# Growth and reproduction of New Zealand *Acaena* (Rosaceae) species in relation to rarity and commonness

Kelvin M. Lloyd[1]*, William G. Lee[2] and J. Bastow Wilson[1]
[1]Botany Department, University of Otago, P.O. Box 56, Dunedin, New Zealand
[2]Landcare Research, Private Bag 1930, Dunedin, New Zealand
*address for correspondence: Landcare Research, Private Bag 1930, Dunedin, New Zealand
(E-mail: LloydK@LandcareResearch.co.nz)

**Abstract:** In New Zealand, as elsewhere, research on rare species has been dominated by autecological studies of individual threatened species. Limitations of this approach are that it involves no comparison with related common species which may have similar traits, and that the minimal sample size prevents generalisation about causes and consequences of rarity. We report on experimentally determined growth and reproductive traits of 10 rare and common *Acaena* (Rosaceae) species from two taxonomic sections (sect. Ancistrum and sect. Microphyllae). We examined the relationship between rarity or commonness and relative growth rate, mode of vegetative expansion, morphology/presentation of reproductive structures and reproductive allocation. Rarity and commonness were defined according to geographic range size, measured as the number of 10-km grid squares containing at least one record of the species. There were tendencies across both taxonomic sections for species with large range size to have higher relative growth rates and in section Microphyllae, faster lateral expansion. Among section Ancistrum species, common species tended to produce inflorescences for a shorter period and held their capitula higher above the canopy, but other reproductive attributes showed little association with range size. In section Microphyllae all reproductive traits tended to be positively associated with range size. This was mainly due to the single very common species having high fecundity. The lack of strong patterns among our results may reflect insufficient sample size or that the rare species represent different types of rarity.

**Keywords:** clonal plant; geographic range; guerrilla growth mode; phalanx growth mode; relative growth rate; reproductive allocation; RGR.

## Introduction

The New Zealand flora provides an excellent opportunity for gaining an understanding of the causes and consequences of rarity in plants. It contains a relatively large proportion of genera in which extensive radiation of species has occurred, probably as a result of new habitats created by tectonic activity in the late Tertiary (Fenner *et al.*, 1997). These speciose genera are well suited to the comparative approach to studying rarity (Cotgreave and Pagel, 1997; Bevill and Louda, 1999) because many contain a mixture of rare or regionally restricted species and common, widespread species.

A general understanding of rare species is lacking (Gaston, 1994), despite many recent single-species autecological accounts, driven primarily by the need for more information on threatened taxa (e.g. Widyatmoko and Norton, 1997; Shaw and Burns, 1997). In studies of single rare species, interpreting traits as causes of rarity is potentially misleading because the same traits may be present in common species. Comparative studies using controlled experiments to test for differences between larger samples of rare and common species (e.g. Kunin and Shmida, 1997) show much promise for identifying general differences between these two groups, but these have rarely been carried out.

While exceptions are common, differences between rare and common species have been observed most often in reproductive traits. Differences have been demonstrated in flowering phenology (Rabinowitz *et al.*, 1989; Lahti *et al.*, 1991), floral morphology (Harper, 1979; Kunin and Shmida, 1997), reproductive allocation (Primack, 1979; Kunin and Gaston, 1993) and dispersal traits (Edwards and Westoby, 1996; Lee *et al.*, 2001). In contrast to the work on reproductive traits, no consistent pattern has emerged from studies that have tested for differences in the vegetative growth traits of rare and common species (e.g. Snyder *et al.*, 1994; Witkowski and Lamont, 1997; Walck *et al.*, 1999). However, these studies have involved few species and in general very little research has examined the topic. This is unfortunate, because relative growth rate (RGR) (Grime and Hunt, 1975) and mode of vegetative expansion (Lovett Doust and Lovett Doust, 1982) are potentially important elements of plant ecology. Particular ecological strategies may be over-represented among rare plants. For instance, it has been suggested that rare species tend to be stress tolerators (Pate and Hopper, 1993; Wisheu and Keddy, 1994) and early successional species (Griggs, 1940; Massey and Whitson, 1980).

In this paper we report on a within-genus comparative study of the vegetative and reproductive growth traits of rare and common species of *Acaena* (Rosaceae). This genus was chosen because it holds a range of rare and common species and the plants are relatively easy to propagate and manipulate in experiments. We used controlled experiments to test for consistent intrinsic differences between the rare and common species. The traits of rare species may be either causes of rarity, or consequences (e.g. traits that promote persistence when rare). As a result there should be no expectation that rare species have trait values "inferior" to those of common species: tests for rare-common differences should be two-tailed. We looked for differences between the rare and common *Acaena* species in relative growth rate, the rate and mode of lateral spread, flowering phenology, reproductive allocation and aspects of reproductive morphology.

## Materials and methods

### Species used

*Acaena* is a predominantly southern-hemisphere genus containing approximately 100 species, with 18 of these indigenous to New Zealand and its outlying islands (Webb *et al.,* 1988; Macmillan, 1989; 1991).

**Table 1.** *Acaena* species used, and their provenances and range sizes. Plants from two populations were available for three species. Range size is expressed as the number of 10-km grid squares in the New Zealand region that contain at least one occurrence of the species.

| Species | Collection locality, habitat and altitude (m a.s.l.) | Map grid reference (NZMS 260) | Range size |
|---|---|---|---|
| Section Ancistrum | | | |
| *A. anserinifolia* | *Nothofagus* forest, Kowai Bush, Springfield, Canterbury (430) | L35: 229 681 | 737 |
| *A. caesiiglauca* | [1] *Chionochloa rigida* grassland, Old Man Range, Central Otago (1200) | H43: 156 339 | 238 |
| | [2] Short tussock grassland, Cave Stream, Castle Hill, Canterbury (680) | K34: 079 782 | |
| *A. juvenca* | Regenerating lowland forest, Trotters Gorge, North Otago (60) | J42: 363 316 | 109 |
| *A. minor* var. *antarctica* | Grown from seed collected from Auckland Island, Southern Ocean | unknown | 14 |
| *A. pallida* | *Ammophila* - dominated sand dunes, Tomahawk Beach, Otago Peninsula (5) | I44: 228 965 | 23 |
| Section Microphyllae | | | |
| *A. buchananii* | Roadside near St Bathans, Manuherikia Valley, Central Otago (520) | H41: 566 877 | 46 |
| *A. inermis* | [1] Roadside at Lake Lyndon, Porters Pass, Canterbury (840) | K35: 055 672 | 234 |
| | [2] Central Otago | unknown | |
| *A. microphylla* var. *pauciglochidiata* | [1] Gravel flat behind dunes, Chrystalls Beach, South Otago (2) | H45: 844 411 | 42 |
| | [2] Exposed cliff top, Cape Saunders, Otago Peninsula (120) | J44: 347 792 | |
| *A. rorida* | *Chionochloa rubra* grassland, Kaimanawa Mts, North Island (1130) | U21: 790 710 | 3 |
| *A. tesca* | Depleted *Chionochloa* grassland, South Rough Ridge, Central Otago (1020) | H42: 588 358 | 23 |

The majority of *Acaena* species are low-growing and mat-forming, and most of the indigenous species have globular capitula bearing spined fruits (Webb *et al.,* 1988). We used five species from each of two sections (sect. Ancistrum and sect. Microphyllae; Table 1). Several anatomical and structural differences in reproductive attributes exist between these two sections (Lee *et al.,* 2001). Capitula comprise a greater number of florets (40-130) in section Ancistrum species than in section Microphyllae (2-20). In section Ancistrum, all species possess elongated scapes (10-30 cm in length), which raise capitula well above the level of the foliage canopy, while in section Microphyllae capitula are often sessile, and where scapes are present they tend to be shorter (2-7 cm). Generally fruits of species from both sections bear four spines: these are barbed with stiff retrorse hairs in section Ancistrum but lack such barbs in section Microphyllae.

Most of the species were represented by plants from only one provenance, but for three species, two provenances were used (Table 1). Most plants were collected as vegetative ramets from wild populations, with the exception of *A. minor* ramets, which were obtained from cultivated plants. Ramets were propagated in fertilised potting mix for 6 months, with the exception of the Castle Hill population of *A. caesiiglauca*, and the Central Otago population of *A. inermis*, which were collected 3 months later than the other populations and thus propagated for only 3 months.

## Relative growth rate (RGR)

All 10 of the chosen *Acaena* species were used, with two populations for *A. caesiiglauca* and *A. microphylla* (Table 1), giving 12 species/population levels in total. Shoot tip cuttings of similar size were taken from several plants of each species and planted in pre-soaked fertilised potting mix in 0.5-litre plastic pots. After an establishment period of 1 month, plants were paired within species on the basis of comparable size and vigour. One member of each pair was randomly selected and harvested above ground level to estimate initial biomass. The remaining plants were randomly arranged into four blocks and grown outdoors in Dunedin (45º 52' S, 170º 30' E) for 4 months (September-December) before a final harvest. Harvested plants were dried at 80ºC for 48 hours, and weighed. The RGR of each species was calculated from the initial and final dry weights of the paired plants.

## Rate and mode of lateral growth

*Acaena* species are clonal, and most are prostrate and tend to spread radially when growing over an unobstructed surface. When growth occurs in this fashion, measuring the change in plant perimeter over time allows the rate of lateral growth to be assessed. An additional feature of spatial arrangement in clonal plants such as *Acaena* is the mode of lateral expansion. The plant perimeter can expand as a broad front with few indentations, by giving equal weight to the growth of many radiating terminal meristems, and filling the gaps between these with growth from lateral meristems. Alternatively, plants may expand by favouring the growth of fewer, relatively fast-growing terminal meristems and reducing lateral growth, leading to a more broken plant perimeter. These strategies were termed "phalanx" and "guerilla" respectively, by Lovett Doust and Lovett Doust (1982).

### *Experiment 1*

*Acaena* plants were grown outdoors in Dunedin, in garden soil over which a layer of non-fertilised organic potting mix had been spread to provide a level surface to grow across, and to restrict establishment of weeds. Two populations were available for three species, giving 13 species/populations in total (Table 1). Four replicate plants of each species/population were arranged into randomised blocks. Accidental contact with herbicide reduced the level of replication in two species. Lateral spread rate was measured by successively recording the dimensions of the minimum rectangle that could fully enclose the two-dimensional extent of each plant. Rectangle sides were oriented east-west or north-south. Minimum rectangles were measured at approximately 2-week intervals over a 14-week period covering the season of peak growth. The densities of plants within their minimum rectangles were estimated by measuring the proportions of line transects, placed across each rectangle, that were covered by plants. Six of these transects were used for each plant, with three oriented east-west and three north-south. Transects were placed by restricted randomisation within each orientation, one within each third of the distance along the rectangle side. Density measurements were made on two randomly selected plants of each species/population, at the same time as minimum-rectangle measurement.

### *Experiment 2*

Because replication in Experiment 1 was reduced in some species, a second experiment was conducted the following year to verify the results. Replication was set at five, and two populations were used for *A. inermis* and *A. microphylla* (Table 1), giving 12 species/population levels in total. Plants were grown in soil from which weeds were removed by hand. Lateral spread was measured in the same way as in Experiment 1. Density measurements were not made throughout the course of the experiment, but at the time of the last extent measurement the density of each plant was measured by superimposing a 20-mm grid over its rectangular extent, and mapping the grid squares occupied by the plant.

## Reproductive growth

Flowering phenology was recorded each week on the plants grown in Experiment 1 (see above). During the flowering period, the number of inflorescences on each plant was counted. Plants of the Castle Hill population of *A. caesiiglauca* and the Central Otago population of *A. inermis* did not flower, possibly because they were more recently propagated, and these two populations were excluded from analyses of reproductive traits. No plants of *A. minor* flowered during Experiment 1 hence no phenological data are available for this species.

In section Ancistrum species, reproductive allocation (reproductive biomass/total biomass) was examined in both Experiment 1 and Experiment 2. Capitula and scapes were harvested and counted as the capitula matured. After the last capitulum had been removed, all plants were harvested at ground level. In Experiment 1 the *in situ* height of each capitulum above ground level and above the canopy was recorded before harvesting. Unless mechanically removed, dead leaves remain attached to stems for a considerable period of time in *Acaena*, facilitating recovery of the total season's vegetative production. Fruits, scapes, and vegetative material were dried at 80°C for 48 hours and weighed.

In Experiment 1, the lengthy flowering period of one species meant that the final harvest was not carried out until spring, when production of the next season's capitula had begun in most of the plants. These immature scapes and capitula were harvested separately and added to the reproductive biomass from the previous season, because reproductive allocation measures the total reproductive output over the entire period of growth. The *A. minor* plants that did not flower in the first season were among the plants producing new season's capitula: these immature scapes and capitula were thus the only contribution made to reproductive biomass in this species.

It proved difficult to recover all the fruits produced by section Microphyllae species when these plants were grown in the ground; accordingly, a pot experiment was established to compare reproductive allocation in these species. Experimental material consisted of small plants of each species, grown outdoors for 6 months in 75-mm-diameter plastic pots, in fertilised potting mix. Before inflorescences appeared, these plants were transplanted to 210-mm-diameter pots containing fertilised potting mix, and grown outdoors. When flowering had finished and all plants were in fruit, they were harvested at soil level and separated into fruits, scapes, and remaining biomass. These components were dried at 80ºC for 48 hours and weighed. On each plant, the total number of capitula was recorded, and the lengths of 10 randomly selected scapes were measured. Where sessile capitula or scapes were borne terminally on short upright branches, "scape" was defined to include these short branches, since the upright branches in these cases serve the same function (i.e. raising the capitulum).

## Data analysis

For most variates, differences between the species were examined using analysis of variance or equivalent non-parametric tests. Spread rate data were analysed by linearly regressing the natural logarithm of extent (minimum rectangle size) on time for each replicate, then performing analysis of variance on the resultant regression coefficients. Taking the natural logarithm of the area variate corrects for the possibility that spread rates are proportional to plant size. From the Experiment 1 data, an estimate of the actual area occupied by each plant was obtained, for each time interval, by multiplying the plant's rectangular extent by its density within that area. Linear regression of the natural logarithm of area occupied on time allowed the species' rates of increase in occupancy to be compared. Analysis of variance was performed on the regression coefficients, in the same manner as the analysis of lateral spread rates.

The phalanx growth form has a lower amount of perimeter per area occupied than the guerilla growth form. Therefore, we examined the tendency of plants to expand by guerrilla or phalanx mode by calculating the proportion of occupied grid squares that occurred on the edge of each plant. These "perimeter" squares were defined as those occupied 20-mm grid squares that were directly adjacent to at least one unoccupied grid square, out of the surrounding eight. Raw perimeter proportions are biased by the inherent negative relationship between perimeter and size. An object of a given shape will have a decreasing proportion of perimeter cells as its size is increased. For this reason, standardisation was carried out by dividing the raw perimeter proportions by perimeter proportions calculated from "null shapes" of the same size (i.e. same number of occupied grid squares), but highly compact shape. The null shape for each plant was generated by a program that sequentially added occupied cells around an initial occupied cell, placed in the centre of a two-dimensional matrix, until the number of occupied cells in the null shape equalled the observed number occupied by the plant. A small corrected perimeter proportion indicates a tendency toward the phalanx growth form, while a large corrected perimeter proportion indicates expansion in the guerilla mode.

Rarity and commonness were defined by geographic range size, which was measured as the number of 10-km grid squares in the New Zealand region that contained at least one occurrence of the species. While geographic range size is a continuous variate, we refer to rare species as those occurring in fewer than 50 10-km grid squares, and common species as those found in over 100 10-km grid squares. Geographic range data were obtained from the four main New Zealand herbaria (AKL, CHR, OTA, WELT), the National Vegetation Survey database maintained by Landcare Research, unpublished species lists, records from the literature and personal observations. The data were mapped and converted to grid square occupancies using ArcView GIS. The *Acaena* species traits were plotted against their log-transformed geographic range sizes. Where trait data were available from two populations, the mean of these was used. On account of the small sample sizes involved (n = 5 in each of the two sections) formal correlations between trait data and geographic range are not presented.

# Results

## Relative growth rate (RGR)

In section Ancistrum, RGR ranged from 0.096 week$^{-1}$ in *A. pallida* to 0.173 week$^{-1}$ in *A. juvenca*, while among the section Microphyllae species, RGR was lowest in *A. microphylla* (0.122 week$^{-1}$) and highest in *A. rorida* (0.169 week$^{-1}$). The common species in section Ancistrum, *A. anserinifolia*, *A. caesiiglauca* and *A. juvenca*, had higher relative growth rates than the rare species, *A. minor* and *A. pallida* (Fig. 1). In section Microphyllae, the rarest species, *A. rorida*, had the highest RGR, but that of the commonest species, *A. inermis*, was also high (Fig. 1), resulting in no trend that could be related to range size.

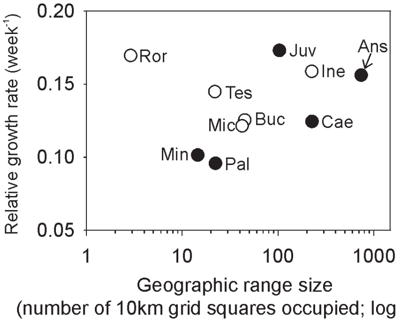

**Figure 1.** Relationship between relative growth rate and geographic range size of *Acaena* species. Species are identified by the first three letters of their specific epithet. ●= sect. Ancistrum, ○= sect. Microphyllae.

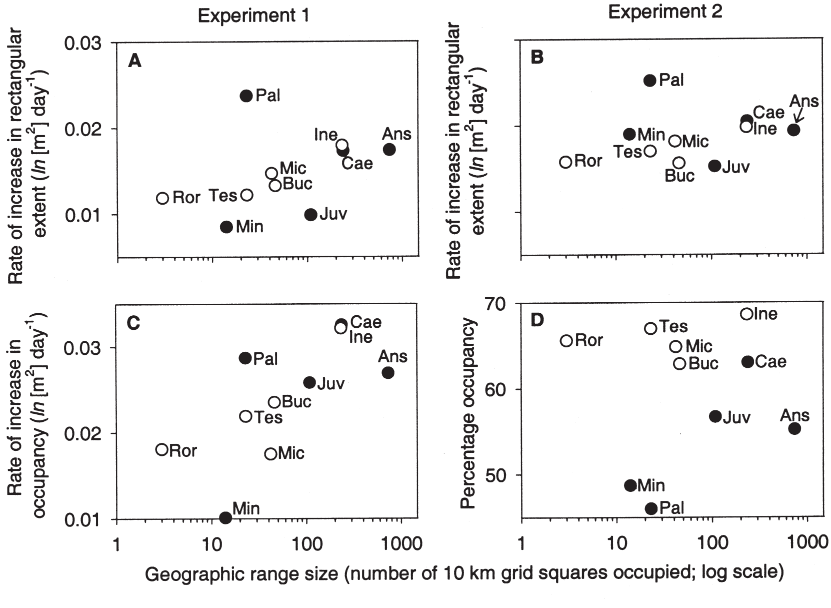

**Figure 2.** Vegetative expansion (increase in rectangular extent and occupancy of 20 mm grid squares) of *Acaena* species grown outdoors in garden soil, plotted against geographic range size. Species are identified by the first three letters of their specific epithet. ●= sect. Ancistrum, ○ = sect. Microphyllae.

### Increase in rectangular extent

In both experiments, the rare *A. pallida* increased its rectangular extent consistently faster (mean 2.4% per day) than the other section Ancistrum species, while the common *A. juvenca* was consistently slow (mean 1.2% per day). However, there was no relationship between geographic range size and increase in extent in either experiment (Fig. 2a,b) because the remaining rare species, *A. minor*, expanded its perimeter slowly. In section Microphyllae, common species tended to increase in extent faster than rare species. This relationship was consistent across both experiments. The most common species, *A. inermis*, expanded its perimeter fastest (Fig. 2a,b).

### Rate of increase in occupancy (Experiment 1)

Common species tended to increase their areas of occupancy faster than rare species, both in section Ancistrum (although the rare *A. pallida* was an exception) and in section Microphyllae (Fig. 2c). The rare *A. minor* increased occupancy particularly slowly, while the common *A. inermis* increased occupancy much faster than the other section Microphyllae species.

### Percentage occupancy (Experiment 2)

At the end of Experiment 2, percentage occupancy of grid squares differed strongly between the two sections of *Acaena* ($F_{1,44} = 67.9, P < 0.001$). Section Ancistrum species tended to occupy a lower percentage of grid squares (mean 54%) within their rectangular extents than did section Microphyllae species (mean 66%), although *A. caesiiglauca* was an exception (Fig. 2d). Within section Ancistrum, the two rare species, *A. minor* and *A. pallida*, had much lower percentage occupancy than the three common species, *A. anserinifolia*, *A. caesiiglauca* and *A. juvenca*. In section Microphyllae, the most common species, *A. inermis*, occupied the greatest percentage of 20-mm grid squares within its rectangular extent, but there were fewer differences between the species than in section Ancistrum (Fig. 2d).

### Proportion of perimeter squares

Corrected perimeter proportions differed strongly among the *Acaena* species/populations ($F_{11,48} = 65.8$, $P < 0.001$), but there was a highly significant interaction between perimeter proportion and taxonomic section ($F_{1,48} = 433.1$, $P < 0.001$). In general the stoloniferous species of section Ancistrum had greater corrected proportions of perimeter squares than did the rhizomatous section Microphyllae species (Table 2), indicating that within *Acaena* the stoloniferous habit leads to expansion in the guerilla mode, while rhizomatous species tend to advance as a phalanx. There was less variation within section Microphyllae than in section Ancistrum, in which *A. anserinifolia* and *A. pallida* had much higher corrected proportions of perimeter squares than *A. caesiiglauca* and *A. minor*, with *A. juvenca* intermediate. No relationship was observable in either section between corrected perimeter proportions and geographic range size.

### Flowering phenology

All species produced their first capitula in October or November, but there were marked differences among species in the duration of inflorescence production. *A. pallida* produced inflorescences over a longer period (32 weeks) than the other section Ancistrum species, with *A. caesiiglauca* and *A. juvenca* intermediate (24-25 weeks) and *A. anserinifolia* having the shortest flowering period (12 weeks). Most of the section Microphyllae species had considerably shorter flowering periods (3-7 weeks), the striking exception being *A. buchananii* which produced capitula for almost as long (30 weeks) as *A. pallida*. Within section Ancistrum, duration of inflorescence production was negatively related to geographic range size (Fig. 3a), although this result is based on the responses of only four species and only one is rare. Duration of inflorescence production was unrelated to geographic range size in section Microphyllae species (Fig. 3a).

**Table 2.** Tendency for "guerilla" or "phalanx" modes of vegetative expansion in *Acaena* species. Values are corrected proportion of perimeter values (see methods). Low values denote "phalanx" expansion, while high values indicate "guerilla" expansion, *sensu* Lovett Doust and Lovett Doust (1982). Within each section, the species are ranked from rare to common according to geographic range size.

| Species | Corrected proportion of perimeter |
|---|---|
| Section Ancistrum | |
| *A. minor* | 2.00 |
| *A. pallida* | 3.43 |
| *A. juvenca* | 2.41 |
| *A. caesiiglauca* | 1.57 |
| *A. anserinifolia* | 3.60 |
| Section Microphyllae | |
| *A. rorida* | 1.37 |
| *A. tesca* | 1.48 |
| *A. microphylla* | 1.50 |
| *A. buchananii* | 1.52 |
| *A. inermis* | 1.33 |

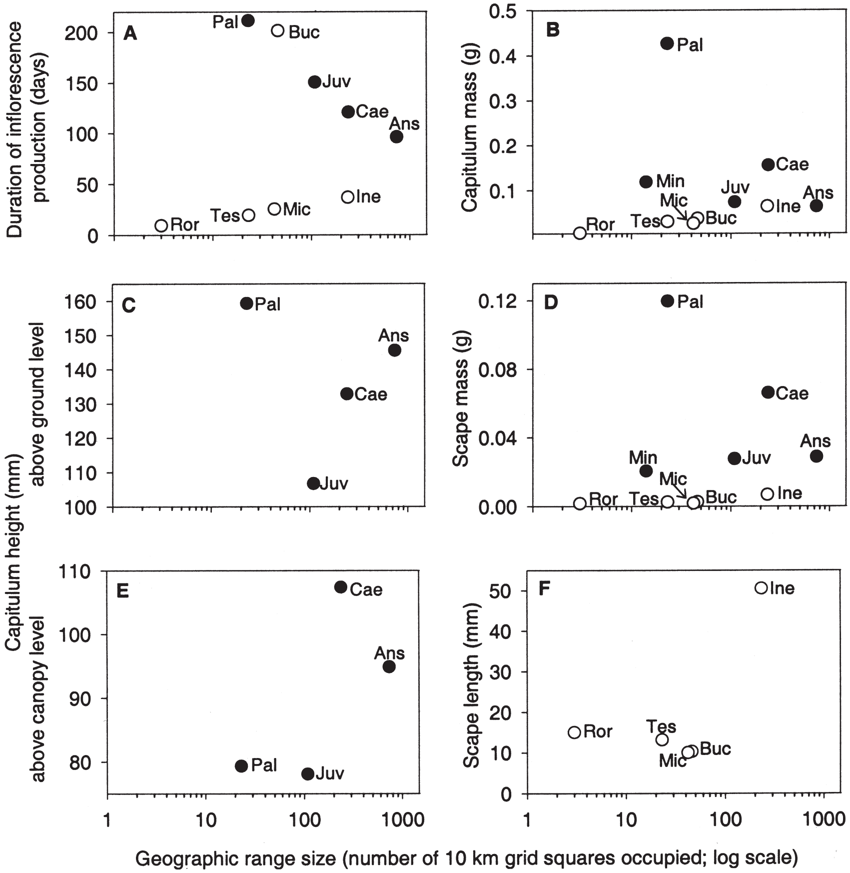

**Figure 3.** Relationships between reproductive traits (phenology, scape features and capitulum mass) and geographic range size of *Acaena* species. Species are identified by the first three letters of their specific epithet. ●= sect. Ancistrum, ○= sect. Microphyllae.

### Capitulum and scape features

Capitulum mass, scape mass and capitulum height above the ground and canopy all differed strongly ($P < 0.001$) among the section Ancistrum *Acaena* species. These traits were not associated with geographic range size (Fig. 3b-d), with the possible exception of capitulum height above the plant canopy (Fig. 3e). In section Microphyllae, capitulum mass was positively related to range size (Fig. 3b). This result, however, was partly due to abortion of fruits in the rarest species, *A. rorida*. Scapes of the most widespread species, *A. inermis*, were much heavier and longer than those of the other section Microphyllae species, which were similar in size (Fig. 3d,f).

### Reproductive allocation

In section Ancistrum, *A. juvenca* had much higher reproductive allocation than the other species in both experiments, with *A. pallida* intermediate, and *A. anserinifolia* and *A. minor* allocating a low proportion of biomass to reproduction. *Acaena caesiiglauca* had the most variable reproductive allocation between years. There was no relationship between reproductive allocation and range size in either experiment (Fig. 4a). There was more variation in reproductive allocation among the section Microphyllae species. The two most common species, *A. buchananii* and *A. inermis*, had greater reproductive allocation than the three rarest species (*A. microphylla*, *A. rorida* and *A. tesca*) (Fig. 4b). The very low reproductive allocation of *A. rorida* was due to abortion of most fruits.

## Discussion

### Research on rare New Zealand plants

While several rare New Zealand plant species have

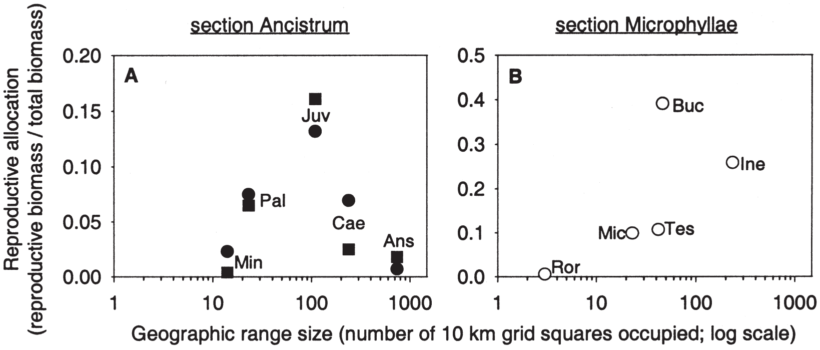

**Figure 4.** Relationships between reproductive allocation and geographic range size of *Acaena* species. Species are identified by the first three letters of their specific epithet. In section Ancistrum, ●= Experiment 1, ■= Experiment 2.

been the subject of autecological studies (e.g. Rogers, 1996; Williams *et al.*, 1996; Widyatmoko and Norton, 1997; Shaw and Burns, 1997), the traits of rare species have hardly ever been given a context by comparing them with those of common species. Generally, rare and common species have been studied in isolation from each other, and even when studies have included both rare and common species [e.g. in *Chionochloa* (Lee and Fenner, 1989; Fenner *et al.*, 1993)], these studies have not been designed to test for rare-common differences. Here we have tried to address this research gap, and in doing so have experimented on a genus of plants which has received relatively little scientific attention in New Zealand.

## Vegetative traits and rarity

Our results show some tendency for common *Acaena* species to have faster vegetative growth than rare species, but this tendency was not always consistent between the two taxonomic sections, and depended on the measure of growth. Very few studies anywhere have compared the vegetative growth characteristics of rare and common species. Witkowski and Lamont (1997) reported similar growth rates from seedlings of a pair of rare and common *Banksia* subshrubs. When resprouting after fire, the common species had faster RGR on a mass basis, but growth rates were similar on a modular basis (e.g. branches per branch). Snyder *et al.* (1994) found no differences in relative growth rate between a rare species of *Echinacea* and two widespread congeners, while Walck *et al.* (1999) observed faster growth rate in a rare *Solidago* species than a common congener. The results with *Acaena* reflect this ambivalent literature. In section Ancistrum, common species tended to have higher RGR and greater increase in occupancy than rare species, but no consistent relationship between increase in extent and range size was evident. In section Microphyllae, *A. inermis*, by far the most widespread species, consistently had the fastest lateral expansion, but it was matched in RGR by the extremely rare *A. rorida*. More evidence is needed to test the hypothesis that growth rates differ between rare and common species. A larger sample of species would be valuable in this regard.

Some of the species' growth responses appear contradictory: for instance we observed the highest RGR in *A. juvenca*, yet this species had relatively low rates of lateral expansion. The reverse was true of *A. pallida*. This may indicate allocation differences. The fast lateral expansion of *A. pallida* occurred at the expense of consolidating space: it had low occupancy and a strong guerilla growth mode. Thus its fast lateral growth was not reflected in high RGR, which measures increase in total plant mass. In *A. juvenca*, emphasis was placed on allocating growth to reproductive structures, and this appeared to be traded off against allocation to vegetative expansion.

Favourable and homogeneous resource conditions, such as those of our experiments, usually result in plants with a compact phalanx growth form (de Kroon and Hutchings, 1995), but high proportion of perimeter values indicated that *A. anserinifolia* and *A. pallida* retained a relatively loose guerilla plant structure. Lovett Doust and Lovett Doust (1980) suggest that guerilla species are opportunistic and predominate in disturbed habitats, perhaps because the spatial dispersion of partly independent ramets increases persistence time of the genet (de Kroon and van Groenendael, 1990). A fixed guerilla strategy accords well with the frequently disturbed habitats of *A. pallida* and *A. anserinifolia*: the former occupies sand dunes (Webb *et al.*, 1988) while *A. anserinifolia* is mostly found beside tracks, roads and streams (K. Lloyd, *unpubl.*).

### Reproductive traits and rarity

The most prevalent differences observed between rare and common species have involved reproductive traits (Kunin and Gaston, 1993). Rare plant species have been shown in one comparison to commence flowering earlier (Rabinowitz *et al.*, 1989) and in another to flower for a shorter period (Lathi *et al.*, 1991) than common species. They may also be more likely to be self-compatible (Harper, 1979; Kunin and Shmida, 1997) and to have lower investment in reproduction (Longton, 1992; Murray and Westoby, 2000). In a survey of the floras of the British Isles and California, Hegde and Ellstrand (1999) observed that rare and common species differed in inflorescence structure, flower colour, and fruit type, although these differences were not always concordant across the two floras.

This study provides limited support for reproductive differences between rare and common species. We observed large differences between the *Acaena* species in all of the reproductive traits examined (flowering phenology, capitulum and scape mass, scape length, reproductive allocation), but while a few of these traits showed some relation to geographic range size, these relationships were generally inconsistent across the two taxonomic sections of *Acaena*.

The negative relationship among section Ancistrum species between duration of inflorescence production and range size was strong, and contrary to that observed by Lahti *et al.* (1991). However caution should be employed when interpreting the *Acaena* relation, as the geographically-restricted *A. minor* did not flower in the season when records were taken, leaving only four sample points. *A. pallida* was in fact the sole rare species. Its very long period of inflorescence production may help it to persist while being rare.

In section Microphyllae, the positive association between capitulum mass and geographic range size owed much to the abortion of fruits that occurred in the rarest species, *A. rorida*. It was clear from observations of plants growing nearby, but in different conditions to those of the experiment, that *A. rorida* is quite capable of producing a sizeable number of relatively large (*c.* 10 fruits) capitula. The reason for abortion of *A. rorida* fruits under experimental conditions is unknown.

In both sections of *Acaena* the most common species held their capitula higher above the plant canopy than did the less common species. Height of diaspore release has been shown to be important for dispersal, both in terms of transport by wind (Sheldon and Burrows, 1973) and by animals such as sheep (Fischer *et al.*, 1996). The greater effective capitulum heights of *A. anserinifolia*, *A. caesiiglauca* and *A. inermis* may promote wider dispersal of their fruits, which is consistent with the larger range size of these species.

Low reproductive allocation in the three rare section Microphyllae species is consistent with evidence from rare British mosses (Longton, 1992) and 'everywhere-sparse' Australian sclerophyll woodland species (Murray and Westoby, 2000). Although Primack (1979) observed lower reproductive allocation in two rare species of *Plantago* than in common congeners, the plants were not grown in standard conditions and as a consequence differences in reproductive allocation could be due to differences in habitat quality.

### Anthropogenic effects on *Acaena* distribution

Prior to human colonisation of New Zealand, a diverse suite of ground-dwelling (or nesting) birds were present, and are likely to have been important dispersers of *Acaena* species, particularly those having barbed-spined fruit (Lee *et al.*, 2001). Many of these birds appear to have occupied the same open riparian habitats (Anderson, 1983; Holdaway, 1989) that are important for *Acaena* species today. The arrival of humans and associated animal predators led to the extinction of many bird species (Holdaway, 1989) but loss of ground-dwelling bird dispersers may have been at least partially offset by dispersal of *Acaena* fruits by introduced animals, including humans, particularly since European colonisation. An early attempt at biocontrol of *A. anserinifolia* is testimony to the ability of this species to attach fruits to sheep's wool (Miller, 1970), while the frequent occurrence of *Acaena* species beside roads and tracks suggests anthropogenic dispersal.

Present-day species distributions must also be interpreted in the light of human-induced landscape changes. Anthropogenic forest fragmentation may have increased the available habitat for species that occur on forest edges, such as *A. anserinifolia*, but could have reduced the amount of habitat for species of forest interiors, such as *A. juvenca*. The tussock grassland species *A. caesiiglauca* may have expanded its range in tandem with the expansion of indigenous grasslands that occurred following anthropogenic fires (McGlone, 2001). Three small and highly disjunct populations of *A. buchananii* in mid-Canterbury and Marlborough may be derived from anthropogenic dispersal events (B.H. Macmillan, Landcare Research, Christchurch, New Zealand, *pers. comm.*), as the species is otherwise restricted to the dry inland basins of Otago and South Canterbury. Anthropogenic effects on species distributions do not necessarily confound associations between geographic range and plant traits. The same traits that allow species to maintain large ranges (e.g. strong dispersal, wide environmental tolerance and high competitive ability) may also mean they are better able to take advantage of human-induced changes (e.g. increases in habitat availability).

### Types of rarity

While some weak patterns are observable in our experimental results, we did not find a consistent, generalisable pattern of trait differences between the rare and common *Acaena* species, suggesting that the rare species might be rare for different reasons. It has been frequently suggested that rare species should not be regarded as a homogenous assemblage, but may represent several different types of rarity, classified not only by geographic range but also by habitat specificity and population size (Rabinowitz, 1981; Fiedler and Ahouse, 1992). Conversely, species may be rare and common for exactly the same reason, e.g. the abundance of habitat specialists may simply reflect the abundance of their habitats. There is no reason to expect species representing different types of rarity to share the same sets of traits. However testing for associations between types of rarity and species traits requires a larger sample of species than we have used here, because the different types of rarity each need to be represented by sufficient numbers of species.

Rabinowitz (1981) did not include a temporal classification of rarity in her typology, but the concept of "old" and "young" rare species was raised early in the study of rarity (Griggs, 1940; Stebbins and Major, 1965) and was revived more recently by Fiedler and Ahouse (1992). A temporal component of rarity need not be restricted to taxon age (i.e. time since speciation) but could also include time since colonisation. The traits of "young" rare species may be no different from the traits of common, widespread species. Newly evolved species and new colonists may simply have had insufficient time to expand their ranges. Among the *Acaena* species, the highly restricted *A. rorida* is similar in morphology to the nearby *A. microphylla* var. *microphylla* (Macmillan, 1991), suggesting that *A. rorida* may be a recent derivative of this taxon. *Acaena pallida* may be another "recent" rarity. This sand dune species has a highly disjunct distribution, being found in Wellington Harbour, on the Chatham Islands, and in the southeastern South Island. Such a distribution could be that of a relict species which has suffered local extinctions from the middle of its range, but its rarity is surprising in view of its strong vegetative expansion, long flowering period, and relatively high reproductive allocation. An alternative hypothesis is that *A. pallida* has colonised New Zealand relatively recently. Phylogenies derived from molecular information could prove useful for testing these hypotheses.

Even within a single rarity type, it may prove difficult to establish links between plant traits and rarity, necessitating further subdivision of the group of rare species. For instance, a great many rare plant species appear to be habitat specialists (Rabinowitz *et al.*, 1986; McCoy and Mushinsky, 1992; Saetersdal, 1994; Linder, 1995), but different habitats may select for different suites of plant traits. This may obscure relationships between plant traits and rarity when a group of rare habitat specialists are specialised to different habitats.

Our study has contributed results from a larger sample of species than has been used in most experimental studies of rare and common plants, but the patterns we found remain weak. Research targeting particular types of rarity may prove more useful for improving our understanding of rare species.

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