

## Fruit features in relation to the ecology and distribution of *Acaena* (Rosaceae) species in New Zealand

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**Abstract:** Fruit features of 17 *Acaena* species in New Zealand were investigated to determine the relations between reproductive allocation patterns, mode of dispersal and species ecology. Three basic morphological types, corresponding to major sections within the genus, are represented: spineless fruits (Sect. *Pteracaena* - one species), spined fruits lacking barbs (Sect. *Microphyllae* - 6 species), and spined fruits with barbs (Sect. *Ancistrum* - 10 species). The presence of terminal barbs on spines enhances fruit adhesion to animals, and is associated with the development of longer scapes, globular many-fruited capitula, and smaller single-seeded fruits. Barb-spined species generally have the broadest geographical range and habitat distribution within New Zealand, and are the only species of *Acaena* to occur in forests or on offshore islands. These species are generally strongly stoloniferous. *Acaena* species with barbless spines and/or no spines are often regional endemics confined to open and/or localised habitats, are rhizomatous, and may be dispersed by water, ingestion or wind. There is a tight correlation between intrageneric classification and species ecology and fruit features which requires testing via independent phylogenetic analysis based on molecular genetic characters. Although avian dispersers have declined since human settlement, introduced mammals may be performing a similar function for barbed *Acaena* species.

**Keywords:** *Acaena*; dispersal; ecology; geographic distribution

## Introduction

Establishing links between modes of dispersal and species ecology is important for understanding the role of dispersal in the diversification of the angiosperms during the Tertiary (Tiffney, 1986), and for assessing the relevance of dispersal modes for the identification of functional types for predicting vegetation responses to extrinsic factors such as climate change (Leishman and Westoby, 1996). Dispersibility may also affect broad geographic distributions, abundance and persistence within habitats, and the genetic structure and size of populations (Webb, 1998). One approach to determining the relevance of dispersal to species ecology is to undertake comparative studies using large genera of species having different dispersal modes.

The native *Acaena* species are long-lived perennials that produce fruits with a range of morphological features. Some species have barb-tipped spines (glochidia) extending from the hypanthium which attach the fruits to passing animals. Other species lack barb-

spines and appear to have limited ability for dispersal by animals. The genus *Acaena* is confined mostly to the southern hemisphere, and comprises approximately 50 species, with greatest species richness in South America (Bitter, 1911; Grondona, 1964). There are 19 species native to New Zealand and 2 naturalised from Australia (Webb *et al.*, 1988; Macmillan, 1989, 1991).

In New Zealand, fruits dispersed via attachment to animals occur as viscid fruits or seeds (e.g., *Pittosporum*), barbs (e.g., *Acaena*), hooks (e.g., *Uncinia*) and awns (many grasses) (Wardle, 1991). Hamlin (1959) doubted the relevance of such structures in the New Zealand flora because of the absence of indigenous terrestrial mammals. However primary dispersers of these fruits in New Zealand must have been ground dwelling and volant birds (Wardle, 1991), as is the case today in subantarctic regions (Walton, 1977a). At the plant community level in New Zealand, adhesion dispersal is relatively uncommon, compared to temperate communities elsewhere in the world, occurring amongst less than 10% of the vascular plant species (Willson *et al.*, 1990).

This study investigates the relation between dispersal features, seed size, habitat, and altitudinal and geographic range of *Acaena* (Rosaceae) species in New Zealand. Our aim is to determine the environmental conditions that favour the development of diaspores dispersing through adhesion to animals (epizoochory) in New Zealand, and to investigate whether there are other fruit and ecological features correlated with this mode of dispersal.

## Methods

The study was restricted to the 17 taxa of *Acaena* that occur on the New Zealand mainland: *Acaena magellanica* and *A. minor*, two species occurring only in the subantarctic bioclimatic zone, were not included.

### Morphological features of fruits

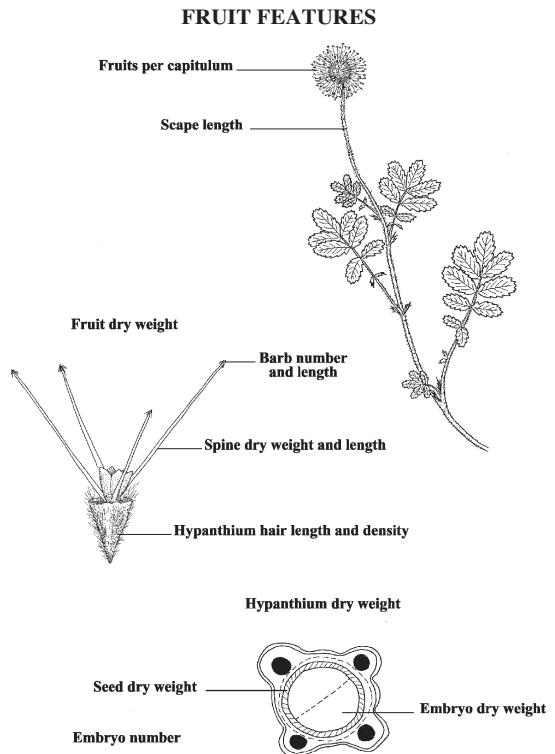
Information on scape length (cm) and fruits per capitulum were obtained from Webb *et al.* (1988), and Macmillan (1983, 1985, 1989, 1991). Fruits of native *Acaena* species were obtained from collections at the Landcare Research herbarium (CHR), Lincoln. A single air-dried sample was selected from a site representative of the range of the species, and the following measurements (Fig. 1) undertaken on 10 individual fruits: Hypanthium hairs (presence, density (number per 250 x 250  $\mu\text{m}$ ) and length  $\mu\text{m}$ ); Spines (presence and length (mm)); Barbs (presence, number, and length ( $\mu\text{m}$ )); Total diaspore weight (after oven drying at 70 degrees centigrade for 24 hours) ; Hypanthium weight (diaspore minus spines); Seed weight (embryo and enclosing fibrous endocarp); Embryo weight (embryo dissected out of endocarp/seed coat); Spine weight. Fruit colour was determined for mature fruits using the following Munsell Colour Company (1975) classification : Dusky red (10R - 2.5/2, 3/3, 3/4); Reddish brown (2.5YR 3/3, 3/4, 4/3, 4/4; 5YR - 4/4, 4/5, 5/4, 6/4); Red (2.5YR - 4/6).

### Ecological features of species

Information on the distribution and ecological range of *Acaena* species was obtained from Webb *et al.* (1988), Macmillan (1983, 1985, 1989, 1991), and various colleagues, and classified as follows:

Distribution: Presence on North Island, South Island, Stewart Island, Chatham Island, Subantarctic Islands (Auckland, Campbell, Antipodes) scored as per Lee *et al.* (1988).

Regional: Number of 10 km grid squares occupied as a percentage of the North Island, South Island and Stewart Island area. Regional distributions determined



**Figure 1.** Fruit features measured for all *Acaena* species.

from circumscribing area within which all CHR herbarium samples were obtained.

Habitat: Forest/Shrubland (1), herbfield (2), and gravel/sand (3).

Altitude: Lowland (1), montane (2), subalpine (3), and alpine (4), after Wardle (1977).

### Phylogenetic features

Subgeneric categories were recognised after Bitter (1911): Section *Pteracaena*, Section *Ancistrum*, and Section *Microphyllae*.

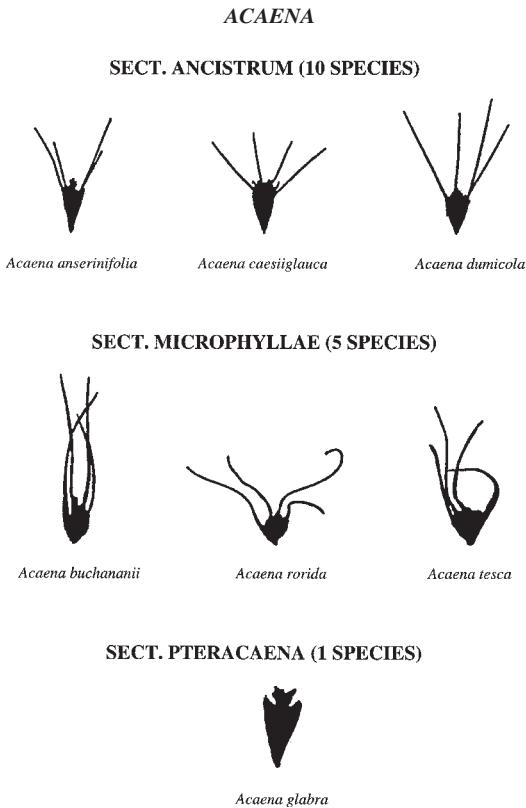
### Statistical analyses

An ordination was performed on the taxa using fruit character data, following standardisation of the character values (division by maximum). Detrended Correspondence analysis was used (Hill & Gauch 1980) in the PATN package (Belbin 1989), with the first two axes being presented. Phylogenetic relations and ecological characters were plotted on the species ordination to see if the gradients of species and

**Table 1.** A summary of the geographic distribution and ecology of *Acaena* species in New Zealand. Location of sample sites is also presented.

Species	Distribution (% 10 x 10 km grid squares occupied)	Habitat	Sample location
<b>Section Ancistrum</b>			
<i>Acaena anserinifolia</i> <sup>1</sup>	Widespread on New Zealand mainland and subantarctic islands, lowland to subalpine. (86%)	Growing along forest margins and in shrubland, grasslands, herbfields and open habitats.	Mount Sinclair, Banks Peninsula.
<i>Acaena caesiiglauca</i> <sup>1</sup>	Widespread in eastern South Island from Kaikoura Mountains to Otago. (25%)	Montane to subalpine tussock grassland and open ground.	Lake Pukaki, Canterbury
<i>Acaena dumicola</i> <sup>1</sup>	Narrow zone east of main divide in South Island from Kaikoura Mountains to Otago. (15%)	In montane scrub on well-drained soil.	Lake Pukaki, Canterbury.
<i>Acaena emittens</i> <sup>1</sup>	Regional endemic in the central North Island with an outlier near Nelson. (2%)	In montane to subalpine open <i>Nothofagus</i> forest, mixed shrubland and disturbed sites.	Taruarau Hill, Taihape.
<i>Acaena fissistipula</i> <sup>1</sup>	Widespread east of the Main Divide in South Island. (21%)	In montane to alpine grassland and herbfield, especially stream sides and seepages and open habitats	Mount Ida, North Otago.
<i>Acaena juvenca</i> <sup>1</sup>	Local in Central and southern North Island and widespread in the South Island east of the Main Divide from north west Nelson to Otago. (25%)	In lowland and montane open broadleaved and <i>Nothofagus</i> forest, along forest margins and in shrubland	Takamatua Valley, Banks Peninsula.
<i>Acaena novae-zelandiae</i> <sup>1</sup>	Widespread in North Island eastern, areas of the South Island. (59%)	In lowland to montane grassland and open habitats	Lincoln, Canterbury.
<i>Acaena pallida</i> <sup>1</sup>	Locally distributed in North Island near Wellington and in the South Island on Otago Peninsula, near Invercargill and on Stewart Island. (<1%)	In open vegetation on coastal sand dunes.	Tomahawk Beach, Dunedin.
<i>Acaena profundeincisa</i> <sup>1</sup>	Sparse in central and lower North Island and widespread in eastern mountains from Nelson to Otago. (35%)	Growing in subalpine and alpine scrub, tussock grassland and herbfield.	Mount Mytton, Nelson
<i>Acaena saccaticupula</i> <sup>1</sup>	Common in South Island in inland eastern mountains. (17%)	In montane and alpine herbfields and open habitats.	Cave Stream, Canterbury.
<b>Section Microphyllae</b>			
<i>Acaena buchananii</i> <sup>1</sup>	Restricted to Central and North Otago Mountains in the South Island. (6%)	Growing in dry lowland and montane grassland and lake communities.	Manuhierikia River, North Otago.
<i>Acaena inermis</i>	Local in central and southern North Island and widespread east of the Main Divide in the South Island from north-west Nelson to Otago. (23%)	In montane and subalpine open grassland sites and along river courses.	Spineless form - Craigieburn Ranges, Canterbury; spined form - Ashburton Gorge, Canterbury.
<i>Acaena microphylla</i> var. <i>microphylla</i>	Regional endemic in Central North Island. (6%)	In lowland and montane grassland and on river terraces.	Waipakihi River, Desert Road.
<i>Acaena microphylla</i> var. <i>pauciglochidiata</i>	Local in South Island confined to coast in east Otago, Southland, and Stewart Island. (2%)	On sand and consolidated gravel.	Colac Bay, Southland.
<i>Acaena rorida</i>	Regional endemic in Central North Island. (<1%)	In subalpine turf on limestone amongst red tussock.	Ruahine Range, North Island.
<i>Acaena tesca</i>	Regional endemic in Central Otago, South Island. (2%) fellfield.	In montane to alpine short and tall tussock grassland and	Old Man Range, Central Otago.
<b>Section Pteracaena</b>			
<i>Acaena glabra</i>	Eastern South Island greywacke mountains from Kaikoura to North Otago. (8%)	In subalpine and alpine screes and well drained stream beds	Porters Pass, Canterbury.

<sup>1</sup>Species with terminal barbs on spines.



**Figure 2.** Outlines of representative fruits of *Acaena* species.

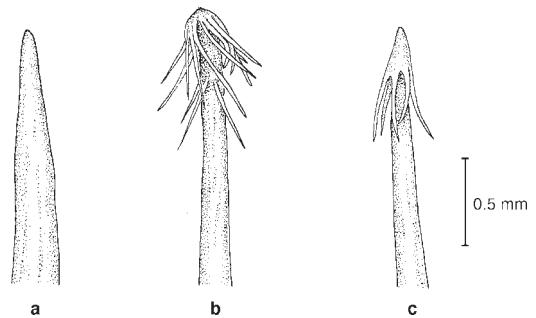
characters represented the same pattern as dispersal features. In addition, the ordination axes were tested against individual characters by regression of ordination scores on the values (continuous variables only). A one way analysis of variance (ANOVA) was undertaken on ecological features against selected fruit features.

Means for all fruit and ecological characters were compared using *t*-tests between species in Section Ancistrum and Section Microphyllae.

## Results

### Species ecology

A summary of the distribution and ecology of *Acaena* species is given in Table 1. The majority of species grow in open habitats, particularly grassland (13 species), frequently as edge species, in montane and subalpine zones (>10 species). Maximum species richness occurs in these habitats east of the Main



**Figure 3.** Terminal processes on spines of *Acaena* species: a. bald spine (*A. microphylla* var. *microphylla*) b. soft hairs (*A. buchananii*) and c. barbs (*A. novae zelandiae*).

Divide in the South Island (15 species). There are four relatively shade tolerant species that grow in forests or shrubland (*A. anserinifolia*<sup>1</sup>, *A. dumicola*, *A. emittens*, *A. juvenca*). Geographic ranges extend from local regional endemics (e.g., *A. rorida*, *A. tesca*) through to species that occur throughout the North and South Islands (e.g., *A. anserinifolia*).

### Fruit features

Representative fruit types are illustrated in Figs. 2 and 3. A summary of measurements of major fruit features are presented in Tables 2 and 3.

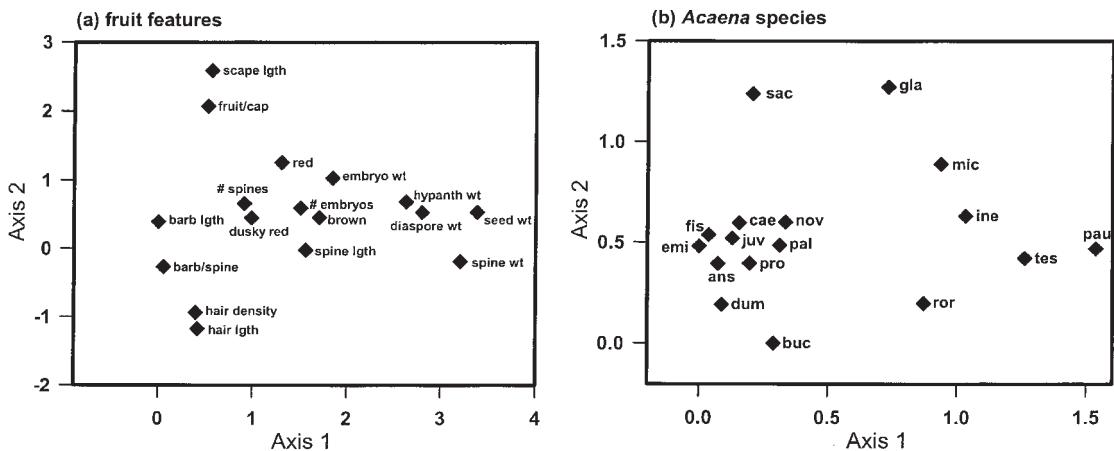
The number of fruits per capitulum range from a low of 10 or fewer (e.g., *A. tesca*, *A. rorida*, *A. microphylla* var. *pauciglochidiata*, *A. buchananii*) to a high of over 100 (e.g., *A. novae-zelandiae*, *A. pallida*). Scape length is similarly variable. In some species (e.g., *A. buchananii*, *A. microphylla*) capitula are sessile while in others the scape elongates to a maximum length of approximately 20 cm (e.g., *A. saccaticupula*, *A. caesiiglauca*, *A. fissistipula*).

Only one species (*A. glabra*) completely lacks external protruding spines (Fig. 2, Table 2). Although spines are present they are enclosed within the hypanthium wings. Other fruits commonly have four spines extending from the hypanthium, although in *A. saccaticupula* the spines are only just emergent from the hypanthium wings. In those species with barbs the spines are uniformly thin whereas the barbless species are associated with bulbous spines that taper towards the tip and often become contorted on maturation (Fig. 2). The hypanthium of most species also supports hairs which vary in length from 0.3 mm (e.g., *A. inermis*) to 1.0 mm (e.g., *A. buchananii*).

<sup>1</sup>Nomenclature follows Allan (1961), Connor and Edgar (1987), Webb *et al.* (1988) and Macmillan (1989, 1991).

**Table 2.** Capitula and spine features of *Acaena* species.

	Number of fruits per cap	Scape length (max) cm	Spines				
			Number of spines	Spine length (mm)	Wt. of single spine (mg)	Barbs per spine	Barb length (mm)
<b>Section Ancistrum</b>							
<i>anseritifolia</i>	50-60	12	4	6.8	0.075	5.6	595
<i>caesiiglauca</i>	50-70	20	4	5.4	0.105	10.2	605
<i>dumicola</i>	40	10	4	5.2	0.09	7.6	435
<i>emittens</i>	40-50	13	4	5.0	0.045	6.8	615
<i>fissistipula</i>	50-60	20	4	4.3	0.055	8.4	610
<i>juvenca</i>	45-60	15	4	4.9	0.103	5.4	545
<i>novae-zelandiae</i>	80-120	15	4	5.1	0.13	7.2	320
<i>pallida</i>	80-115	18	4	8.9	0.143	6.6	615
<i>profundeincisa</i>	40-50	12	4	4.7	0.1	5.6	660
<i>saccaticupula</i>	80-100	30	4	2.9	0.04	5.6	410
<b>Section Microphyllae</b>							
<i>buchananii</i>	10	0	4	11.9	0.44	20	825
<i>inermis (spineless)</i>	20	7	0	NA <sup>1</sup>	NA	NA	NA
<i>inermis (spines)</i>	20	7	4	11.4	0.215	0	0
<i>microphylla</i> var. <i>micophylla</i>	20	2.5	4	9.3	0.355	0	0
<i>microphylla</i> var. <i>pauciglochidiata</i>	2-4	0	4	14.6	0.78	0	0
<i>rorida</i>	10	2	4	9.0	0.18	0	0
<i>tesca</i>	10	0	4	15.5	0.4	0	0
<b>Section Pteracaena</b>							
<i>glabra</i>	60-100	9	0	NA	NA	NA	NA

<sup>1</sup>NA = not applicable**Figure 4.** Ordination diagrams of (a) fruit characters and (b) *Acaena* species. Fruit characters include scape length, number of fruits per capitula, mature fruit colour (red, dusky red, and reddish brown), barb length and number, spine number, length and weight, and weight of diaspore, hypanthium, seed and embryo(s). First three letters of specific epithet are used to identify species. For further details see methods section.

The nature of the spined tip and the barb processes are illustrated in Fig. 3. Barbs are typically terminal, stiff and reflexed at a low angle pointing down the spine. They vary in number from 2-12, and are between 300-900  $\mu\text{m}$  long. Some species also have terminal processes on spines, but these are usually soft retrorse hairs (Fig. 3) which have a variable orientation (e.g., *A. buchananii*). One taxon (*A. microphylla* var. *pauciglochidiata*) has relatively stiff retrorse hairs. *A. inermis* has individual plants that produce either spined (lacking barbs) or unspined fruits, and samples of these were measured separately (Tables 2, 3). *A. microphylla* var. *microphylla* and *A. buchananii* sometimes have individual plants within a population which produce unspined fruit.

*Acaena* species have either one or two seeds per fruit. Seed weight (embryo plus endocarp) averages 0.30 mg, with the biggest embryos reaching over 0.6 mg (e.g., *A. pallida*, *A. novae-zelandiae*). Embryo

weight represents between 10% (e.g., *A. buchananii*) and 31% (e.g., *A. saccaticupula*) of the total diaspore weight.

### Species and fruit features

An ordination diagram using all species and all fruit characters is presented in Fig. 4a, b. The first axis differentiates between those species (*A. fissistipula*, *A. emittens*) with numerous long terminal barbs on spines and relatively light diaspores, to the left on axis 1, and those lacking barbed spines, but having heavy individual fruits due to well developed fibrous endocarps and bundles associated with the spines, around the embryo (*A. microphylla* var. *pauciglochidiata*, *A. tesca*). The second axis segregates species with many red fruits clustered in capitula on long scapes (top) (*A. saccaticupula*, *A. glabra*) from those with few fruits on or near the ground

**Table 3.** Hypanthium features of *Acaena* fruits

	Hypanthium hairs		Hypanthium weights				
	Hair density 250x250 $\mu\text{m}$	Hair length ( $\mu\text{m}$ )	Total diaspore weight (mg) <sup>1</sup>	Hypanth. weight (mg) <sup>2</sup>	Seed weight (mg) <sup>3</sup>	Embryo weight (mg) <sup>4</sup>	No. of embryos
<b>Section Ancistrum</b>							
<i>anseritifolia</i>	4	750	1.39	1.11	0.6	0.21	1
<i>caesiiglauca</i>	3	562	1.89	1.47	1.05	0.43	1
<i>dumicola</i>	8	750	1.54	1.18	0.93	0.24	1
<i>emittens</i>	4	375	0.95	0.77	0.47	0.15	1
<i>fissistipula</i>	6	425	1.33	1.11	0.78	0.36	1
<i>juvenca</i>	4	525	1.59	1.18	0.76	0.21	1
<i>novae-zelandiae</i>	5	575	2.79	2.27	1.83	0.59	1
<i>pallida</i>	7	875	3.68	3.12	2.27	0.62	1
<i>profundeincisa</i>	5	625	2.08	1.68	1.42	0.32	1
<i>saccaticupula</i>	0	0	1.43	1.27	1	0.44	1
<b>Section Microphyllae</b>							
<i>buchananii</i>	6	1000	2.97	1.39	1.39	0.31	2
<i>inermis</i> (spineless)	2	300	3.68	3.68	3.68	0.55	2
<i>inermis</i> (spines)	5	250	5.58	4.04	4.04	0.33	2
<i>microphylla</i> var. <i>micophylla</i>	0	0	3.37	1.95	1.95	0.37	2
<i>microphylla</i>	0	0	9.64	6.48	6.48	0.99	2
var. <i>pauciglochidiata</i>							
<i>rorida</i>	4	500	3.16	2.44	2.44	0.36	2
<i>tesca</i>	2	175	6.6	5	5	0.96	2
<b>Section Pteracaena</b>							
<i>glabra</i>	0	0	2.2	2.2	0.97	0.55	1

<sup>1</sup>hypanthium + spines and sepals where these adhere to fruit

<sup>2</sup>hypanthium - spines

<sup>3</sup>seed - hypanthium; involves removing brown flaps (epidermis of hypanthium, fibrous bundles of spines, and associated parenchyma) around seed

<sup>4</sup>embryo, dissected out of endocarp; note this may refer to 1 or 2 embryos

NOTE: 2-3 = weight of hypanthium flap

(*A. buchananii*, *A. rorida*, *A. dumicola*), and relatively dense long hairs on the hypanthium.

### Fruit features in relation to geographic distribution

To test the relation between geographic range and fruit features, a one-way analysis of variance was carried out on the species distributions, based on percentage of 10 km grid squares occupied in New Zealand, versus the barb length. This showed a highly significant difference between the two largest Sections ( $P < 0.001$ ) once *A. buchananii* had been excluded (its barbs are non-functional for dispersal by attaching). Likewise there was a positive correlation ( $P < 0.001$ ) between barb length and ordination position on axis 1 of the Detrended Correspondence Analysis (Fig. 4). These patterns are the same as those derived if the two main sections within *Acaena* were to be compared, as the barb characters match that separation.

Both of the two trans-Tasman non-endemic species (*Acaena novae-zelandiae* and *A. pallida*) have barbed spines, although the latter is locally distributed in New Zealand. Overall, the top five most widespread species in New Zealand all have barbed spines (Table 1). In contrast, six out of the eight taxa with the smallest distributions in New Zealand (present in less than eight percent of 10 km grid squares) have spines without barbs. Regional endemics are far more common amongst barbless species (4) than amongst those with barbs (1). Amongst *Acaena* in New Zealand only barb-fruited species occur offshore on the subantarctic islands. Distributions (using 10 km grid squares) within either North Island or South Island, or based on the total number of islands occupied, failed to show any significant differences between species with and without barbs on spines.

### Fruit features in relation to habitat

The relation between fruit features and habitat is shown in Fig. 5a using the species ordination scores outlined previously (Fig. 4b). The three predominantly shrubland and forest species on the lower left of the ordination diagram characteristically have fruits with numerous long barb-spines, a dense covering of long hairs over the hypanthium, and many-fruited capitula (e.g., *A. emittens*, *A. juvenca*, *A. anserinifolia*).

### Fruit features in relation to rooting habit

The major difference in habit amongst *Acaena* species relates to their mode of vegetative reproduction (either via stolons or rhizomes). Rhizomatous species (e.g., *A. tesca*, *A. rorida*) are segregated on the right of Fig. 5b. Strongly stoloniferous species (e.g., *A. emittens*,

*A. anserinifolia*), and those which typically produce shorter stolons (e.g., *A. saccaticupula*, *A. caesiiglauca*) are both clustered on the left hand side of the ordination (Fig. 5b). *A. glabra* produces few adventitious roots, and occupies an immediate position.

### Fruit features in relation to altitude

There was a significant trend for an increase in barb number ( $P < 0.01$ ), scape length ( $P < 0.01$ ), and the number of fruits ( $P < 0.01$ ), with increasing altitude, and a decrease in barb length ( $P < 0.01$ ).

### Fruit features in relation to phylogeny

Patterns found in fruit characters are strongly constrained by the intrageneric classification, with species in Section Ancistrum on the left of Fig. 5c and those in Section Microphyllae nearly all on the right. The position of *A. buchananii* amongst species in the section Ancistrum appears to be due to the presence of long, soft hairs at the tip of the spines (Table 2; Fig. 3), which are not functionally equivalent to barbs. *A. glabra* (Section Pteracaena) occupies an intermediate position on axis 1 but is distinguished as different from most species (with the single exception of *A. saccaticupula*) on axis 2. Segregation on the second axis is less clear for the two major sections with species from both groups represented at both ends of the axis. Overall, species in Section Ancistrum differ significantly ( $P < 0.01$ ) from those in Section Microphyllae in having more fruits per capitulum (mean 72 vs 12), longer scapes (mean 16 cm vs 2 cm), and lighter fruits (mean 1.8 mg vs 4.9 mg) and spines (mean 0.103 mg vs 0.431 mg).

## Discussion

*Acaena* species in New Zealand have adopted two contrasting pathways in relation to dispersal and habitat specialisation. One group (Section Ancistrum) has developed fruits with single, large, poorly protected embryos enveloped in an elaborate light-weight hypanthium with barb-tipped spines suitable for attachment to animals. These species are strongly stoloniferous, are successful in both open and forest habitats, and in general have achieved broad geographic ranges. The second group (Section Microphyllae), in contrast, maintained two embryos, heavily encased in fibrous endocarps, and generally supporting thick, long, barbless spines. Fruits are typically heavy and remain at ground level. These species are rhizomatous, are mainly in non-forest habitats, and are more likely to have restricted geographic ranges.

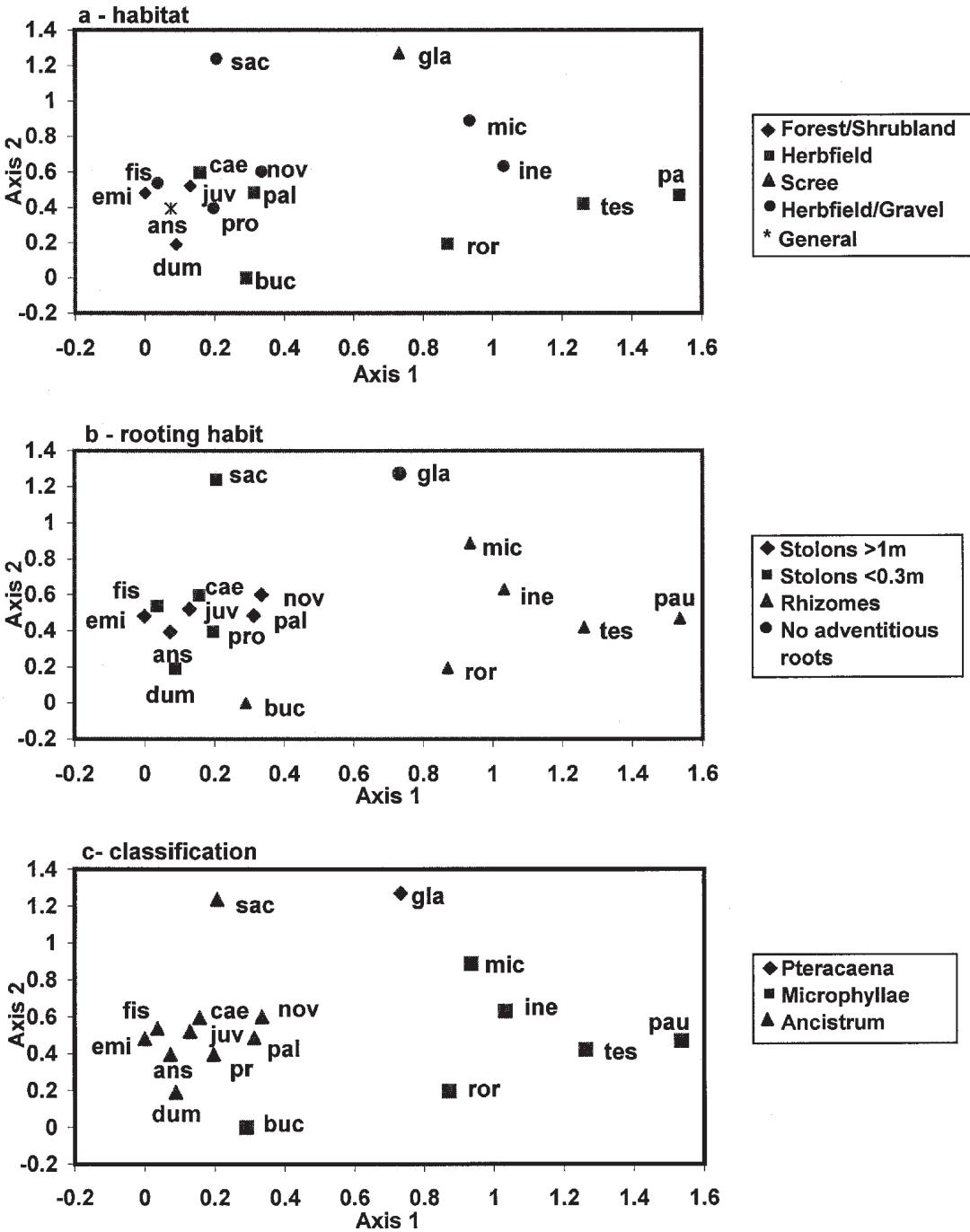


Figure 5. (a) Habitat, (b) rooting habit, and (c) taxonomic classification of *Acaena* species on an ordination of species based on fruit characters.

### Barb-fruited species

Several types of evidence suggest that barb-fruited species have greater dispersibility, through attachment to animals, than those species with fruits which lack barbs. In experimental studies in other taxa diaspores with straight spines had lower adherence and retention rates than those with hooks or barbs (Shmida and Ellner, 1983; Carlquist and Pauly, 1985). Barbed or hooked diaspores are common amongst fruits found on animals (Agnew and Flux, 1969), and there is also biogeographic evidence of the effectiveness of epizoochory in long-distance dispersal (Ridley, 1930; Taylor, 1954; Falla, 1960; Carlquist, 1967, 1983). Seed shadows for *Acaena novae-zelandiae* show that most of the disseminules are initially deposited within the area occupied by the plant (Gynn and Richards, 1985), while around 25% moved over 3 metres, and some up to 18 metres from the parent plant.

The importance of multiple and sequential pathways for dispersal of adhesive fruits have been highlighted by Liddle and Elgar (1984). For example, barbed-fruited *Acaena* species are undoubtedly dispersed through attachment to animals, but they may also be carried large distances by wind and water, often as a ball of intact, interlocked capitula.

The development of more and longer barbs on taller scapes in species characteristic of shrubland and forest habitats may reflect the larger size of the indigenous birds found in these communities, as fruit attachment height on dispersers controls the amount of settlement in vegetation of different structure (Bullock and Primack, 1977). The relatively large embryos in these species would assist with early establishment and growth of plants in low-light environments, although seed germination in *Acaena* species generally appears to be favoured by light (Conner, 1987).

The barb-fruited types of *Acaena* are also found in other countries, especially South America where they are dispersed by both birds and mammals. A noticeable difference from the New Zealand forms is the development of greater ornamentation and types of barbs, which may reflect the local importance of mammals. However, while different morphologic devices are suited to attachment on different surfaces (Carlquist and Pauly, 1985), there is no evidence of such differences affecting adhesion either to fur or feathers.

Overall, barb-fruited *Acaena* species in New Zealand are adapted to both long-distance seed dispersal via attachment to animals, and short-distance colonisation via stolons. The demise of most flightless and many ground dwelling native birds in New Zealand since European settlement may not have markedly reduced the dispersal potential for epizoochorous plant species as many of the fourteen widespread introduced

mammals (King, 1990) could perform analogous functions. Dawson (1960) suggests that mammalian dispersal of diaspores accounts, in part, for overlapping distributions and subsequent hybridisation of *Acaena anserinifolia* and *Acaena novae-zelandiae* in habitats created by human destruction of forest.

### Barbless-fruited species

The dispersibility of barbless-fruited species is probably limited, as the spines are unlikely to enable attachment to animals. Some of these *Acaena* species are associated with periodically inundated turf communities (e.g., *Acaena microphylla* var. *pauciglochidiata*, *Acaena buchananii*) and may depend on water or wind to disperse seeds. Their colour (dusky red) when mature and the presence of a thickened endocarp may also adapt the seeds to ingestion and dispersal by birds.

Raven (1973) considered that *Acaena* was of great antiquity in New Zealand based on their diversity, disjunct distribution, and distinctiveness. Within the genus, Bitter (1911) suggested the barbless-fruited *Acaena* species (i.e. section Microphyllae) to be distinctive to New Zealand and to have had a long line of independent evolution. The group is unrepresented in South America (Grondona 1964), although they do have a spineless species of *Acaena* (e.g., *Acaena lucida* - Section Pleurocephala) which has a very limited habitat and geographic range (Marticorena - pers. comm. 1997). *Acaena inermis* produces both spined and spineless fruits throughout its distribution in New Zealand and within communities (Conner, 1981; B. Macmillan, unpubl.), although the spined form appears to be less common.

Carlquist (1966a, b) has proposed a correlation between the diminution of hooks on fruits of *Sanicula* (Apiaceae) and narrowness of habitat, suggesting that a loss of dispersal ability can occur in species with narrow potential niche breadth. Cody and Overton (1996) demonstrated clear and rapid (<30 years) shifts in diaspore morphology of wind-dispersed, annual and biennial, Asteraceae on an island system in response to strong selection for reduced dispersal potential. A similar process could have occurred in barbless *Acaena* species which tend to occupy insular habitats. Geritz *et al.* (1984) argue on theoretical grounds that when safe sites for seedling establishment are either small or confined to an area around the parent plant or propagules are few in number, dispersal curves with very small tails are most efficacious. Ellner and Shmida (1981) suggest that in some environments anti-dispersal mechanisms are favoured. In deserts there are very few epizoochoric species, and these are mainly in more mesic sites. They show that amongst desert plants a variety of dispersal-restricting seed-containers have

developed that protect the seed from predation and flooding, regulate the within-season timing of germination, and spread dispersal and germination over several years. Each of these criteria apply to the majority of the barbless *Acaena* species, and suggest that the reduced dispersal ability may be a strategy associated with survival in restricted habitats.

### Other factors

Walton (1976, 1977a, b, 1979, 1980) believes that within sections of the genus containing barbed spines subtle differences in dispersal ability are probably a secondary factor in determining species geographic range in *Acaena*. He compared the reproductive biology and ecology of two *Acaena* species with contrasting distribution patterns in the subantarctic area: *A. magellanica*, with a broad circum-polar distribution, and *A. tenera* which is restricted to South Georgia. Although the two species differed in some aspects of their reproductive biology (e.g., in *A. magellanica* scape elongation occurred before anthesis, promoting outcrossing, and there were more fruits per capitulum), he suggests that genetic adaptability, environmental tolerance, and competitive ability were of greater consequence in accounting for the differences in geographic range. Conner (1981) undertook a comparative study of the ecology of five subalpine *Acaena* (*A. glabra*, *A. fissistipula*, *A. inermis*, *A. caesiiglauca* and *A. profundeincisa*) species in Canterbury and found differences in water tolerance and competitive ability that correlated with species habitat associations.

Clearly more information on seed germination and establishment characteristics, seed shadows, and relative competitive ability of *Acaena* species in New Zealand is required to assess the relative importance of the ecological correlates revealed in this study. A phylogeny for the genus based on molecular characters would also be helpful to determine the frequency of origin of different dispersal modes, and to clarify the selective forces involved in their development.

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