

Short communication

A natural hybrid between *Raoulia bryoides* and *R. grandiflora* (Compositae-Gnaphalieae) from Mt St Patrick, Canterbury, New Zealand

ROBERT J. MCKENZIE

JOSEPHINE M. WARD*

School of Biological Sciences
University of Canterbury
Private Bag 4800
Christchurch, New Zealand
Email: josephine.ward@canterbury.ac.nz

STUART M. MURRAY

Old Quarry Farm
R.D. 1
Lyttelton, New Zealand

Abstract The morphology of a putative hybrid from Mt St Patrick in the South Island of New Zealand is described. Morphology is consistent with the parentage *Raoulia bryoides* × *R. grandiflora*. The pollen of the plant appears to be highly fertile. This is the first authenticated record of a wild hybrid between these species.

Keywords Asteraceae; Compositae; Gnaphalieae; hybridisation; New Zealand flora; *Raoulia bryoides*; *Raoulia grandiflora*

INTRODUCTION

Raoulia Hook.f. (Compositae, tribe Gnaphalieae) is New Zealand's largest endemic flowering plant genus, with 23 described species and 8 additional entities that may warrant species status (Ward 1997). *Raoulia* species have long been known to form natural hybrids, not just among themselves, but also with closely related genera (Cockayne & Allan 1934; Allan 1939, 1961; Ward 1997; McKenzie 2001).

Three intergeneric hybrid combinations involving alpine species of *Raoulia* have been the subject of recent unpublished studies (Falvey 1996; McKenzie 2001). Numerous intrageneric combinations between *Raoulia* species have been reported (Cockayne & Allan 1934; Allan 1961; Ward 1997), but little substantive evidence has been published. Chromosome numbers have provided evidence for the occurrence of hybrids between *Raoulia* species of differing ploidy (Dawson et al. 1993). A natural hybrid between *R. eximia* Hook.f. and *R. petriensis* Kirk has been described from cultivated material (Tan & McBeath 1988).

In this paper we describe a putative hybrid between *Raoulia bryoides* Hook.f. and *R. grandiflora* Hook.f. from Mt St Patrick, Canterbury, South Island, New Zealand. Both *R. bryoides* and *R. grandiflora* are alpine species belonging to subgenus *Psychrophyton* Beauverd. *Raoulia bryoides* is a cushion-forming species found on rocky outcrops east of the Main Divide in the northern half of the South Island. *Raoulia grandiflora* forms mats or dispersed clumps in tall-tussock grassland, herbfield, and fellfield from the central North Island southwards. Putative hybrids between cushion and mat species of subgenus *Psychrophyton* are rarely seen in the wild. The only other such putative combination we have encountered is *R. grandiflora* × *R. mammillaris*, comprising three individual plants at a single site. The single putative *R. bryoides* × *R. grandiflora* was not flowering when discovered and determination of its identity was not possible from vegetative morphology alone. A cultivated clone of the hybrid flowered for the first time during the spring of 2002, allowing the parentage to be determined.

MATERIALS AND METHODS

A single plant of the putative hybrid was discovered on Mt St Patrick, St James Range, growing on rock on a south-east-facing slope in a clump of *Leucogenes grandiceps* (Hook.f.) Beauverd.

*Author for correspondence.

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Cuttings were collected and grown in a shadehouse in Christchurch. The morphology of the putative hybrid is described from one of these cultivated plants which bore four capitula in October and November 2002. A voucher (CANU 38701) is lodged with the University of Canterbury Herbarium. Pollen stainability was assessed with Alexander's differential stain (Alexander 1980) and pollen viability estimated with the fluorochromatic reaction (Heslop-Harrison & Heslop-Harrison 1970). Freshly presented pollen was collected from six florets. For each procedure 200 pollen grains per floret were scored.

RESULTS AND DISCUSSION

The putative hybrid has densely tufted branches and forms a hard compact mat (Fig. 1). The plant has two distinct shoot types: short upright shoots with indistinct internodes and prostrate shoots with longer internodes. The leaves are 3.2–3.6 mm long \times 1.3–1.4 mm wide, narrowly obovate-oblong with an obtuse to acute apex. A short mucro 70–120 μ m long is present at the leaf apex. The leaf bases are appressed to the stem and imbricate. The lamina is usually horizontal on the upright shoots and recurved on the prostrate shoots. The leaves are commonly uninervate, but bi- and trinervate leaves are present on the largest vegetative shoots and the flowering shoots. Dense indumentum covers the adaxial and abaxial leaf surfaces. The clothing trichomes are interwoven, appressed to the leaf surface and comprise a mixture of narrow and broad hairs 8–40 μ m wide, all with a single basal cell. The conspicuous capitula are terminal and borne on the short upright shoots (Fig. 2). The capitula are solitary, 5.5–5.9 mm long \times 4.5–4.9 mm wide and large for the size of the shoots. Each capitulum contains 18–19 female florets around the periphery and 21–24 hermaphrodite florets in the centre. The inner involucre bracts are 4.9–5.5 mm long \times 0.8–1.2 mm wide. The bract lamina is white and non-hygroscopic, so does not radiate outwards during sunny weather. The corolla lobes and style arms are white. The hermaphrodite florets have short style arms 0.28–0.42 mm in length. The pollen is yellow and the anthers are translucent and colourless. The pappus hairs are dimorphic. The apical cells are rounded in female florets, and rounded to clavate in hermaphrodite florets. The cells below the apex are predominantly obtuse and non-projecting in female florets, but rounded and projecting in hermaphrodite florets. The apical cells

have reticulate wall thickening. The upper portion of the pappus hairs is not distinctly flattened in either floret type. In both floret types the ovary epidermis bears twin hairs 0.15–0.37 mm long with obtuse to acute apices.

A comparison of selected morphological features in *Leucogenes grandiceps*, *Raoulia bryoides*, *R. grandiflora*, and the putative hybrid is presented in Table 1. Some characters are identical in the three sympatric species and the putative hybrid, such as pollen and anther colour. No character state unique to *L. grandiceps* (e.g., multicapitulate inflorescences, greenish yellow corolla lobes and style arms, uniform thickening of pappus apical cell walls, and brown involucre bract lamina) is expressed in the putative hybrid. No novel or extreme character states were observed. In all characters recorded, the putative hybrid is either intermediate between *R. bryoides* and *R. grandiflora* or identical to one or both species.

The putative hybrid is intermediate between *R. bryoides* and *R. grandiflora* in numerous floral characters, including involucre bract dimensions, length of the style arms of hermaphrodite florets, and length of twin hairs on the ovary. Variation in the number of leaf traces in the putative hybrid is interpreted as an intermediate state between *R. bryoides* (uninervate leaves) and *R. grandiflora* (trinervate leaves). The leaf apex shape of the putative hybrid is also intermediate between *R. bryoides* and *R. grandiflora*. In many vegetative and floral characters the putative hybrid is more similar to *R. bryoides* than to *R. grandiflora*. This is especially true for vegetative characters, such as the dimensions and shape of the leaves. The clothing trichomes are similarly variable in width in the putative hybrid and *R. bryoides* (although broad trichomes predominate in *R. bryoides*), but always narrow in *R. grandiflora*. Only *R. bryoides* and the putative hybrid have clothing trichomes with a single basal cell. The putative hybrid resembles *R. grandiflora* in the number of female and hermaphrodite florets per capitulum. In different pappus characters the putative hybrid is similar to either *R. grandiflora* or *R. bryoides*. The pappus hairs are monomorphic in *R. grandiflora* but dimorphic in the putative hybrid and *R. bryoides*. The putative hybrid is more similar to *R. bryoides* in the shape and degree of protrusion of the cells below the pappus apex, but more similar to *R. grandiflora* in the shape of the pappus apical cells, and the absence of distinct broadening and flattening of the pappus hair below the apex.

Fig. 1 Growth form of natural hybrid between *Raoulia bryoides* and *R. grandiflora*, from cultivated clone. Scale bar = 5 mm.

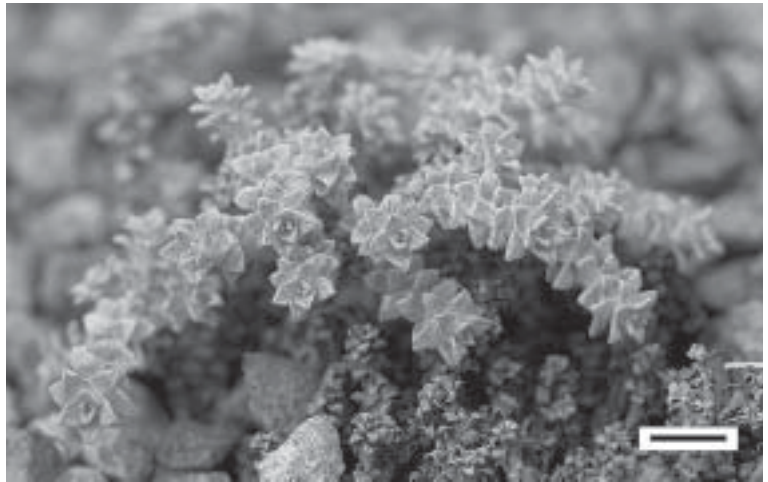


Fig. 2 Flowering shoot from natural hybrid between *Raoulia bryoides* and *R. grandiflora*, from cultivated clone. Scale bar = 5 mm.



The pollen appears to be highly fertile. Alexander's differential stain indicated 86% of the grains were normally developed. Abnormal grains were smaller and the cytoplasm was either shrunken or poorly stained. A similar percentage of pollen grains (83%) exhibited moderate to strong fluorescence with the fluorochromatic reaction. The capitula were fixed prior to seed maturation, so ovule fertility is unknown.

The putative hybrid does not fit into any currently defined species. No novel character states were recorded and only a single plant was discovered, suggesting that it does not belong to an undescribed taxon. The possession by the putative hybrid of qualitative characters shared with either *R. bryoides*

or *R. grandiflora*, and of character states intermediate between these species, is supportive of hybridity. This evidence also suggests that phenotypic plasticity in either *R. bryoides* or *R. grandiflora* is unlikely to account for the putative hybrid's morphology.

In this instance, the field evidence, gross vegetative morphology, and prior knowledge of hybridisation in New Zealand Gnaphalieae led to an incorrect initial hypothesis concerning the putative hybrid's parentage. Hybrids often occur close to the maternal parent; the hybrid in question was growing within a patch of *Leucogenes grandiceps*. Hybrids have been reported between all geographically feasible combinations of *Leucogenes* Beauverd and the pulvinate species of *Raoulia*, with those between

Table 1 Selected morphological characters in *Leucogenes grandiceps*, *Raoulia bryoides*, *R. grandiflora*, and putative *R. bryoides* × *R. grandiflora*.

Character	<i>L. grandiceps</i>	<i>R. bryoides</i>	<i>R. bryoides</i> × <i>R. grandiflora</i>	<i>R. grandiflora</i>
Growth form	clump or mat	cushion	mat	mat
Leaf dimensions (mm)	5.2–7.7 × 2.2–3.4	2.2–3.6 × 0.9–1.4	3.2–3.6 × 1.3–1.4	7.3–12.3 × 1.0–3.3
Leaf shape	obovate to obovate-oblong	obovate to narrowly obovate-oblong	narrowly obovate to oblong	narrowly rhombic
Leaf apex	obtuse to rounded	obtuse	obtuse to acute	acute
Leaf venation	trinervate	uninervate	uni- to trinervate	trinervate
Clothing trichome width (µm)	7–18	12–35	8–40	9–16
Number of basal cells in clothing trichomes	2–3	1	1	2–3
Leaf glandular trichomes	biseriate	biseriate	biseriate	mainly uniseriate
Number of capitula per flowering shoot	5–11	1	1	1
Involucral bract dimensions (mm)	4.3–5.5 × 1–1.9	3.8–4.4 × 0.6–1.1	4.9–5.5 × 0.8–1.2	7.5–12.2 × 0.9–1.8
Involucral bract lamina colour	pale to dark brown	white	white	white
Involucral bract lamina hygroscopic	no	no	no	yes
Number of ♀ florets per capitulum	8–22	4–8	18–19	9–22
Number of ♂ florets per capitulum	11–51	4–11	21–24	9–28
Corolla lobe and style arm colour	greenish yellow	white	white	white
Style arm length in ♂ florets (mm)	0.38–1	0.12–0.28	0.28–0.42	0.38–0.75
Pappus hairs dimorphic	yes	yes	yes	no
Pappus hairs apical cell shape (♀ florets)	obtuse to rounded	obtuse	rounded	rounded
Pappus hairs apical cell shape (♂ florets)	obtuse to rounded	rounded	rounded to clavate	rounded to clavate
Pappus apical cell wall thickening	uniform	reticulate	reticulate	reticulate
Pappus shape of cells below apex (♂ florets)	obtuse to rounded	obtuse to rounded	obtuse to rounded	rounded
Pappus cells below apex projecting (♀ florets)	yes	no	some	yes
Pappus hairs broader below apex	yes	yes	no	no
Pappus hairs flattened below apex	yes	yes	no	no
Ovary twin hair length (mm)	0.18–0.78	0.31–1.3	0.15–0.37	0.12–0.22
Ovary twin hair apex	acute	acute	obtuse to acute	obtuse

L. grandiceps and *R. mammillaris* Hook.f. (a very close relative of *R. bryoides*) reported frequently from the well-botanised Craigieburn Range. Gross vegetative morphology does not discount a *L. grandiceps* × *R. bryoides* combination. However, vegetative micromorphology and floral morphology do not support such a conclusion. For example, in other hybrids between *L. grandiceps* and a species with solitary capitula, the number of capitula per shoot is variable (1–5) on the same plant (Falvey 1996; McKenzie 2001). All four of the features unique to *L. grandiceps* are absent in the putative hybrid, whereas four features unique to *R. grandiflora* (acute leaf apex, pappus not broadened or flattened below the apex, clavate apical cells in pappus, and obtuse twin hairs) are present.

The combination *Raoulia bryoides* × *R. grandiflora* is listed by Cockayne & Allan (1934), and Allan (1961) noted that certain specimens from Mt Patriarch have leaf morphology strongly suggestive of *R. bryoides* × *R. grandiflora*. However, the leaf figured by Allan (1939) is much more similar to *Leucogenes leontopodium* than to *R. grandiflora*. This similarity, the relative frequency of reported hybrids between species of *Leucogenes* and cushion-forming *Raoulia*, and the abundance of both *Leucogenes leontopodium* and *Raoulia bryoides* on Mt Patriarch make it very likely that the second parent of the plant figured by Allan (1939) was *L. leontopodium* rather than *R. grandiflora*. It is, however, difficult to ascertain parentage with confidence in the absence of flowering or fruiting parts.

Since *R. bryoides* and *R. grandiflora* frequently grow in close proximity, the paucity of known hybrids suggests the presence of strong reproductive barriers between the two species. Numerous pre- and post-pollination barriers may prevent hybridisation between two plants (Levin 1978). Given the experimental cross-compatibility of many New Zealand Gnaphalieae (McKenzie 2001), overlap in flowering periods of the two species, and their likely possession of a generalist pollination system, post-pollination isolation might be most likely. It is possible that hybrids arise more frequently but most are not sufficiently well adapted to survive the rigours of the alpine environment.

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