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**The Alpine Ranunculi of New Zealand.**

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This information explains in great detail the landscape in which our Alpine plants have adapted to and grow in.

New Zealand is a small country and is one of the newest land masses in the world. Crammed between the Pacific Plate and the Australian Plate it is particularly active with constant earth movement eg earthquakes.

### Ranunculus haastii

The long, loose slopes of stony debris, known in New Zealand as shingle slides, which cover a large proportion of the higher mountain slopes of the eastern ranges of the South Island (Fig. 9), are inhabited by a specialised community of plants, of which few are able to tolerate the conditions of more stable situations. A more complete account of this community has been published elsewhere (Fisher 1952) but it is relevant here to summarise certain features bearing on the natural history of *R. haastii*.

The extensive development of debris slopes in certain parts of New Zealand is largely due to the nature of the parent rock, which consists of indurated sedimentary material known as greywacke. Mechanical weathering along numerous cracks and shatter zones is rapid, and the rate of accumulation of the resulting debris on any hillside greatly exceeds its rate of removal by chemical weathering or by alluvial transport. Such heaps of debris lie at an angle of repose close to 32° above the horizontal, a slope of about 1 to 1·6.

In the Central Otago region, a number of ranges similar in height and climate to many of those further north, occur in the mica-schist belt. Owing to their more gently sloping flanks and to the greater coherence of their rocks, these mountains undergo physical disintegration at a rate more closely approaching their rate of chemical weathering, so that massive accumulations of unweathered debris are lacking, and a gap is produced in the distribution of the scree plants. Further south on the Eyre Mountains fairly large scree slopes have developed on schist with slightly different properties and in this region a distinct subspecies, *R. haastii* subsp. *piliferus*, occurs. On the Takitimu Range, again to the south, the recurrence of *R. haastii* subsp. *haastii* corresponds with a return to greywacke.

Although there is no difficulty in explaining the absence of *R. haastii* and the other scree species from the mica-schist area of north Otago, it is less easy to explain the apparent absence of the species from the Inland Kaikoura Range where screes are abundant. Other species of scree plant have been recorded in this region, and *R. haastii* itself is present on the Seaward Kaikoura Range immediately to the south-east. Climatic differences may be able to account for the absence of *R. haastii* from the high rainfall area of the central Alps and also from the West Coast side of the mountains, but differences in climate between adjacent slopes of the Seaward and Inland Kaikoura Ranges are much smaller. One explanation might be that the range of *R. haastii* is expanding and has not yet reached its potential limit in the northern part of the South Island. But it is also possible that the Inland Kaikoura region has not yet been adequately explored botanically.

More than 10 species from almost as many different families are regular inhabitants of unstable debris slopes. Few other species ever successfully establish themselves in this habitat and few of the scree plants succeed in more stable situations. Such clear-cut specialisation is uncommon and provides an unusual opportunity for studying the physiological ecology of a group of unrelated plants utilising similar adaptations.

The surface of the unstable scree is a layer of loose stones; some of these may be more than a foot in diameter, but most are considerably smaller. Movement of this top layer intermittently destroys the upper parts of most herbaceous plants growing through it. The roots and storage organs of the scree plants are embedded deeply in a moist, stable zone containing fine materials sifted down from the mobile layer above, and possessing a tightly packed surface over which the mobile sheet slides. The silty particles in the packed surface of this layer become temporarily cemented together when dry, so that during the summer the stability of the scree increases. When saturated by rain, and particularly when snow falls during the winter, these layers loosen, and localised movements of patches of the surface, become more frequent. The slight downhill readjustments which even the compacted layers undergo, result in the downhill orientation of the rhizomes, which usually lie just beneath this compacted surface.

Like most of the other scree plants, *R. haastii* is a fleshy, summer-green perennial with large rhizomes and an extensive root system. That spring growth of new leaves and scapes is probably controlled by soil temperatures was shown when, in a heated green-house (*ca.* 60°F), spring development was advanced five weeks over plants outdoors (soil temp. *ca.* 40°F). The flowers open at the end of a further six to eight weeks, which under natural conditions is generally early in November. The mature fruits begin to be shed towards the end of January, but whole heads may become detached by surface movements and the fruits scattered by the wind over distant parts of the scree slope. From any growing point, of which a branching rhizome may have half a dozen or more, rarely more than a single vegetative leaf or a single scape is formed. The large bract of the inflorescence is more similar to a vegetative leaf in shape and texture in this species than in any other member of the *alpine* group. Young rhizomes, and small branches from larger rhizomes, usually bear only leaves, but large rhizomes may produce at the end of each branch a scape with as many as five flowers, so that it is possible for single plants with well branched rhizomes, to bear as many as 20 blooms. More commonly, however, a smaller number of flowers is produced by a single vegetative colony.

Characteristic of all the scree species are their fleshy, thickened leaves, glabrous in most, and usually covered with a heavy glaucous bloom. Even when the leaves are large, as in *R. haastii*, it is usual for them to be well divided and hence effectively microphyllous (subsp. *piliferus* is an exception). External features such as extensive root systems and microphyllous leaves, together with anatomical features such as strong vessel development and high stomatal frequencies, suggest a general adaptation to a swift transpiration current from soil to atmosphere. Detached shoots wilt rapidly. Nothing resembling the stomatal control and epidermal protection from water loss that occurs in the desert-succulents of other countries is present. The nature of the scree environment makes such a swift passage of water readily possible: an abundant supply of moisture, even in dry seasons, is available in the deeper layers of the soil where the roots penetrate, while high winds (Foehn), low atmospheric humidities, high temperatures at the soil surface, and strong insolation, all contribute to high evaporation rates at the level of the foliage.

From an examination of the above characteristics of the scree plants and their environment it is not difficult to formulate a physiological explanation of their ecological specialisation. Where accelerated erosion produces repeated movements of stony debris around woody plants or evergreen herbs, extensive damage is usually caused. The summer-green habit, with rhizomes buried in a stable zone, permits the specialised scree plants to undergo such intermittent destruction of their fleshy shoots without substantial loss of elaborated material. Spring growth is more rapid in the scree plants than in other alpine plants, and storage organs are more strongly developed. Such fast growth suggests high efficiency on the part of the scree plants in exploiting the high temperatures and bright illumination of the screes, which would make possible a more rapid accumulation of assimilated materials in the storage organs than would be normal for other, non-adapted species. Under such conditions of high illumination it is not improbable that a major factor limiting photosynthesis would be the rate of $CO_2$ uptake, necessitating as rapid a turnover of air in the intercellular spaces of the leaves as possible. Only by providing ample water would the consequent dehydration of these tissues be averted. To obtain water in quantity from the soil, extensive root systems, of the kind found, would be required; to transport it to the leaves an efficient conducting system would be necessary; and to reduce damage in the peripheral parts of the leaf, a microphyllous leaf form, as found in most scree plants, with mesophyll more or less evenly collected around the major veins, would be an important advantage.

If the foregoing is correct the critical requirement is abundant water in the deeper layers of the soil; comparison of such layers in neighbouring stable habitats with those enclosing the roots of the scree plants revealed that water is usually much less freely available under more stabilised conditions. Certain contributing factors are obvious. First, the concave slopes that favours debris accumulation also guides the draining moisture into the scree area. Secondly, stabilised conditions compared with unstable ones support a much greater density of plants, often in closed communities, and hence a much greater consumption of water. Thirdly, the long continued presence of vegetation in a stable site leads to the development of true soils with increasing proportions of fine mineral and organic materials. Such soils have a greater field capacity for water, but owing to colloidal properties most of this water is held much more firmly than by the immature stony soils of the screes. The high water requirements, which according to the above hypothesis must be possessed by the scree plants, would thus be difficult to meet in many stable habitats, and accordingly the hypothesis outlined is able to account not only for the success of the scree plants on the water-abundant screes, but also for their failure in other places.

It may be noted that recent studies by Molloy *et al.* (1963) show that many fully unstable screes in Canterbury contain deep soil layers possessing strong indications of having been formed under dense vegetation. Whether such origins are necessary for the establishment of specialised scree communities remains to be shown.

### Variation

Two subspecies with separate ranges of distribution have been distinguished in *R. haastii*. The more widespread and better known subspecies *haastii* is fairly abundant on larger screes of the eastern ranges of the alps from Wairau Gorge to the Takitimu Range of Otago. The other, subspecies *piliferus* is so far known only from the Rough Peaks Range in the Eyre Mountains south-west of Lake Wakatipu.

**Ranunculus haastii** subspecies **haastii**

It is suspected that the slight amount of variation observable in natural populations of this subspecies is mainly due to differences in vigour, caused by site conditions and age, rather than to genetic differences. As cultivation of any of the specialised scree species has been found to be particularly difficult, however, it has not been possible to distinguish the sources of variation with any certainty. What variation does occur is confined mainly to correlated size differences in leaves and flowers, to the depth of cutting of the leaves, and to the number of branches of the scape. According to Kirk (1899), who had no Eyre Mountains material, Otago specimens of *R. haastii* tend to be less deeply divided in the leaves, to have wider petals, and scapes more strongly villous at the base, than specimens from Canterbury or Nelson. Cheeseman (1925) was unable to confirm such differences between Canterbury and north Otago specimens, but during the present study a leaf specimen from the Takitimu Range was found to differ in the way described by Kirk.

The absence of observable variation of any apparent significance in Canterbury populations of subsp. *haastii* may be related to the stringently selective conditions of the very uniform scree environment. Evidence for strong selection pressure is apparent in the convergence of many characteristics in the species of different families specialised for life on the screes (Fisher 1952). Besides the Ranunculaceae (*R. haastii*), such divergent groups as the Umbelliferae (*Anisotome carnosula*), Caryophyllaceae (*Stellaria roughii*), Campanulaceae (*Lobelia roughii*), Cruciferae (*Notothlaspi rosulatum*), Onagraceae (*Epilobium pycnostachyum*), and Compositae (*Cotula atrata*) are among those represented. It appears that any advantages of variation in these species have been largely sacrificed in favour of increased efficiency in adaptation to a particularly uniform habitat, none of the species showing the intraspecific variation typical of their nearest relatives inhabiting other alpine situations.

**Ranunculus haastii** subspecies **piliferus**

The leaves of this subspecies differ from those usual in subspecies *haastii* by the less deeply notched margins of their three lobes. The single Takitimu specimen, though lacking hairs, approached this shape (Fig 9). In ssp. *haastii*, folding of the lobes usually obscures their shape but in ssp. *piliferus*, the lobes tend to lie flat so that their separately orbicular form is more clearly visible (Fig. 103). Whereas the leaves of ssp. *haastii* bear a small amount of silky hair only at the base of the petiole where it joins the rhizomes, and are otherwise completely glabrous, ssp. *piliferus* bears hairs, although sparingly, on the foliar surfaces particularly near the insertion of the petiole, and also on the bracts and sepals. Of the two colonies examined only one shows considerable variation.

The scree slopes at Rough Peaks west of Lake Wakatipu where this subspecies was first found by Simpson and Thomson (1926) and which were again visited during this study, are composed of coarser debris than is commonly occupied by the species in north Otago or Canterbury. Simpson and Thomson suggested the term rock slide for this type of slope to compare with shingle slide used for the more familiar type in Canterbury. The lower margin of the rock slide at Rough Peaks lies in a herbfield basin at an altitude of about 5,000 ft, and its slopes begin below the cliffs of a high cirque with a summit at about 6,000 ft. *R. haastii* subsp. *piliferus* occurs quite abundantly on a west-facing scree slope, while scattered colonies of *R. buchananii* occur on ledges and cracks on the sheltered face of the cliffs on the north side of the basin. Interspersed among subsp. *piliferus* on the scree, are plants of a hybrid swarm linking *R. haastii* and *R. buchananii* (p. 120), and these are most numerous in the last 40 yards of the scree slope lying nearest the cliff. As *R. buchananii* regularly bears a rich vestment of silky hairs on its leaves and as subsp. *piliferus* occurs in such close association with *R. buchananii* it is reasonable to attribute the presence of hairs on what is elsewhere a glabrous species to local introgression. However, a separate colony of ssp. *piliferus* on a north-facing slope a mile further westwards along the Rough Peaks Range, shows little variation in hairiness or leaf shape among its members, and contains no plants recognisable as recent hybrids.

It must be concluded that the silky-haired forms of *R. haastii*, whatever their original source, are now widespread in at least the Rough Peaks Range and probably throughout the Eyre Mountains of which Rough Peaks is a small north-eastern extension. Accordingly, subspecific rather than hybrid status has been provided. Its difference from *R. haastii* subsp. *haastii* is possibly associated with an ecotypic adaptation to the "rock slides" of the region. The probability that the differences have an introgressive origin in *R. buchananii* is regarded as very strong.