Curator of the John Ray Herbarium for permission to study their specimens; to Jan Jacobs, Brian Mitchell and Fred Morrison for collecting some of the seeds and specimens; to Tony Auld, Kerri Gallagher and Louisa Murray for assistance and companionship during many of the collecting trips; to Bruce Maslin for taxonomic and nomenclatural guidance; and to Tony Auld, Mike Crisp and Bruce Maslin for commenting on the manuscript.

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Manuscript received 17 January 1995, accepted 21 June 1995