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The genus *Hebe*

A botanical report

Linda Noack Kristensen
Afdeling for Blomsterdyrkning
DK-5792 Årslev

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Hebe hulkeana

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Chapter 1. Introduction

> “Are the alpine and subalpine flora of New Zealand alpine at all, or are the plants just forced into these conditions by competition?”
>
> Phil Garnock-Jones
> 6 June 1989

The New Zealand flora evolved in isolation from other floras from the split up of the Gondwana Supercontinent about 100 million years ago. The flora is rich in endemic plant species, with relatives in both tropical, subtropical and temperate floras.

Hebe is an example of a large plant genus widely spread throughout New Zealand, although it is also found in two other countries.

In Europe *Hebe* is widely used as garden plants and pot plants, being exotic and valuable. For more than 15 years, the Danish pot plant growers have produced cultivars of *Hebe* as flowering pot plants. The interest for these plants is increasing, and with the genetic variation within the genus more species and varieties could be developed for commercial production in future.

Linda Noack Kristensen
July 1989

Chapter 2. Summary

The genus *Hebe (Scrophulariaceae)* was first separated from the genus *Veronica* in 1926. All taxa, except two, are endemic to New Zealand and outlying islands.

The exact number of taxa is not known at present, and a major taxonomical revision has recently been started by Dr. P. Garnock-Jones, Botany Division, DSIR, Lincoln, New Zealand.

Both the present and the suggestions for new taxa are presented in Appendix 1. The suggested new taxa are based on interviews with Mr. A.P. Druce, Pinehaven, Upper Hutt, New Zealand.

Evolution of the genus is discussed. The most supported theory is that *Hebe* originated in New Zealand after the split of Gondwana. The two species shared with South America and Falkland Islands are suggested to have originated in New Zealand and to have become established else where as a result of long distance dispersal.

The genus is grouped into ten botanical sections. The major features are the presence of a sinus, the structure of the capsule and the type and position of inflorescence.

Within each section, the growth form, habitat and distribution of the taxa vary. *Hebe* taxa are found from alpine to lowland altitudes and in various land forms. The most common land forms are cliff and rock. The distribution of a taxon is often local in "pockets".

The reliability of the present sections, and an alternative separation into groups on the basis of chromosome numbers are discussed.

Very little is known about the physiology of the genus. Growth rate, presence of growth rings and persistence of foliage have been studied for two subalpine species.

Hebe tolerates frost to some extent. Much are yet to be studied in terms of lower and upper temperature tolerance, and optimal temperature for growth, flowering and fruiting.

Studies of the apical meristems indicate that much can be learnt about these structures. The structure of an apical meristem in the section "Paniculatae" is shown to be totally different from anything previously known.

Flowering in *Hebe* occurs all year round in one species or another, and intensity of flowering has been shown to increase with latitudes.

A high degree of gender dimorphism, self-compatibility and self-fertilization is found in *Hebe*. The relationship between these features is discussed. Breeding systems in the genus have not been studied. Pollination is carried out by flies, beetles and native bees.

Hybridization occurs frequently in nature, and the presence of both monoploids, diploids and triploids indicates that taxa have developed and adapted to the changeable New Zealand environment. In culture, hybrids are very common.

Chapter 3. Identification and history of the genus *Hebe*

Hebe Comm. ex Juss., 1789, belongs to the tribe *Veroniceae* of the family *Scrophulariaceae* (Moore in Allan, 1961) and all species except two are endemic to New Zealand and outlying islands (P. Garnock-Jones, pers. comm.).

Hebe is the largest genus of plants in New Zealand in terms of species number. The plants are evergreen shrubs or small trees with opposite leaves. They are found from sea-level to the alpine altitude, and range in height from a few centimetres to 7 meters. Leaf size varies widely. The smallest leaved species occur at the higher altitudes. The flowers are 4-5 lobed, small, mostly born in spikes or racemes. Flower colours range from white to blue, mauve, purple and red.

The history of the genus *Hebe* formerly started in 1926, 63 years ago. The name *Hebe* was suggested a few years earlier. The important botanical papers are:

1921 *Hebe* was regarded as a genus distinct from *Veronica* for the first time by Pennell.

1925 The genus *Veronica* was treated as three "divisions", *Hebe, Pygmea, Euveronica* by Cheeseman. He admitted: "The arrangement and limitation of the species, and the preparation of the necessary diagnoses, has proved to be a most difficult and perplexing task, and I am far from satisfied with the result".

1926 New Zealand species of *Hebe* were taxonomically described for the first time by Cockayne and Allan. They were firmly convinced that: "*Hebe* and other polymorphic genera are separable into definite easily-recognizable groups by the "natural" method of field-taxonomy". They separated 70 species into the new genus. 29 species remained as *Veronica* because of insufficient or faulty evidence.

1928 The diversity of *Hebe* was described by Laing and Blackwell, who wrote: "They (the species) show such an extreme diversity, that it is possible to describe only the chief forms. From a piece of ground a few yards square may sometimes be taken a dozen specimens, all showing differences of shapes and structure, that in another genus would entitle them to varietal, or even specific range".

1961 The last completed revision of *Hebe* was published by Moore in Allan's "Flora of New Zealand. Volume 1".

She wrote: "Perhaps c. 100 species, mostly endemic in New Zealand but two shared with South America and one of them extending to Falkland Islands; a few species in Tasmania, south-east Australia and New Guinea". Moore described 79 species and separated the genus into ten botanical sections. She further described 12 taxa as "Incertae Sedis", 12 as hybrids and 16 as horticultural forms.

Moore stated: "Since the second edition of Cheeseman's Manual (1925) some 26 new taxa have been proposed in N.Z. *Hebe*."

1986 Named and unnamed taxa of the genus *Hebe* are described and painted by Eagle. She noted: "The identification of *Hebe* species is often difficult, especially if plants are not in flower. ... there are about 90 species in New Zealand, (some of these are not yet named)." Sixteen unnamed forms are described out of 122 taxa in total. Of these, 5 taxa are of dubious specific or varietal standing.

The latter reference is the most up to date published version of the diversity in *Hebe* taxa. An extensive taxonomic revision is now being undertaken by P. Garnock-Jones (pers. comm.).

The exact number of species in the genus is not known at present, but suggestions have been made (A.P. Druce pers. comm., P. Garnock-Jones pers. comm.).

I have therefore interviewed the principals, Dr. Phil Garnock-Jones, Botany Division, DSIR, Lincoln, and Mr. Anthony P. Druce, 123 Pinehaven Rd, Pinehaven, Upper Hutt, New Zealand, to achieve the latest views of:

- taxonomical status (though the aim of this report not is taxonomy)
- variation
- habitats and distribution
- physiology

The literature has been studied and mainly references from 1950 and later has been cited, again to achieve newer evidence and avoid taxonomical confusion because of name changes.

3.1 Variation, including worldwide distribution

In New Zealand, *Scrophulariaceae* is represented by 11 genera. They are *Jovellana, Gratiola, Glossostigma, Limosella, Euphrasia, Mimulus, Ourisia, Mazus, Pygmea, Parahebe* and *Hebe*. The three genera listed last are closely related, and *Hebe* contents of the largest number of species. This report concentrates on the genus *Hebe*.

3.1.1 How many species?

The number of species in the *Hebe* genus has varied since the genus was first accepted.

Since 1961, a number of taxa have been investigated. Some are suggested to be new species or new varieties. Some existing species and varieties are suggested to be only forms of other species (van Royen 1972, Eagle 1986, Heads 1987, Druce 1989, P. Garnock-Jones pers. comm.)

In 1972, van Royen suggested to transfer 12 *Hebe* species occurring in the alpine regions of New Guinea to the genus *Parahebe*. Previously the species were assigned to firstly to the genus *Veronica*, later to the genus *Euveronica* and by Pennell (1943) transferred to the genus *Parahebe*. Pennell (1943) described 14 and van Royen (1972) noted that the species number at the moment is 12, but "it is likely that this number will increase with further explorations". van Royen's arguments for recognizing the

New Guinea *Hebe* genus as *Parahebe* are based on leaf margin, capsule and chromosome number differences, but he was also aware of numerous similarities like axillary inflorescences, growth form and woody appearance.

The number of Australian *Hebe* species is noted to be "Possible 6 endemic species, mainly at higher elevations in Australia and Tasmania (Burbridge 1963, Beadle et al. 1982). The Australian and Tasmanian species of *Hebe* are now thought to belong to the genus *Parahebe* (P. Garnock-Jones pers. comm.).

The two species shared with South America are well accepted to be species of *Hebe.*

Heads (1987) has considered *Leonohebe* to be a genus separate from *Hebe*, but no evidence has been given for the separation. Therefore, I retain the name *Hebe* for species considered by Heads to be *Leonohebe.*

In Appendix 1, the present taxa in the genus *Hebe* are presented. Furthermore, the taxa thought to get species or variety status are presented. The number of taxa in Appendix 1 is 113, of which 98 is considered to be species (Druce 1989).

3.1.2. Worldwide distribution

According to Garnock-Jones (1976), the following species of *Hebe* are found on islands in the Pacific Ocean and the Tasmanian Sea: *H. insularis, H. elliptica, H. salicifolia, H. macrocarpa var. latisepala, H. breviracemosa, H. bollonsii, H. dieffenbachii, H. barkeri, H. chatamica, H. rapensis, H. odora* and *H. benthamii.*

The two species shared with Chile in South America are *H. elliptica* and *H. salicifolia,* while the one shared with the Falkland Islands is *H. elliptica* (Garnock-Jones 1976).

The worldwide distribution of *Hebe* species, excluding specification of the New Zealand mainland distribution, is illustrated in Fig. 3.1.

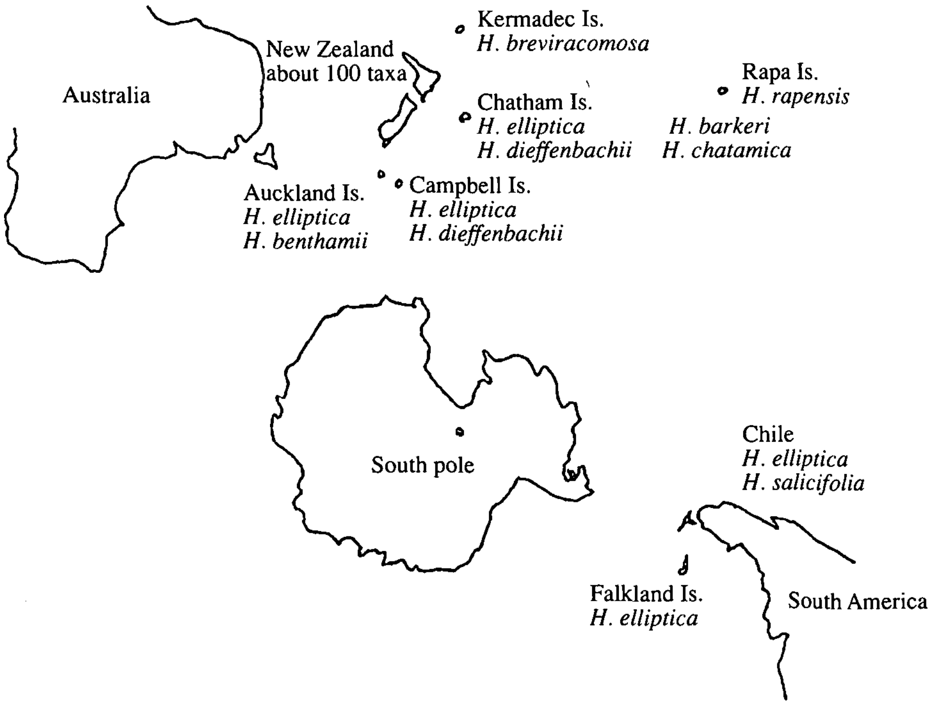


Fig. 3.1. Worldwide distribution of species in the genus Hebe. *(Modified after Allan 1961 and Garnock-Jones 1976).*

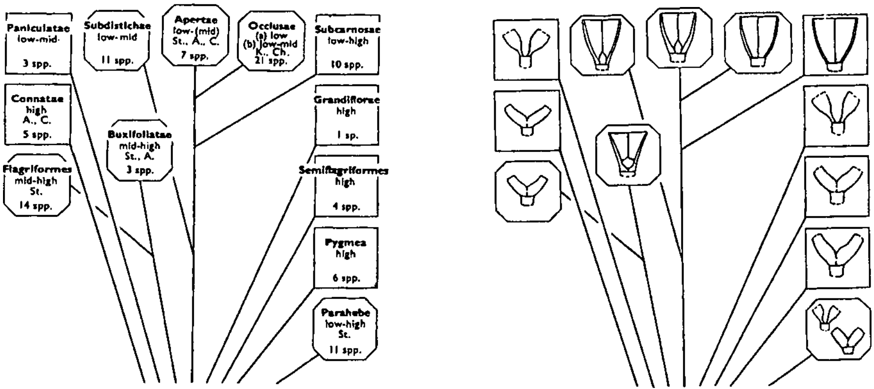
3.2. Classifications and sections, morphological variation and chromosome numbers

Moore (Allan 1961) classified 79 New Zealand *Hebe* species in ten sections, mainly by differences in sinus size and form, inflorescence type and position and by differences in growth form.

Moore (1967) pointed out the differences of the sections within *Hebe* and the relations to the genera *Parahebe* and *Pygmea* (now *Chionohebe*) in four drawings. They illustrate distribution, base of leaf bud (sinus), capsule in traverse section and position and type of inflorescence (Fig. 3.2).

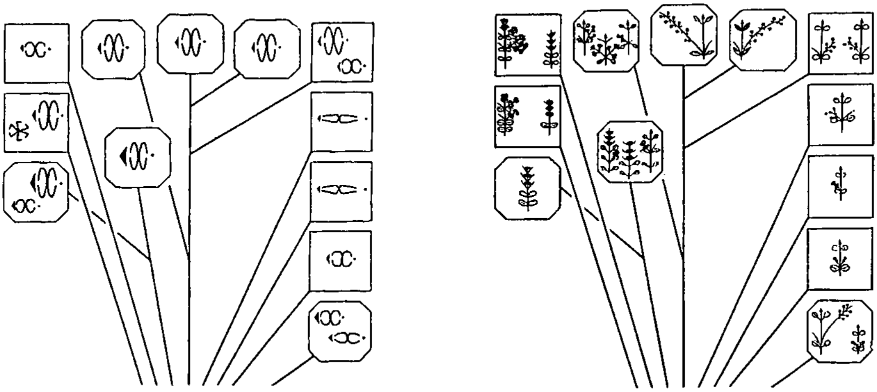
The ten sections are widely accepted, though Metcalf (1987) uses only nine sections.

Morphological characteristics of the ten sections, the species and the chromosome numbers of the species, as published by Hair (1967), (Appendix 1) show large variation from large-leaved lowland taxa in sections "Apertae" and "Occlusae" to taxa with miniature leaves and whipcord-like branches in section "Flagriformes". Also within the sections, large variation in habit and leaf shapes are found. One of the main criteria for separating the sections is the presence and shape of a sinus (Fig. 3.2). The stability of this feature is now coming into doubt (A. P. Druce pers. comm., P. Garnock-Jones pers. comm.), for example A. P. Druce (pers. comm.) found both presence and absent of a sinus in popu-



1: *Hebe* groups, *Pygmea* and *Parahebe*: Names, distributions, numbers of species.

2: *Hebe* groups, *Pygmea* and *Parahebe*: Bases of leaf buds.



3: *Hebe* goups, *Pygmea* and *Parahebe*: Capsules in transverse section.

4: *Hebe* groups, *Pygmea* and *Parahebe*: Inflorescences - position and types.

Fig. 3.2. Botanical sections of the genera Hebe, Parahebe *and* Pygmea *(now* Chionohebe*) as illustrated by Moore (1967).*

lations of *H. stricta, H. corriganii* and *H. glaucophylla.*

3.3. Evolution from Gondwana or long distance dispersal?

Did the genus *Hebe* exist before the enormous land masses of Gondwana split up about 100 million years ago? (See Appendix 2).

Or did ancestors of *Hebe* originate in New Zealand?

Skipworth (1974) suggested that the genus *Hebe* originated during the fragmentation of the Gondwana Supercontinent (see Fig.3.3).

How the two species shared with Chile and the Falkland Islands were spread is not known. But they are believed to have originated in New Zealand and have dispersed from there.

Ways of long distance dispersal are:

- Seed floating in water. Weight, size, form, persistence of seed surface and viability of seed after floating should be evaluated. Seeds of *Hebe salicifolia* and *Hebe elliptica* showed to be viable after nearly two years storage at room temperature, other *Hebe* species to survive even longer (Simpson 1976).
- Seed carrying in wind. Weight, size, form of the seed are of importance. Seeds of *H. salicifolia* and *H. elliptica* were up to 10 times lighter than seeds from other *Hebe* species studied by Simpson (1976).
- Seed hidden in mud on birds feet. Weight, size and form matters, and the smaller and lighter the seed the more easily can the seed be transported this way. Kennedy (1978) noted that broad-billed prions and diving petrels construct burrows among plants of *Hebe elliptica* on North Island, Foveaux Strait, and in this way seed might have been carried.

Time for dispersal from one location to another as well as where the seed lands, the climate, the competition with the local vegetation, the risk of the first plant(s) to being eaten by animals or insects are all important factors involved in the survival of the first plants which become established not only millions of years ago, but also in recent times in nature. For a plant to become successfully estab-lished and grow to maturity, the climate should be similar to the original centre of dispersal, the competition from local plants and plant communities and damage from animals, insects and pathogens should be marginal. It therefore seems probable that *Hebe* seeds were spread by birds, perhaps colonies of birds drifted with a western wind all carrying mud on their feet from their last rest on the coast of New Zealand.

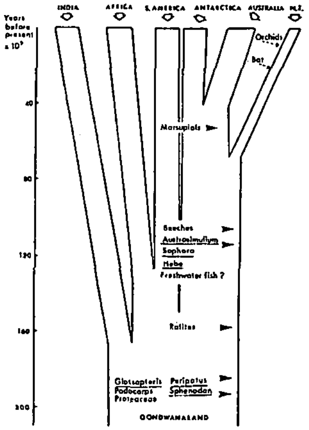


Fig. 3.3. Possible times of arrival in Australasia of some well known taxa, in relation to the fragmentation of the Gondwana Supercontinent (After Skipworth 1974).

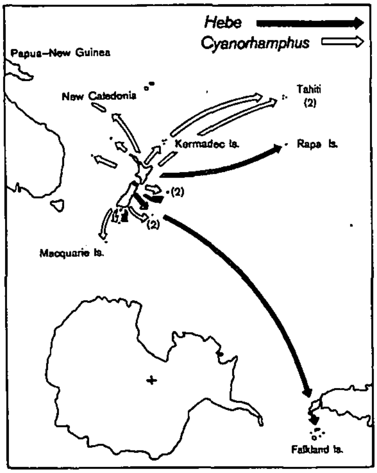


Fig. 3.4. Distribution of the New Zealand parakeet, Cyanorhamphus, *and* Hebe *(Modified after Fleming 1976).*

Fleming (1976) regards the New Zealand *Hebe* species as showing every indication of active evolution, high variability, and of incomplete speciation. Therefore he implies the occurrence of two indistinguishable derivative populations in South America as being of a geological recent date of colonization. Seeds caked to the feet or feathers of seabirds is suggested by Fleming (1976), Godley (1967) and Falla (1960), and two beetle genera, *Kenodactylus* and *Oopterus*, show a zoological parallel by having migrated transoceanically from New Zealand to Falkland, Kuerguelen and South Georgia islands. A New Zealand parakeet, *Cyanorhamphus,* is represented (or was formerly) on all offshore islands as *Hebe* species (Fig. 3.4). This can explain how *Hebe* species were dispersed to offshore islands, but not the dispersion to South America.

P. Garnock-Jones (pers. comm.) supports the theory of long distance dispersal of the two *Hebe* species in South America:

"Until the phylogeny is understood we can only guess, but I suspect *Hebe* evolved after the break up of Gondwana and that *H. elliptica* and *H. salicifolia* in South America result from long distance dispersal. They are unlikely to be the oldest species as they have many derived character states".

A "west wind drift" has been shown to have influenced the distribution of echinoderms (sea stars, sea eggs) in southern latitudes. Effects of the "west wind drift" are illustrated in Fig. 3.5. An indication of the time it takes for distribution in the "west wind drift" was investigated by sending up a big weather balloon in Christchurch. It took the balloon just over five days to get to reach South America, and as the

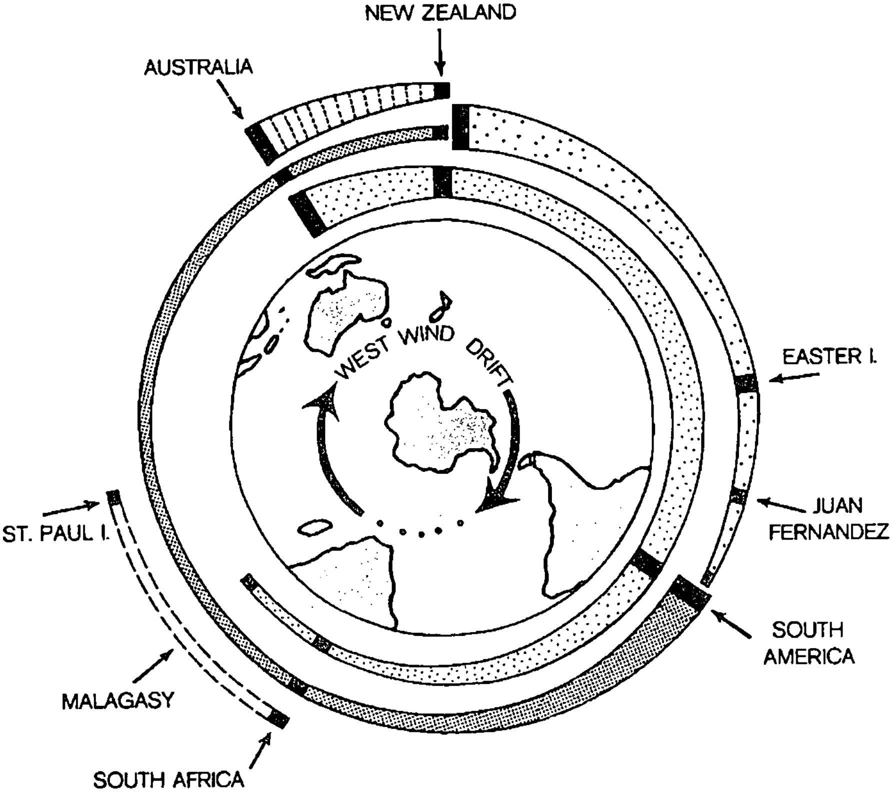


Fig. 3.5. The "west wind drift" as it has influenced the distribution of echinoderms in southern latitudes. The thicker the bars, the more species have been spread. (After Stevens 1985).

balloon circled it reached land again and again for 102 days (Stevens 1985).

Ancestors of the Southern Hemisphere Beech, *Nothofagus*, are found by fossil records to have been distributed in large areas of the Gondwana Supercontinent. Similar evidence of ancestors of *Hebe* has not been found, and therefore we are only able to put up a question mark on the map showing distribution of *Hebe* for example 100 million years ago (Fig. 3.6).

The phylogenetic relations of the *Hebe* genus have been suggested by Moore (1967) (Fig. 3.2) but P. Garnock-Jones (pers. comm.) has recent ideas of the phylogeny, and will be testing them in his present work concerning updating and renewing the taxonomy of the genus. These studies will hopefully lend support for one of the evolution theories.

Chapter 4. Habitat and distribution within the New Zealand Botanical Region

Description of habitat is subdivided into:

- altitudinal zones
- land forms
- hydrology
- growth forms
- plant heights

Distribution is shown on New Zealand maps ordered on the basis of:

- chromosome numbers
- botanical sections

The characteristics on habitat and distribution of 113 *Hebe* taxa are given in Appendix 1.

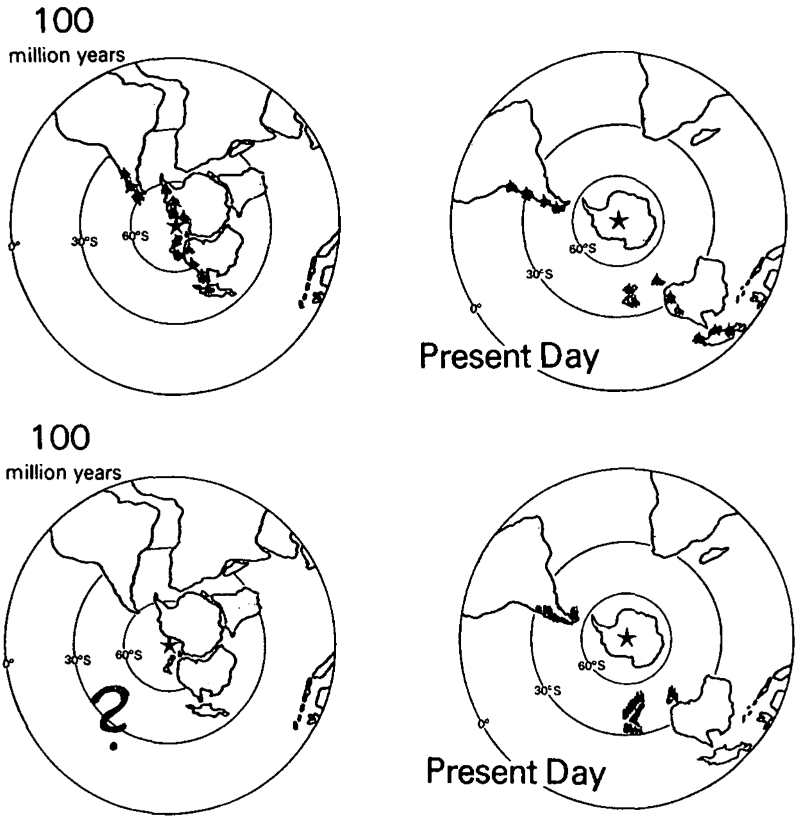


Fig. 3.6. Probably distribution and dispersal of southern beech, Nothofagus sp., *and* Hebe. *Present day distribution is compared with Middle Cretaceous, approximately 100 million years ago during the split of Gondwana. (Modified after Stevens 1985 and Poole 1987).*

4.1. Habitat, growth form and flowering

In the genus *Hebe*, a woody appearance is general, and the plants grow into decumbent forms, taller shrubs or small trees.

Habitats vary from alpine to subalpine, montane and lowland altitudes (Fig. 4.1).

Further, habitats can be categorized into wet and dry positions (hydrology) and into forest, forest margin, scrub, tussock, rock, cliff, maritime cliff, calcareous cliff and bog (land forms) (Fig. 4.2).

Growth form and plant height is also described (A.P. Druce pers. comm., Eagle 1986). In the following descriptions, these characteristics are used to show the different habitats, Appendix 1.

The distribution of taxa in the altitudinal zones is very even (Fig. 4.3).

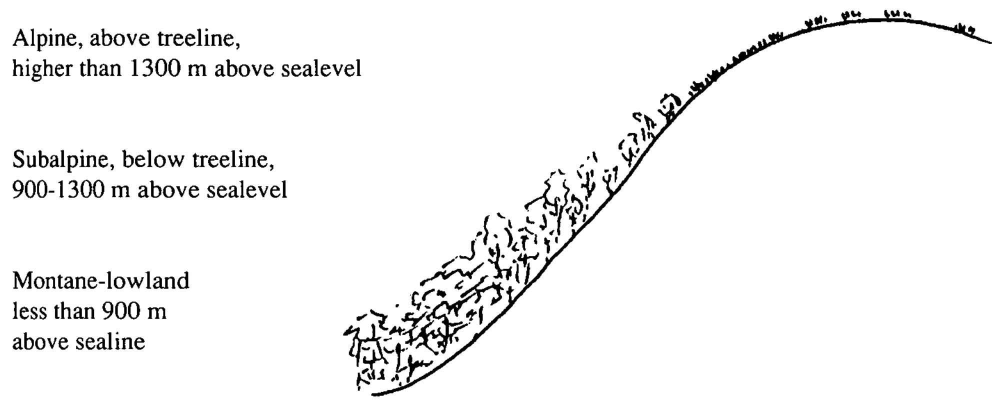


Fig. 4.1. Definition of altitudinal zones describing distribution of taxa in the Hebe *genus. (Modified after Moore 1967).*

Hydrology:	
WET	600 mm precipitation per year, western side and top of mountains and ranges.
DRY	less than 600 mm precipitation per year, eastern side of mountains and ranges.
Landform:	
FOREST	tree and shrub cover more than 80%,
CLIFF	steep rock trees > shrub
FOREST MARGIN	borders, openings
MARITIME CLIFF	coastal cliff
SCRUB	shrub and tree cover more than 80%,
CALCAREOUS CLIFF	cliff primarily of shrub > trees limestone
TUSSOCK	tussock covers 20-100%
BOG	bog and swamp
ROCK	open sites above treeline or where forest has been destroyed; rock-, boulder-, stone-, gravel- and sandfields

Fig. 4.2. Definition of hydrology and land forms used for description of habitat for taxa in the Hebe *genus. After A.P. Druce (pers. comm.).*

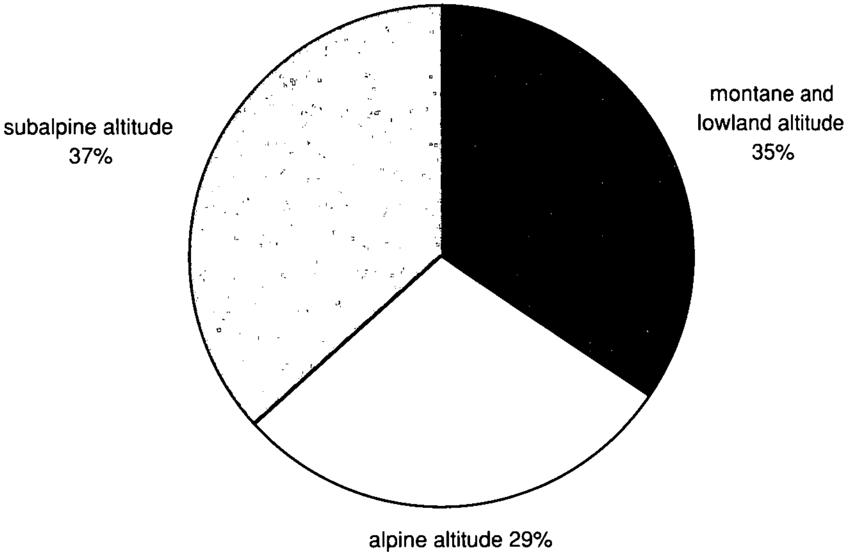


Fig. 4.3. Distribution of Hebe *taxa in altitudinal zones. For details, see Appendix 1.*

A majority of taxa (44%) are 50-200 cm tall shrubs (Fig. 4.4). The next largest growth form (expressed as plant height) is 0-50 cm and 200-400 cm shrubs with 26% taxa in each group. The least common growth form is 400-700 cm trees with only four taxa.

The taxa endemic to the outlying islands are included in this large group of compact, low growing taxa between 50 and 200 cm height. The climate of the islands is temperate to subantarctic, and must have favoured development of low growing shrubs as did the climate in the higher altitudes of the main land.

The growth form of four alpine and subalpine species was studied in an experiment in controlled environment rooms. The growth form persisted well under high temperatures (25/19°C, day/night) for the alpine and subalpine taxa *H. topiaria, H. venustula* and *H. macrantha.* In contrast, *H. cupressoides* seemed to change growth form from an adult (much-reduced "whipcord" leaves) to a softwood growth similar to the juvenile growth (small leaves) (Kristensen, Warrington and Plummer 1989, unpublished). Species of the botanical section "Flagriformes" (where *H. cupressoides* belongs) were investigated and described in 1899 by Cockayne. A juvenile and adult stage were found to be typical for the species. Resemblance were not noticed by Cockayne. Further studies in *Hebe* on temperature, growth forms and plant maturity would give indication on adaptability and flexibility to the different New Zealand land forms.

Fig. 4.5 shows the distribution of taxa in nine land zones, as defined by A.P. Druce (pers. comm.). A majority of taxa (29%) are restricted to the rocky land zone, while 23% are typical on the different types of cliff and 17% grow in tussock.

Summarized, this shows that 69% of the described *Hebe* taxa are to be found in rock, tussock and cliff land zones, in all of which harsh exposed and low temperature conditions are typical. Only 14% of the taxa are competitive and adapted to the sheltered growing conditions as in forest and forest margin.

Distribution of monthly flowering (Fig.4.6) shows a significantly large number of taxa (45-52) in flower in December - February. But right throughout the year at least 8 taxa are to be found flowering in their natural habitat.

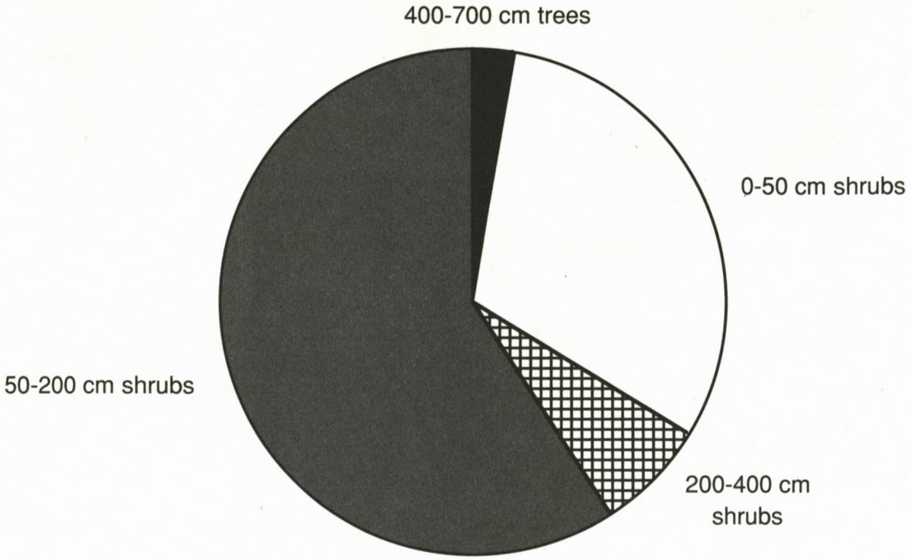


Fig. 4.4. Distribution of growth forms, expressed as plant heights, in the genus Hebe. *For details, see Appendix 1.*

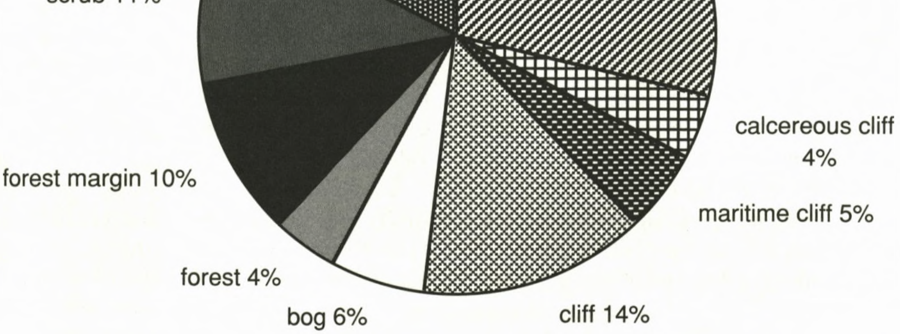


Fig 4.5. Distribution of Hebe *taxa in New Zealand land zones. For details, see Appendix 1.*

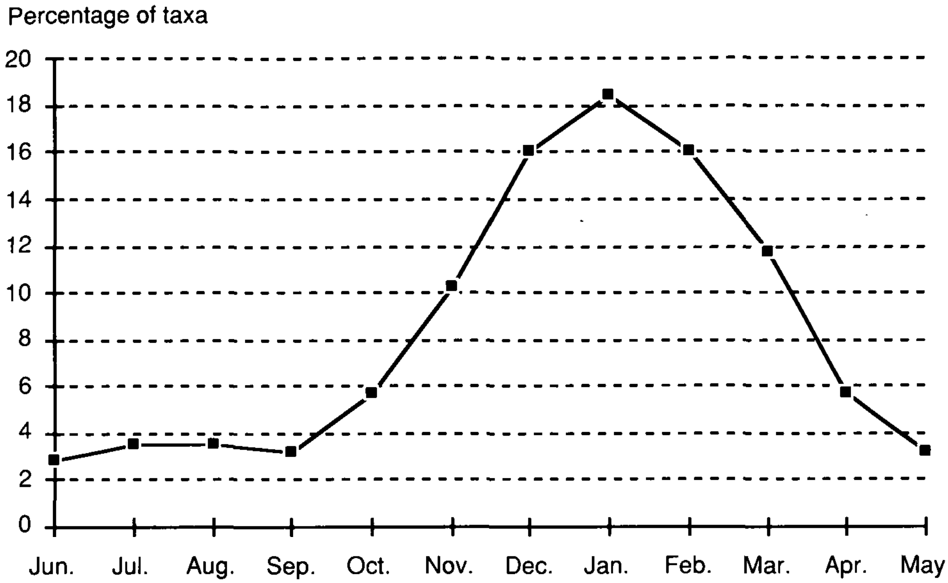


Fig. 4.6. Distribution of monthly flowering in the genus Hebe *in the natural habitats. (Modified after Moore (Allan 1961).*

4.1.1. Alpine

According to Druce (pers. comm., Appendix 1) 29% of the *Hebe* taxa are distributed in the alpine zone.

The alpine altitude is characterized by being above the tree line, open, exposed, harsh and mostly wet. Specialized low growing and cold tolerant genotypes are common in the alpine zone.

Most alpine taxa are also found at the subalpine altitude, but all taxa except two in the section "Connatae", one taxa in section "Subcarnosae" and three species in section "Subdisticae" are strictly alpine. Four species are very flexible, and are found right from the alpine to the lowland zone.

Of the extreme alpine taxa, the average plant height is 0.35 cm and the typical land form is rock. Of the flexible taxa, the average plant height is 1.5 m and typical land form rock and cliff.

A high proportion (24%) of the alpine taxa are monoploids, n=20 and n=21, while very few are diploids and triploids (Fig. 4.7). The typical altitudinal distribution of polyploid and monoploid plant species in the world would be more poly-ploids in higher altitudes (P. Garnock-Jones pers. comm.). The *Hebe* genus does not follow this pattern. Therefore this feature would be of value for further studies.

The time for flowering in the alpine zone is significantly seasonal. Data from Moore (in Allan 1961) show that at least three months of the year are without any alpine taxa flowering (Fig. 4.8). The distinct flowering season is probably even shorter, because Moore's data on flowering are arrived from herbarium specimens (P. Garnock-Jones pers. comm.). Field studies of peak flowering will be valuable.

Leafs are often extremely small, thick, waxy and fleshy. A majority of the "whipcord hebes" (section Flagriformes and Semiflagriformes) belongs to the alpine category. As an example of an alpine decumbent species, the form and variation in leaf shapes of *H. buchananii* is illustrated in Fig. 4.9a. Leaves of a taller alpine shrub, *H. pinguifolia*, are shown in Fig. 4.9b.

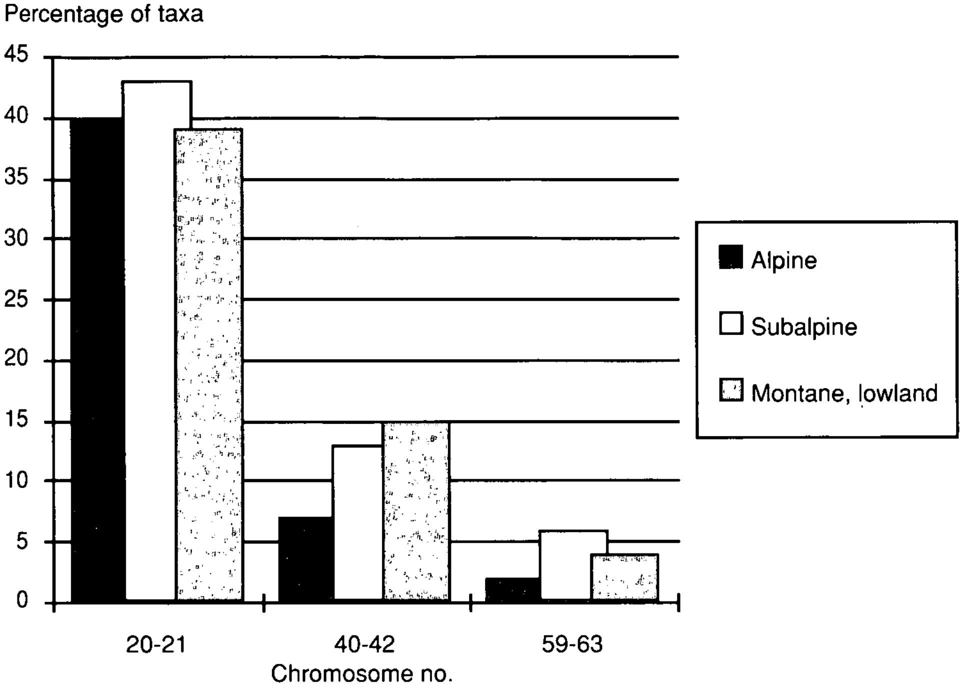


Fig. 4.7. Distribution of Hebe *taxa in monoploids (n=20 and n=21), diploids (n=40 and n=42) and triploids (n=59, n=60, n=61, n=62 and n=63) and altitudinal zones. For details, see Appendix 1.*

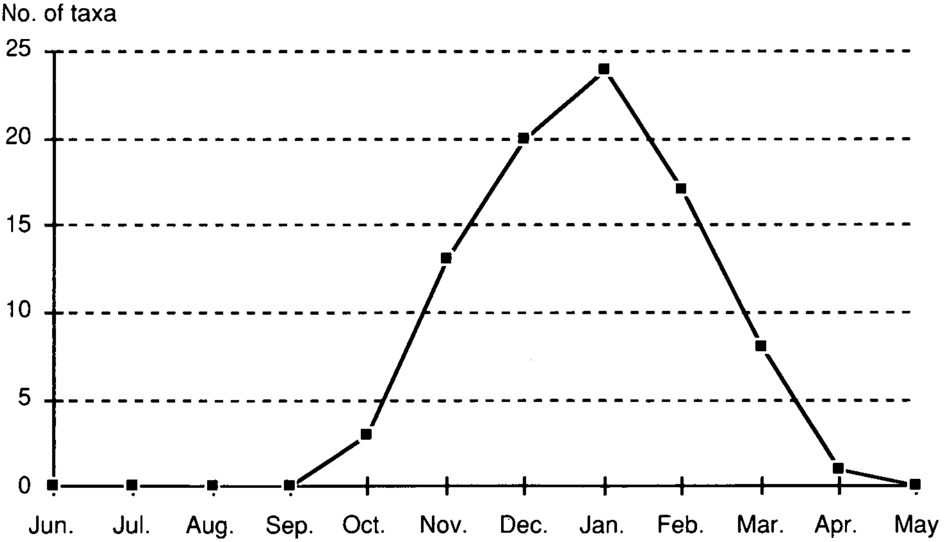


Fig. 4.8. Distribution of monthly flowering in alpine Hebe *taxa. (Modified after Moore (Allan 1961)).*

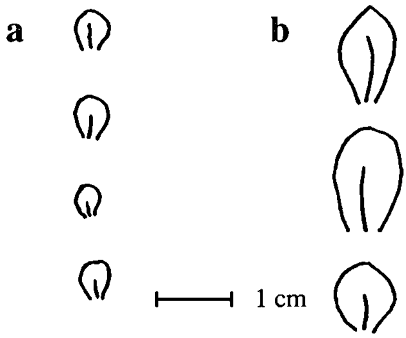


Fig. 4.9. Variation of mature leaf shape and size within a population of a) Hebe buchananii *collected at Old Man Range, Otago, South Island on 7 January 1989. b)* H. pinguifolia *collected at Mt. Hutt, Canterbury, South Island on 11 January 1989. Each leaf represents one plant.*

4.1.2. Subalpine

Hebe is most commonly found in a subalpine habitat: 37% of taxa described by A.P. Druce (pers. comm., Appendix 1) grow in this zone.

The subalpine habitat is characterized by being below the tree line, typically at 900 to 1300 m altitude. The land forms vary from forest to bog, tussock and rock (Fig. 4.1 and Fig. 4.2). Both wet and dry positions are found.

A majority of subalpine *Hebe* taxa also grow in the alpine zone (56%) or the montane-lowland zone (20%). The plant height varies from 0.2 m to 3 m, and the average height is 1 to 1.5 m.

Subalpine monoploids account for more than 25% of the total number of taxa; diploids and triploids are represented by 10% in the subalpine zone (Fig. 4.7).

The size and shape of leaves is larger than for alpine taxa. It varies from 1 to 5 cm. Examples of mature leaves from *H. albicans* and *H. rakaiensis* show that size and shape variation within a population of a species is large (Fig. 4.10a and 4.10b).

Flowering time is seasonal, and distributed over almost exactly the same range of time as the alpine taxa, Fig. 4.11. It must be remembered that the representage of alpine taxa in the subalpine habitat is more than 50%. Again, field studies of the peak flowering time would probably result in a more narrow distribution curve around December-January.

For alpine and subalpine taxa, an extension in open exposed areas is typical. Scott (1977) has analysed plant frequency and site factors of species growing above the timber line on Mt Ruapehu in the North Island. He found, that *H. tetragona* grew with a high frequency in sites with high solar radiation and high available soil potassium. Also soil depth to rock seemed to have an influence on frequency, as 100-200cm soil sites had the highest frequency.

An extreme tolerance of minerals can also be found within the categories of the alpine and subalpine zones. Lyon et al. (1971) found that *H. odora* in an extremely high mineral site, Dun Mountain Mineral Belt, South Island, uses a mechanism to exclude chromium from uptake, a mechanism that is opposite correlated to a high magnesium uptake. Lee et al. (1975) support this statement, and conclude that the competition between species becomes stronger in soils with lower magnesium content where *H. odora* is also to be found.

4.1.3. Forest and lowland

Forest, forest margins (up to the tree line), lowland and coastal positions are given a separate category, as the areas are less exposed than alpine and subalpine positions. Many coastal and maritime taxa, for example taxa endemic to outlying islands are found in the montane and lowland zone. A.P. Druce (pers. comm., Appendix 1) states that 35% of the *Hebe* taxa belong in the montane to lowland zone. Of these, 16% are endemic to the outlying islands (Fig. 3.1).

Plant height varies from decumbent 0.2 m shrubs to small trees up to 7 m tall. A majority of taxa grow into 2-4 m tall shrubs. Leaf size varies from approximately 1 cm to 15 cm in length, with the leaves being mostly 8-12 cm long.

Flowering occurs all year round, but with a majority flowering in January and February (Fig. 4.12). The taxa described to flower in winter might well be odd examples collected and included as herbarium specimens which are used for the describtion of flowering time (P. Garnock-Jones pers. comm.). Flowering occurs all year for taxa endemic

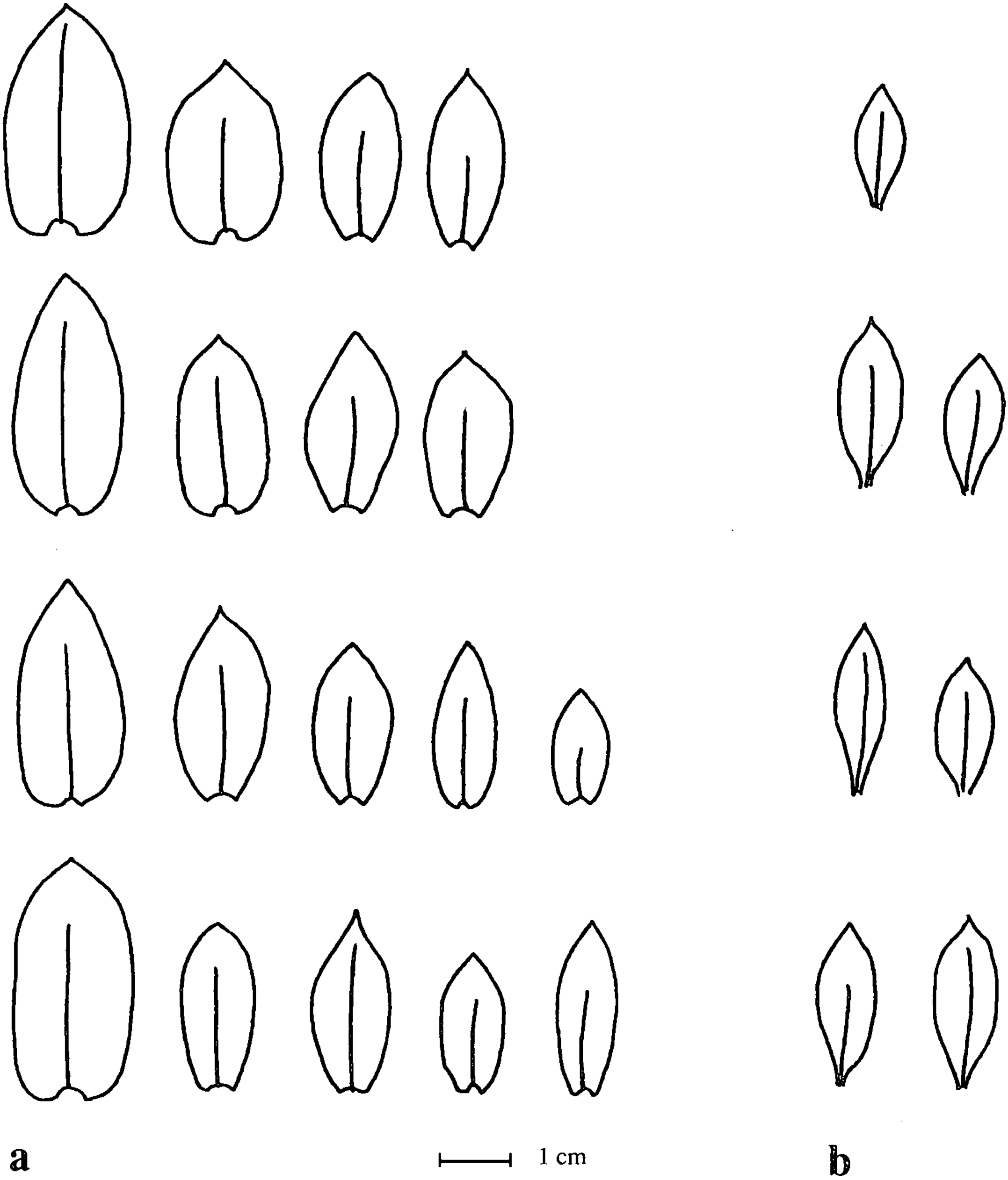


Fig. 4.10. Variation of mature leaf shape and size within a population of a) Hebe albicans *collected in Cobb Valley, North West Nelson, South Island on 27 December 1988. b)* H. rakaiensis *collected at Mt. Hutt, Canterbury, South Island on 11 January 1989. Each leaf represents one plant.*

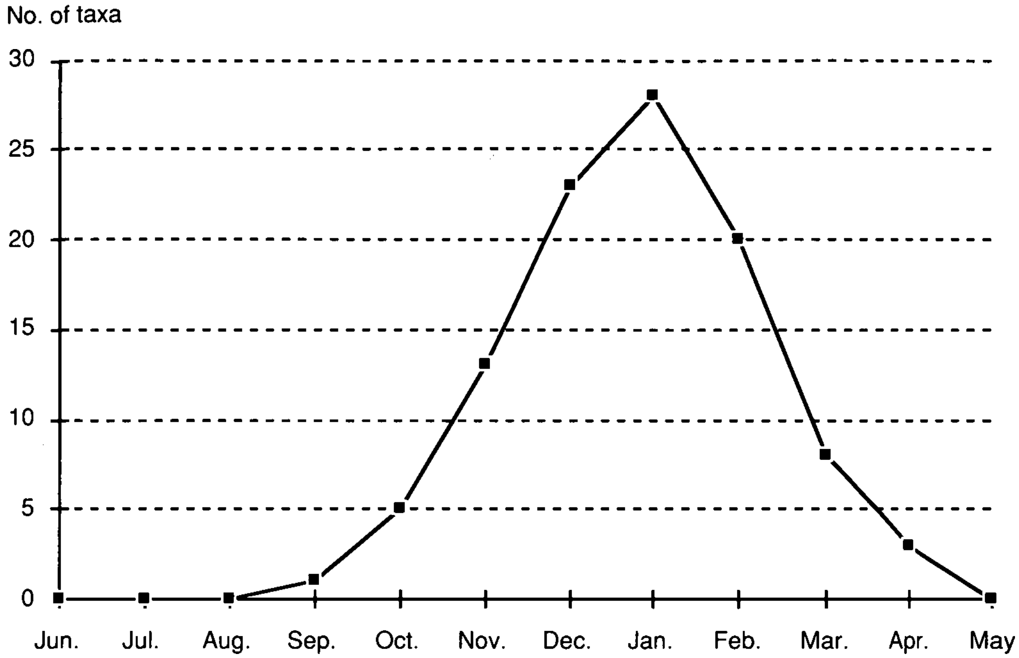


Fig. 4.11. Distribution of monthly flowering in subalpine Hebe *taxa. (Modified after Moore (Allan 1961)).*

to the outlying islands, with a slight peak in November and December. Further studies in the field would probably provide better data.

4.2. Distribution in words and maps

The genus is confined to the Southern Hemisphere temperate zone. On the New Zealand mainland and the outlying islands various *Hebe* species have adapted to the local edaphic and climatic conditions and have reached relative stability with other vegetation.

Recent disruption of the vegetation cover mainly in the last century caused dramatic changes in climate and habitat distribution.

When the Europeans in last century burned of scrub and forest to establish farmland, the native vegetation was either destroyed or remained in remnant pockets. Further, the introduction of plants and animals has changed conditions for the native vegetation (see Appendix 2).

Some taxa of *Hebe* described by early European botanists have for years been unknown in their original areas. For example, *H. matthewsii* is noted by Moore (Allan 1961) being "best known from garden plants and specimens labelled as from Humboldts Mts, all apparently from one collecting". A single plant of *H. matthewsii* has been rediscovered a few months ago by A.P. Druce in the Nelson Mountains (pers. comm.).

Latitudinal distribution of *Hebe* taxa as listed and mapped in Appendix 1, show that 70% of the taxa are found in the South Island, and 30% in the North Island of New Zealand.

Most taxa are restricted to either of the two main islands or Stewart Island, but 8 taxa are distributed on both. Further, seven taxa in section "Flagriformes" are considered to be one species, *H. tetragona*, with a wide latitudinal distribution and a further three taxa are considered to be one species, *H. lycopodioides* (A.P. Druce pers. comm., see Appen-

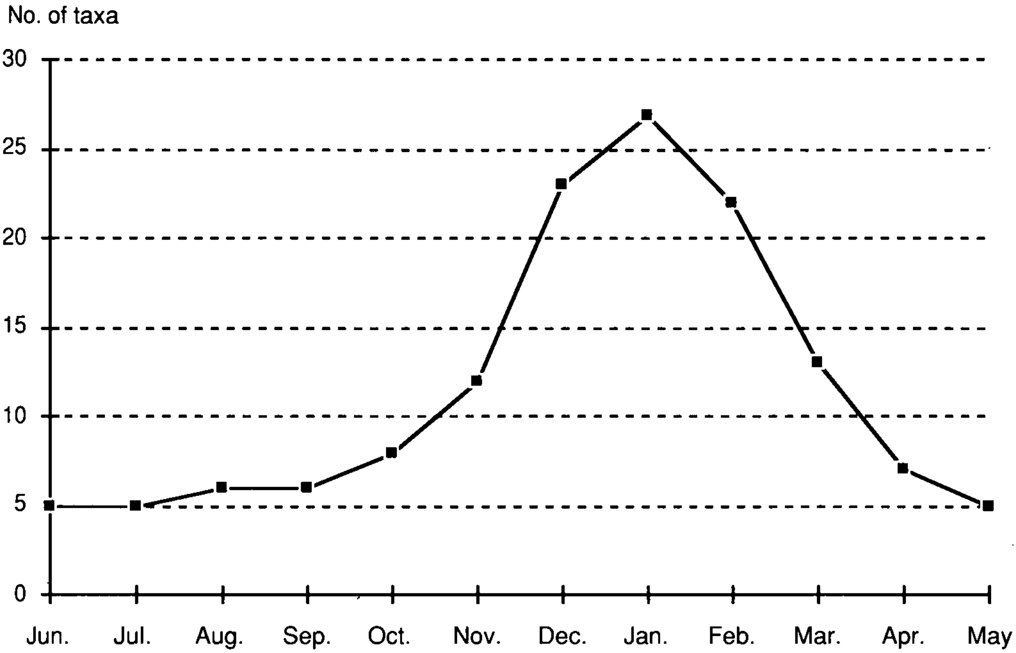


Fig. 4.12. Distribution of monthly flowering in montane and lowland Hebe *taxa. (Modified after Moore (Allan 1961)).*

dix 1). If this becomes true in Garnock-Jones' taxonomical revision, the species of "Flagriformes" will be widely spread along the alpine and subalpine areas of both main islands.

The area where most *Hebe* taxa are distributed is the Northern third of the South Island, with 48% of the taxa being found. The area with the fewest is the Rotorua - Bay of Plenty region with only two taxa (2%).

The geological changes in New Zealand (Appendix 2) has probably meant a limited distribution of taxa and spreading has become rare as the plants have evolved in pockets surrounded by ecological barriers.

4.3. New views

Traditionally, taxa in the genus *Hebe* have been treated as stable and constant. Especially, when plantspeople/botanists from the Northern Hemisphere are evaluating a plant genus, they would like the characteristics of a taxa to be stable and constant. These expections confused me for a while, being one from the Northern Hemisphere.

4.3.1. A stable or still developing genus

The fact that the exact number of species in the genus *Hebe* is not known until a major revision the taxonomy has taken place, and that the number of species and hybrids has fluctuated up and down since the genus was first established in 1926 (see Chapter 3) gives evidence for a plant genus still in the course of developing in a changing environment. The most up to date version of taxa (Appendix 1) compared with the number described by Moore (Allan 1961) indicates that as many as 19 new species are suggested including a few suggested to lose status as species. This fact should be seen both in the light of a still developing genus, but also in the light of a genus being endemic to a country where the first botanical observations were made only 220 years ago. . Since Dr. Daniel Solander on Captain James Cook's first voyage to New Zealand from Britain in 1769, the whole flora has been studied closely, but a lot still remains to be done (H.A. Outred pers. comm.).

4.3.2. Botanical sections - a slender or firm foundation

The major characteristics that have been used to separate *Hebe* taxa into botanical sections are sinus, capsule and type and position of inflorescence (Moore 1967) (Fig. 3.2). Since this publication, chromosome numbers have been counted for most taxa (Hair 1967), and it is found that the chromosome numbers vary widely within sections of especially "Subdisticae", "Occlusae", "Buxifoliatae" and "Flagriformes" (Hair 1967 and A.P. Druce pers. comm., Appendix 1).

The distribution of taxa in the botanical sections shows that "Occlusae" and "Flagriformes" are the largest sections (Fig. 4.14). It should be remembered that the suggestion from A.P. Druce to reduce eleven present taxa into two species would decrease the number of taxa in "Flagriformes" dramatically.

The relationship between number of *Hebe* taxa and various land forms indicates that the first four sections are found widely while the last six sections include taxa growing at distinct land forms (Table 4.1). This suggests that the separation of taxa in the last 6 sections is more reliable than the first four. But further evidence should be gathered before any changes are made.

The altitudinal zones in comparison with the botanical sections (Fig. 4.15) again show large variation. At least two zones are represented in nine of the ten sections. Only the taxa in "Apertae" are restricted to the montane and lowland zone.

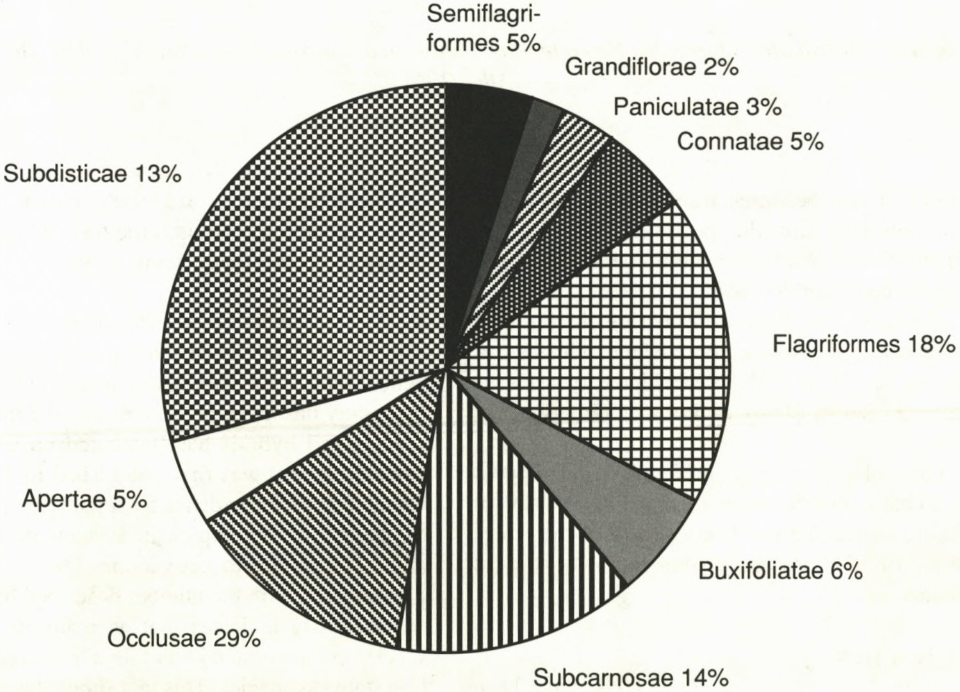


Fig. 4.14. Distribution of Hebe *taxa in Moore's botanical sections. For details, see Appendix 1.*

Table 4.1. Distribution of landforms in the botanical sections of the *Hebe* genus. For further details on species and land forms, see appendix 1.

Botanical section	No. of taxa	Land form Forest	Forest margin	Scrub	Tussock	Rock	Cliff	Maritime cliff	Calcare-ous cliff	Bog
Subdisticae	15	1	4	0	4	7	3	1	1	0
Apertae	7	0	3	0	0	1	2	2	1	0
Occlusae	36	5	8	11	2	9	9	4	1	0
Subcarnosae	13	0	0	0	0	12	6	0	1	1
Buxifoliatae	6	0	0	2	5	0	0	0	0	5
Flagriformes	17	0	0	2	12	1	0	0	0	3
Connatae	8	0	0	0	0	8	0	0	0	0
Paniculatae	5	0	0	0	0	3	1	0	1	0
Grandiflorae	2	0	0	2	2	0	0	0	0	0
Semiflagriformes	4	0	0	0	0	4	0	0	0	0
Summarized no. of taxa	113	6	15	17	25	45	21	7	5	8
per cent taxa	100*	4.0	10.1	11.4	16.8	30.2	14.1	4.7	3.4	5.3

*) 100% = 149 representative taxa in the *Hebe* genus

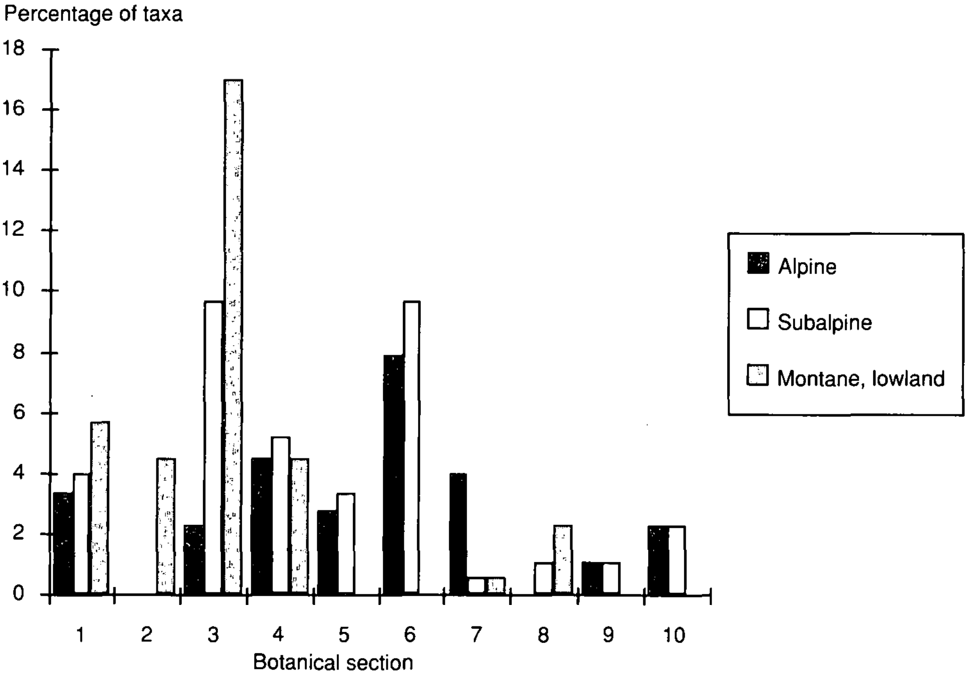


Fig. 4.15. Distribution of Hebe *taxa in botanical sections and altitudinal zones. The botanical sections are numbered in the same order as listed in Appendix 1.*

Another way of making sections could be on the basis of chromosome number or pollen characteristics. Comparing the relationship between altitudinal zones and chromosome number groups (Fig. 4.7), however indicates little distinction. The same conclusion can be made when comparing land zones and chromosome number groups (Fig. 4.16). The major land forms on which the monoploids grow are rock and cliff, while the major land forms for the triploids are scrub and forest. But again, no clear grouping can be made.

Pollen characteristics are as well as the chromosome number of a species, more stable than for example presence of a sinus or type of inflorescence. In the Southern Hemisphere genus *Nothofagus*, pollen characteristics are used to separate the taxa into sections of similar status (Poole 1987). Studies of pollen in the genus *Hebe* show that the pollen grain is very small and the only distinctive character is the sculture of exine. Further more detailed studies might provide more information.

In conclusion, taxa of the genus *Hebe* can be found right throughout the New Zealand mainland and the outlying islands. A large proportion are positioned on rock and cliff and at higher altitudes. The growth form varies from decumbent shrubs to rounded shrubs and small trees. The growth form of alpine and subalpine species tested in an artificial warm environment (25/19°C, day/night) was the same as the natural cool environment.

One of the questions to ask is: - are the alpine and subalpine flora of New Zealand alpine at all, or are the plants just forced into these conditions by competition? (P. Garnock-Jones pers. comm.).

The botanical sections are created to give an indication of the phylogeny, but are weak in the stability of the key characters, sinus, capsule and inflorescence. Nine chromosome numbers are present in the genus and they vary from n=20 to n=63, a fact that indicates natural hybridization. If chromosome numbers should be used for separating the *Hebe* taxa into sections, a wide range of altitudinal, latitudinal and land forms should still be tolerated within the sections. This might though be more correct in terms of evolution than using morphological characteristics. The reason is that morphologically different species adapted to similar environments and with the same chromosome numbers and pollen grain structures can develop more than once over time. Therefore, the most constant diagnostic features to separate groups are chromosome numbers and pollen grain structure. It should also be noted that all data presented treat taxa as individuals, whereas they are linked in the evolution.

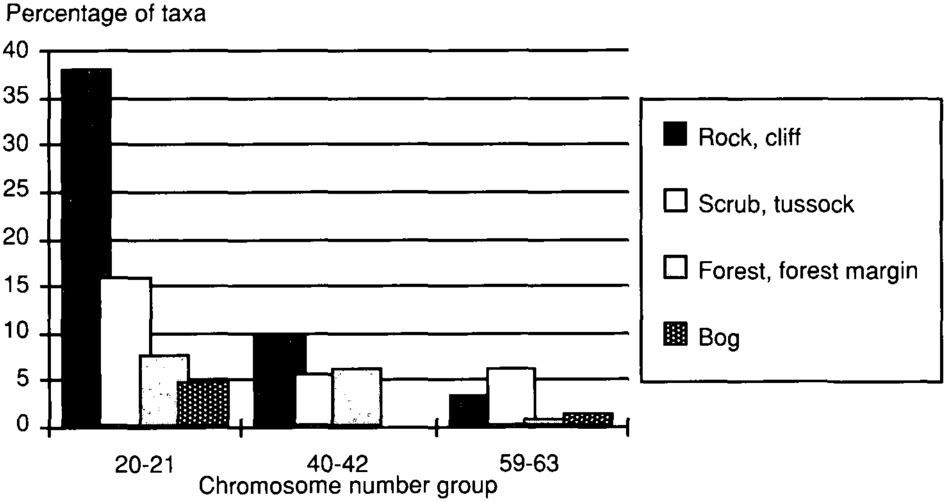


Fig. 4.16. Distribution of Hebe *taxa in monoploids (n=20 and n=21), diploids (n=40 and n=42) and triploids (n=59, n=60, n=61, n=62 and n=63) and land forms. For details, see Appendix 1.*

Chapter 5. Physiology

Generalization of the physiology in the *Hebe* genus would be very interesting but is not possible. Firstly, the genus is so widely spread over mainland New Zealand and outlying islands. It is therefore adapted to various climates, levels of precipitation and ecological systems. Secondly, scientific investigations of physiology in the *Hebe* genus are extremely limited. This chapter can only give examples of physiological studies and suggest avenues worthy of investigations.

Physiological studies should for example include investigations of germination, dormancy, juvenility, apical dominance, vernalization, photosynthesis, phytochrome, photomorphogenesis, phototropism, water relations, flower initiation, flower induction and development, ionic relations, translocation of nutrients and hormones, nitrogen fixation, the nature of auxin-gibberellin-cytokinin-ethylene-inhibitors and other hormones, circadian rhythms, senescence, abscission and death. Only some very basic studies have taken place for species of *Hebe*.

5.1. Rates and periodicity of growth, photosynthesis and transpiration

The age of woody plants can be measured by counting number of growth rings and leaf scars. Measures of yearly shoot growth can also be made. An attempt to describe vegetative growth of two *Hebe* species among other subalpine shrubs and trees, *H. pinguifolia* and *H. odora*, was made by Wardle (1963B). Wardle stated that New Zealand subalpine woody plants show a well-marked annual periodicity in growth, but found it difficult to recognise four distinct seasons as experienced in the Northern Temperate Zone. He therefore referred to two seasons, summer (warmer portion of year when plant growth, flowering and fruiting takes place) and winter (colder portion, when plants are 'inactive').

Wardle's investigations showed that growth may begin later in wet cloudy districts than in drier sunnier districts at similar elevations. Also, it was found that growth rates did not change steadily with changes in altitude. Instead, growth occurred stepwise. These observations are supported by Primack (1983) saying that slope changes and elevational differences over a short distance of subalpine areas can have major influences on micro-climate of the plants and therefore also on their time of flowering.

Wardle (1963B) found reasonably distinct growth rings in *H. odora* and *H. pinguifolia*, and that slowly-grown shoots of *H. pinguifolia* perhaps completely lack secondary xylem in their one-year-old portions.

In Fig 5.1., growth rates are expressed as monthly summer shoot growth for *H. pinguifolia* growing at 1180, 1575 and 1890 m altitude along Broken River, South Island, New Zealand, and compared with those of *H. odora* growing at 1025 m altitude. Growth at the highest altitude occurred later and for a shorter period than at lower altitudes for *H. pinguifolia*. *H. odora* and *H. pinguifolia* from the lowest altitudes showed similar patterns of growth over a long period, from September to April. Wardle (1963) found that on average the annual shoot elongation of *H. pinguifolia* was 0.5-2.5 cm and there were 30-40 growth rings/cm of radius. In *H. odora*, shoots elongated 4.5-9.7 cm and had 20-25 growth rings/cm of radius. *H. odora* was recognised to have the fastest growth of 10 subalpine shrub species, while *H. pinguifolia* was the slowest. Their habitat explains the cited differences in growth rates: moist well-drained sites at relative low altitudes and exposed sites at high altitudes, respectively. Studies on growth rate, transpiration and photosynthesis of the different taxa of *Hebe* in their natural environments as well as under controlled environments would result in valuable information for comparison between taxa and for variability within taxa under various environments.

None of the *Hebe* taxa have deciduous habits. Wardle (1963B) found that leaves of *H. pinguifolia* persisted for 2-3 years from the time they were fully expanded. Both *H. odora* and *H. pinguifolia* appeared to shed their old leaves mainly during the period of most rapid growth. Indeed, further studies on leaf persistence, visibility of leaf scars, growth rings, node numbers per season, periodicity and dormancy during winter, hormonal effects, abscission, senescence and maximum plant age would make valuable knowledge.

Hair on the surface and on the ventral side of leaves occur in a few species, such as *H. gibbsii, H. allanii, H. pubescens* and *H. dieffenbachii*. Hairs on twigs are common, occurring for example, in *H.*

evenosa, H. canterburiensis, H. recurva, H. odora, H. pauciramosa, H. divaricata, H. carnosula, H. venustula, H. pimeleoides, H. topiaria, H. cockayniana, H. lavaudiana, H. raoulii, H. haastii, H. ramosissima. Variation of hairiness within the species *H. amplexicaulis* (including *H. allanii*) is studied by Garnock-Jones and Molloy (1982). A frequency histogram (Fig. 5.2) shows that hairy plants in a population are mostly found in 1200-1400 m altitude, while glabrous plants are found as low as 490 m above sealevel. Reasons for hairiness are not reported.

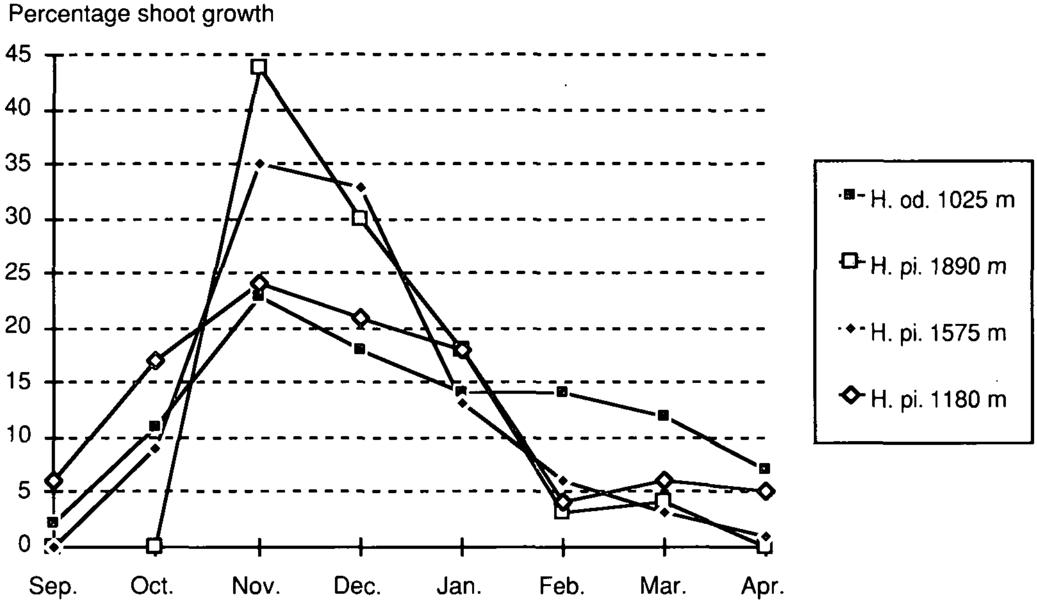


Fig. 5.1. Monthly distribution of summer shoot growth in two species, H. odora *at 1025 m altitude and* H. pinguifolia *studied at 1180, 1575 and 1890 m altitude along Broken River, South Island, New Zealand 1959-60. (Modified after Wardle 1963B).*

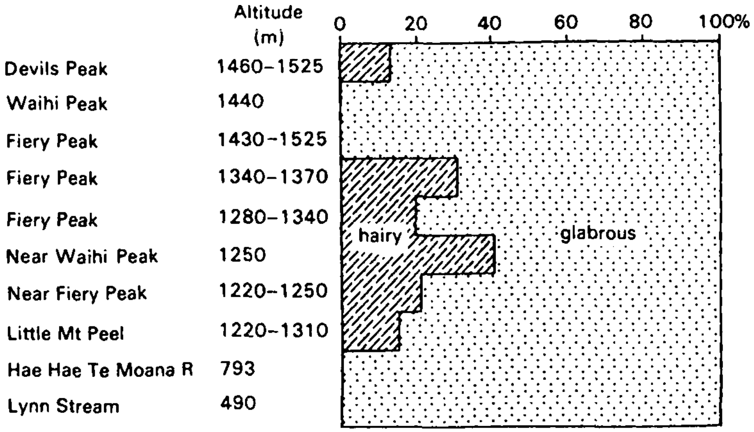


Fig. 5.2. Frequency of hairiness in populations of H. amplexicaulis *in various altitudes at the Mt. peal and Four Peaks Ranges, South Island, New Zealand. (After Garnock-Jones and Molloy 1982).*

5.2. Cold tolerance

The changeable climate of New Zealand (see Appendix 2) including periods of arctic, periods of temperate and periods of subtropical climates together with Ice Ages (the most recent of which lasted till 10,000 years ago) has probably favoured flexibility of taxa and easy adaptability to changing environments. Yearly, monthly and daily variation in temperature are higher than similar latitudes in the Northern Hemisphere. At an altitude of 250 m in Canterbury, South Island (43° latitude), for example, summer temperatures up to 44°C and winter temperatures down to -12°C are recorded (Rooney 1987). The variability among the more than 100 taxa *Hebe* and the limited distribution of most taxa, also indicate flexibility and easy adaptability.

Specific studies of temperature tolerance are very limited, but comparison of distribution with minimum temperature of the area should give an indication of cold tolerance. Also measurements of frost tolerance after standard treatments in a controlled environment would be valuable for further understanding of the physiology of the genus *Hebe*. Sakai and Wardle (1978) have investigated a range of New Zealand trees and shrubs for freezing resistance. It was found for *H. brachysiphon* (syn. *H. venustula*) collected at an altitude of 610 m along Waimakariri River in mid-winter (July) that leaves resisted -13°C, buds -10°C and twigs -15°C for 4-10 hours in an artificial environment. Recorded grass minimum winter temperature at the location was -15.4°C.

Observations on hardiness in young plants of *H. breviracemosa*, endemic to the sub-tropical Kermadec Island, indicate that hardened plants can survive -7°C ground frost and -3°C air frost for one night (Heenan 1989). Damage occurred on lower leaves, resulting in leaf drop. Ground frost of -5.5°C should be the lower temperature limit for damage according to Heenan.

Other observations from the high plain of Canterbury (Rooney 1987) suggest that all *Hebe* taxa in section "Flagriformes" and in addition *H. haastii, H. epacriadea, H. pinguifolia, H. buchananii, H. amplexicaulis, H. pareora* and *H. pimelioides* can tolerate at least -12°C in winter. It is suggested that taxa with bigger leaves, section "Subdistichae", "Apertae", "Subcarnosae" and partly "Occlusae" are less frost tolerant than taxa with smaller leaves. Also their natural distribution (Appendix 1, Chapter 4) supports such a relationship, but no evidence is available.

5.3. The unspecialized apical bud

Apical buds of many woody species of the New Zealand mountains are protected, others are not. The protection is afforded by special structures like bud scales (modified leaves, lasting for two to several years) or caducous stipules. Wardle (1963B) identifies the apical buds of *Hebe* as unspecialized buds, where older developing leaves protect younger developing leaves. *H. odora* and *H. pinguifolia* were found to have unspecialized apical buds with complete enclosure of buds by developing foliage leaves.

The form of the buds is distinct in most taxa, as they consist of almost fully developed leaves. The buds also for a number of taxa have a distinct sinus, the variation of which was used by Moore to separate the *Hebe* genus into botanical sections (in Allan (1961), Moore 1967) (Fig. 3.2).

Inside an apical leaf bud are several developing leaf pairs (Fig. 5.3). Representative samples of apical buds were examined in summer (21 February 1989) from a collection growing in Palmerston North. The number of developing leaf pairs within the apical bud varied from 3 in *H.* 'Bishopiana', 4 in *H. topiaria*, 5 in *H. hulkeana* to 6-8 in *H. recurva* and *H. venustula* (Kristensen 1989, unpublished). The form of the apical meristem varies with the species. In *H. topiaria* and *H. recurva* the leaves sit tight together, while in *H. hulkeana* the leaves overlap and permit air and moisture to move (Fig. 5.4). Neither *H. topiaria*, section "Occlucae", nor *H. recurva*, section "Subcarnosae", have a sinus and even in the very young leaf pairs the buds are tightly appressed. *H. hulkeana*, section "Paniculatae", is recognised to have leaf pairs that diverge in an early stage instead of remaining together (Moore 1967) (Fig. 3.2), but studies of the apical meristems in scanning electron microscope (SEM) show that the leaves are closely appressed and overlapping at this stage (Kristensen, Warrington and Hopcroft 1989, unpublished). Because this discovery indicates a significant meristematic difference between taxa

(Fig. 5.4) and perhaps can give evidence in the evolution of *Hebe*, it is thought to be of importance in the taxonomical revision of the genus and the studies on phenology (P. Garnock-Jones pers. comm.). Further studies of apical bud and leaf development would give an indication of the value of presence or absence of a sinus as a taxonomic criterion. Further studies of the other taxa in the section "Paniculatae" would also provide understanding of characteristics of unspecialized apical buds and the ways in which they differ from typical apical buds in *Hebe*, for example *H. topiaria* and *H. recurva* (Fig. 5.4).

Humidity in an apical bud seems to be relatively high, for example in *H. salicifolia* the inside of the outermost protective leafpair is moist. Also, in *H. salicifolia* there is air between the developing leaf pairs, while leaf buds of smaller leaved taxa leave little room for air. Further studies would help us understand the effect of leaves as protection against wind, humidity and temperature and other features.

There seems to be no clear relationship between the type of overwintering bud and hardiness (Wardle 1963B). The unspecialized apical bud must provide some protection for the apex and developing leaves, though, and further studies on characteristics of the apical bud would indicate why the bud develops in this specific way.

Fig. 5.3. Cross section of unspecialized bud of H. pinguifolia. *Developing leafpairs are completely protected by almost mature leaves still covering the bud. x 2. (Modified after Wardle 1963).*

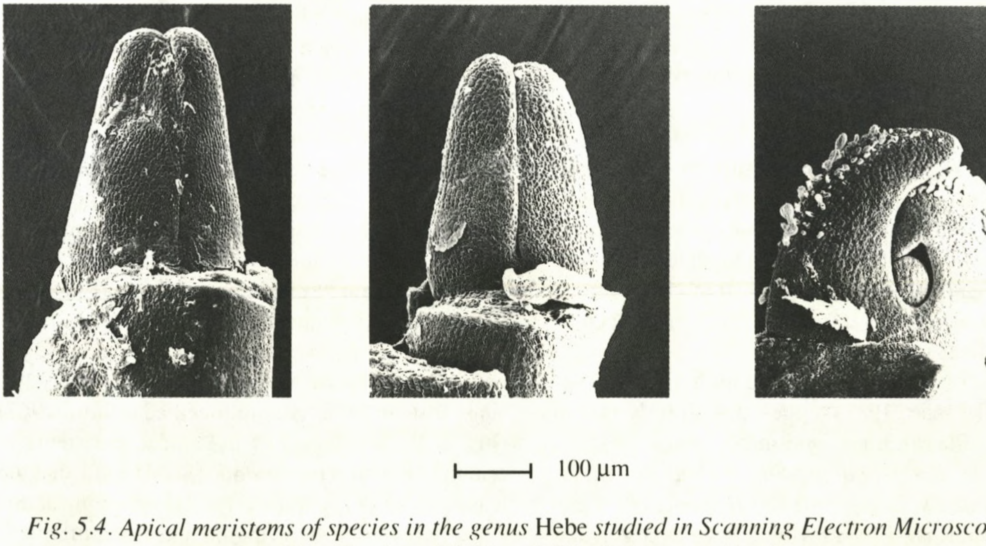


Fig. 5.4. Apical meristems of species in the genus Hebe *studied in Scanning Electron Microscope at Biotechnology Division, DSIR, Palmerston North.*
a) H. topiaria, *4th leaf pair under development, x 150. b)* H. recurva, *7th leaf pair under development, x 160. c)* H. hulkeana, *4th leaf pair under development, x 160.*

Table 5.1. Intensity of flowering in *Hebe* taxa at plantings at Auckland Regional Botanic Gardens (Hobbs 1988, J. Hobbs pers. comm.), Pinehaven, Wellington (A.P. Druce pers. comm.), Christchurch Botanic Gardens (Metcalf 1987) and Queens Park, Invercargill (L.J. Metcalf pers. comm.).

No flowering = 0. Flowering = 1.

Covering of flowers at main flowering time (Invercargill):
excellent = 90-100%, almost the whole bush covered with flowers;
very good = 75- 90%, most of bush covered but foliage showing
good = 60- 75%, a good quantity of flowers but more foliage showing between
fair = 40- 60%, flowers more scattered with larger amounts of foliage showing between

Name	Auckland	Wellington	Christchurch	Invercargill	Altitudinal zone in nature*
***Hebe* taxa flowering in all 4 locations**					
H. macrantha	1	1	1	very good	alpine-subalpine
H. odora	1	1	1	fair-good, seasonal	alpine-subalpine
H. albicans	1	1	1	very good	subalpine-lowland
H. diosmifolia	1	1	1	very good	montane-lowland
H. bishopiana	1	1	1	very good	montane-lowland
H. macrocarpa var. latisepala	1	1	1	very good	montane-lowland
H. recurva	1	1	1	very good	montane-lowland
H. townsonii	1	1	1	fair	montane-lowland
***Hebe* taxa flowering in less than 4 locations**					
H. buchananii	0	1	1		alpine-subalpine
H. cockayniana	0	0			alpine
H. decumbens	0	1	1	good	alpine-subalpine
H. pauciramosa	0			good	alpine-subalpine
H. aff. rigidula	0				alpine-subalpine
H. topiaria	0	1	1	fair, seasonal	alpine-lowland
H. venustula	0	1	1	very good	alpine-lowland
H. rakaiensis	0	1		very good	subalpine-lowland
H. rauolii	0	1		very good	subalpine-lowland
H. rigidula	0	1			subalpine-lowland
H. subalpina	0	0	1	very good	subalpine-lowland
H. vernicosa	0	1	1	very good	subalpine-lowland
H. barkeri	0				montane-lowland
H. bollonsii	0	1			montane-lowland
H. breviracemosa	0	1			montane-lowland
H. chatamica	0	1	1		montane-lowland
H. dieffenbachii	0	1	1		montane-lowland
H. elliptica	0	1			montane-lowland
H. lavaudiana	0	1			montane-lowland
H. pareora	?	1			montane-lowland
H. salicifolia	0	1	1		montane-lowland

* According to Druce, pers. comm.

5.4. Intensity and time of flowering

The main flowering season is December to February for more than 50% of 63 described *Hebe* taxa flowering in their natural environment. Year round, taxa in the *Hebe* genus are flowering, with a minimum of 9 in June and September (Moore in Allan 1961) (Fig. 4.6). The environmental factors that determine flowering of specific genotypes are being investigated. A low temperature period seems to have an effect on flowering, and an effect of photoperiod can not at this stage be rejected (Kristensen 1988, unpublished; Kristensen, Warrington and Plummer 1990, unpublished).

Flowering time and intensity of *Hebe* taxa in plantings at sealevel in the northern, middle and southern of New Zealand mainland (Table 5.1) indicates that 78% of taxa grown in Auckland (humid, subtropical climate, 37° latitude) form flowers, while 88% of recorded taxa do so in Wellington (temperate climate, 41.3° latitude) while 100% of recorded taxa flower in Christchurch (temperate climate, 43.6° latitude) and in Invercargill (cool, temperate climate, 46.5° latitude). Other alpine and subalpine taxa would be of interest to list for flowering, but they tend to grow poorly in the humid Auckland and Wellington climates and for this reason records have not been made.

5.5. Discussion

Studies of physiology in the genus *Hebe* are extremely limited. Monthly shoot growth in two *Hebe* species shows variation with altitude which is expected. P. Wardle (pers. comm.) finds it difficult to measure small details of growth in field studies, and for that reason only a few measurements were made in his investigation (Wardle 1963). Further studies in all altitudes, latitudes and landforms are highly wanted to understand the physiology of the genus. And studies in controlled environments would give us more evidence on the details which are difficult to measure in the field. For example,

- what is the lower frost limit and is there a time limit in addition to the temperature?
- what is the optimum temperature for growth?
- does the protective mechanism of the meristem in the apical bud vary with the season?
- what are the structures of the apical meristems?
- what is the advantage/disadvantage of hairs?
- what are the detailed structures of leafs, stomata, sunken stomata, wax, thickness of leaves, petiole form, colour...?
- what variations are there in the readiness to initiate roots on branches and the relationship with growth hormones (preliminary studies has been carried out but have remained unpublished (P. Wardle pers.comm.)).
- what are the patterns of seasonality in growth, flowering and fruiting?
- what influences the initiation, development and intensity of flowering

Chapter 6. Breeding systems and hybridization

6.1. Flower structure and fertility

A general description of the typical floral structures in the genus *Hebe* is given by Moore (Allan 1961):

"Flowers in axillary or terminal racemes or spikes, inflorescences sometimes compound. Ca-lyx usually deeply and almost equally 4-lobed, the fifth lobe when present usually smaller. Corolla short- or long-tubed, with 4 subequal spreading lobes. Stamens 2, anthers held above tube. Style long, stigma capitate. Capsule dehiscing by the sagittal splitting of the septum and each carpel opening by distal median suture through the septal wall and in varying degrees also through the locule wall; septum usually across widest diameter and capsule + dorsally compressed; seeds usually flatted and smooth."

Inflorescences in *Hebe* are typically racemes and spikes, but panicles are also found. Types of inflorescences characteristic for the botanical sections in the genus are described by Moore (1967) and illustrated in Fig. 3.2. The length and number of florets per inflorescence vary from a few millimetres in inflorescences with 2-6 florets, e.g. *Hebe tetrasticha*, to 10-12 cm in inflorescences with 80-120 florets, e.g. *H. obtusata* and *H. stricta var. macroura*, and up to 30 cm in inflorescences with up to 300 florets in *H. hulkeana* (Kristensen 1989, unpublished) (Fig. 6.1).

Variation of inflorescence type within a species is described by Hamann (1960) in *H. diosmifolia*. He states that both florets and inflorescences can vary, even within the same plant (Fig. 6.2). Similarities were found in an experiment with cold treatments and flowering. It was observed that more inflorescences and more florets per inflorescence occurred in lowland *Hebe* cultivars when cold treat-ment was moderate (15.5/9.5°C day/night) and its duration was 2-3 month compared with shorter durations (Kristensen, Warrington and Plummer 1990, unpublished).

An example of the structure and a floral diagram of a typical floret is shown for *H. diosmifolia* (Fig. 6.3). A typical floret in cross section is shown for *H. hulkeana* (Fig. 6.4). Unusual florets sometimes occur as exemplified by Eagle's drawing of *H. benthamii* with 5-6 calyx and corolla lobes, Fig. 6.5, and by the floret of *H. hulkeana* with 5 calyx lobes which is described by Saunders (1934).

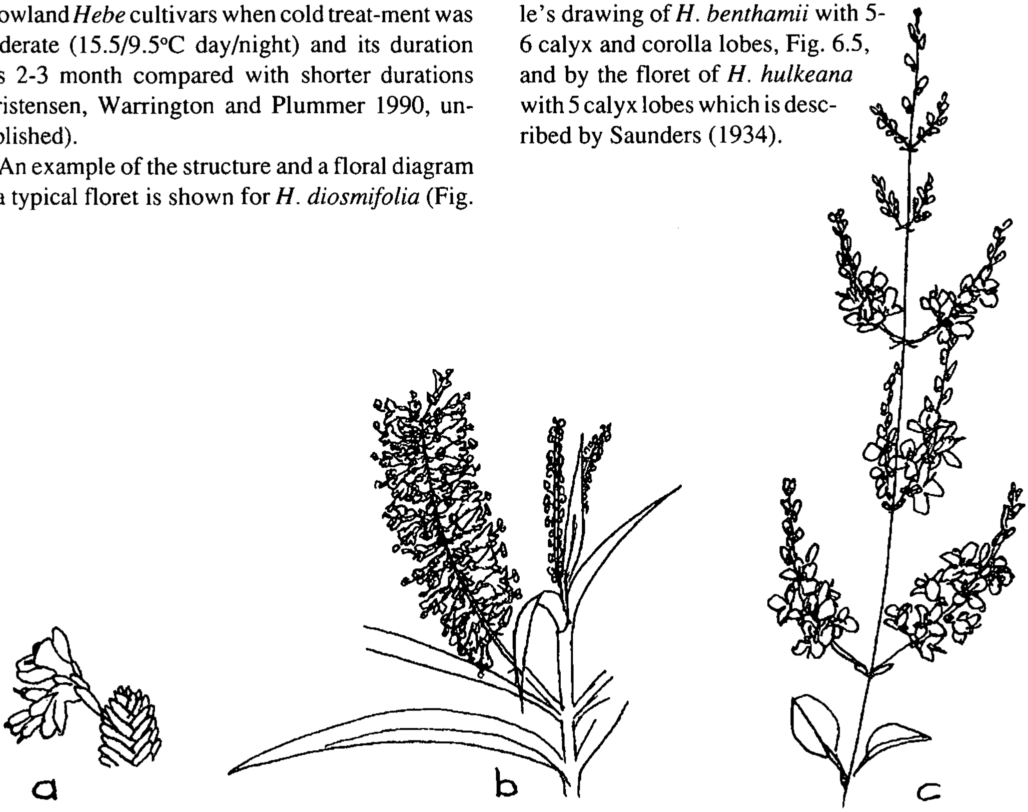


Fig. 6.1. Types of inflorescences in the genus Hebe. *From left, raceme of* H. tetrasticha *(enlarged), spike of* H. stricta var. macroura *(reduced), and panicle of* H. hulkeana *(reduced). (Modified after Eagle 1986).*

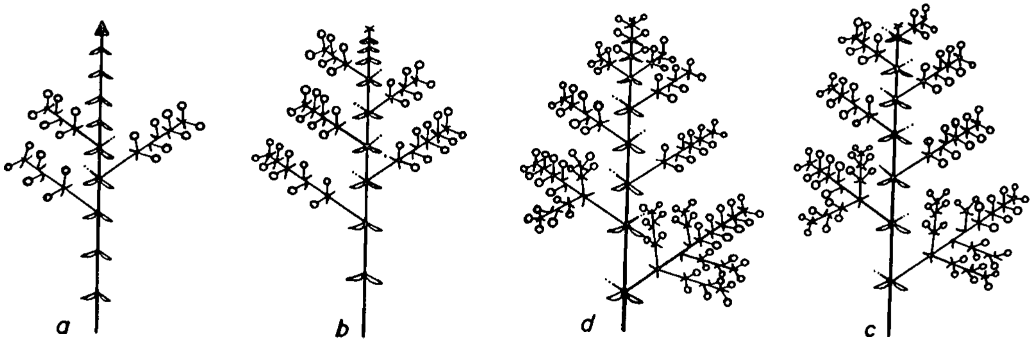


Fig. 6.2. Differences in flowering and branching of inflorescences in four shoots from the same plant of H. diosmifolia. *(After Hamann 1960).*

Fig. 6.3. Structure of floret and floral diagram of H. diosmifolia, *enlarged. (Modified after Hamann 1960)*

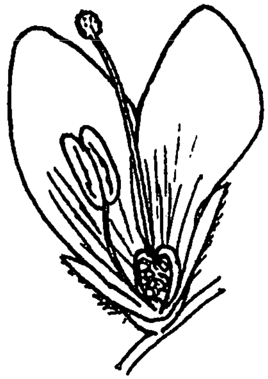


Fig. 6.4. Cross sectioned floret of H. hulkeana, *enlarged. (Modified after Eagle 1986).*

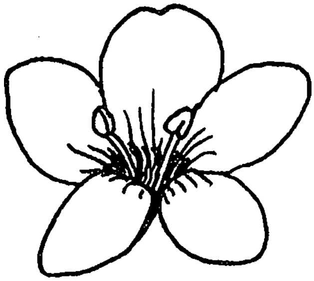


Fig. 6.5. Floret structure of H. benthamii *showing the atypical 5 corolla lobes. (Modified after Eagle 1986).*

6.2. Breeding systems

Most *Hebe* species are self-compatible and a higher proportion of species than in an average genus are dimorphic (two sexual morphs) (Delph unpublished PhD-thesis 1988).

Male sterility is reported by Frankel (1940) and is suggested to be an adaptive mechanism. Frankel also found that male sterility serves as a mechanism which reduces self-fertilization, and that male-sterility in *H. townsonii* is associated with a major physiological disturbance (in meiosis).

Gender dimorphism in the *Hebe* genus has been studied by Delph (1988). She stated that the sex conditions range from monomorphism to the most extreme form of dimorphism: dioecy. In addition, she stated that dimorphism is correlated with altitude, and she hypothesizes that separate sexes evolved in higher altitudes in response to the increased level of self-pollination occurring at the higher altitudes. Delph found a relationship between altitude and the frequency of female-fertile plants: the frequency increases with altitude. She also showed that *Hebe* exhibits inbreeding depression by gender dimorphism, for example studied in *H. subalpina.*

6.3. Pollination

Hebe inflorescences are conspicuous with tightly clustered smaller flowers arranged in spikes and racemes. Small flowers are often pollinated by wind, but the arrangement in inflorescences indicates that they are also likely to attract pollinators. Thomson (1927) reported a great number of insects visiting flowers of *H. salicifolia, H. elliptica, H. traversii, H. pimelioides* and other unidentified species of *Hebe*. Heine (1937) reported "how the flowers of New Zealand are particularly well adapted for pollination by the insects to be found here".

Type of insect	Area	Insects visiting *Hebe* flowers, in percentage 0 10 20 30 40 %
Native bees	Mt. Cook	*********************
	Cr. Mt's	
Wasps	Mt. Cook	****
	Cr. Mt's	****
Bumble bees	Mt. Cook	
	Cr. Mt's	
Syrphid flies	Mt. Cook	********************
	Cr. Mt's	*************************
Other flies+	Mt. Cook	***
	Cr. Mt's	***

Mount Cook: *H. macrantha, H. salicifolia and H. subalpina*, 67 samples=100%.
Craigieburns Mountains: *H. epacriadea, H. odora* and *H. subalpina*, 56 samples=100%.

+) mainly tachinid and muscid flies. Tachinid flies are characterized by hairy bodies and legs, carrying pollen easily and foraging on cold, rainy days when other insects are not present.

Fig. 6.6. Percentage of insects (excluding thrips) visiting flowers of Hebe *species at Mt. Cook (subalpine grassland and scrub, elevation 1100 m), and at Craigieburn mountains (Cr. Mt's) (subalpine grassland and rocky cliffs above tree line, 1600-1800 m elevation). Modified after Primack 1983.*

The original New Zealand insect fauna lacked long-tongued bees, and therefore it is much more likely that flowers are adapted to be pollinated by various flies, short-tongued bees, lepidopterans, beetles (Primack 1983, Heine 1937) and thrips (Heine 1937). These observations are supported by Delph (1988) who investigated natural populations of various species.

The distribution of insects that visited *Hebe* species in two alpine-subalpine sites (Fig. 6.6), shows that visits by tachinid and syrphid flies together account for more than half of the insect visits. Native bees also make up a large proportion of the insect visits at sites where native bees were present. Bumble bees were not observed to visit *Hebe* flowers, and neither in other native plant species investigated (Primack 1983).

Pollination in cool, rainy and misty conditions is very limited. Primack (1983) examined flower longevity and found that flowers were fertile for in average 8.5 days (range: 3-15 days) on plants of a wide range of species at the Craigieburn Mountains (subalpine grassland and scrub). Flower longevity was increased with periods of bad weather, and Primack suggested that increased flower longevity is caused by a low respiration and transpiration rate.

The florets of the taxa in "Paniculatae" are reported by Moore (1973) to be protogynous, meaning that the female parts become fertile first (Fig. 6.7).

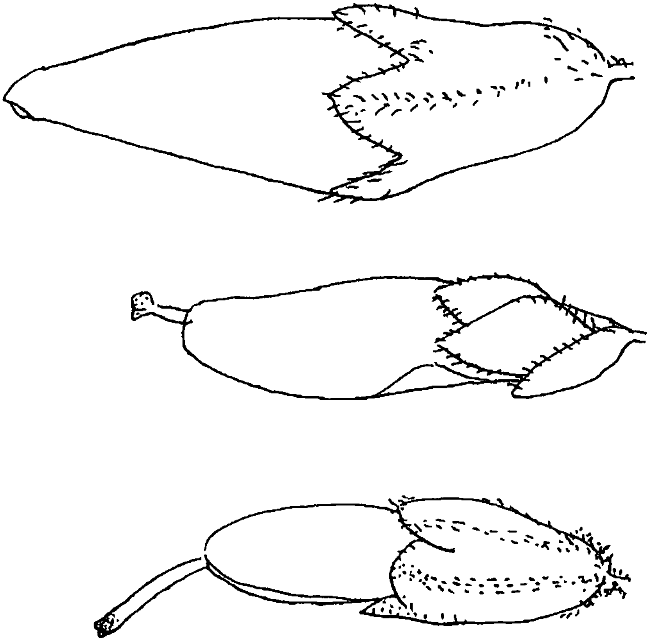


Fig. 6.7.a. Protogynous florets of Hebe *"Paniculatae". The exserted style is not yet visible in* H. raoulii var. raoulii *(top), but visible in* H. lavaudiana *(middle) and* H. hulkeana *(bottom). (Modified after Moore 1973).*

Most *Hebe* flowers from alpine and subalpine zones are white, whereas montane and lowland *Hebe* taxa have a higher proportion of blue, purple and red flowers. Heine (1937) states that the high proportion of white flowers in the New Zealand flora is related to the New Zealand insects:

"...white is the colour most attractive to the majority of New Zealand insects. It attracts a large number of native bees, more Lepidoptera than any other colour, besides a large number of beetles and flies."

A red flower colour is said to be attractive to birds and short-tongued bees (Heine 1937), and the red to purple flowered *H. speciosa* might be bird pollinated according to Garnock-Jones (pers. comm. in Delph 1988).

The effect of wind on degree of pollination has not been studied, neither has degree of self-pollination. Delph (1988) suggested that self-pollination is increased at higher altitudes.

6.4. Seed and fruit structure

The structure of capsules varies with species, and typical types are shown in Fig. 6.8. The types are used as one of the characters in the botanical sections (Moore 1967).

The size, form and other characteristics of seeds were investigated for some species of *Hebe* by Simpson (1976). He found that the number of fresh seeds per gram varied from approximately 2,200-2,500 in *H. lavaudiana* and *H. raoulii* (section: "Paniculatae") to 5,300 in *H. pinguifolia*, 14,000 in

H. traversii and 21,000 in *H. salicifolia*. The form and size varies too (Fig. 6.8) as well as viability. Simpson found that while seeds of *H. amplexicaulis* lost viability immediately after harvest, seeds of *H. salicifolia* and *H. elliptica* remained viable for 2 years.

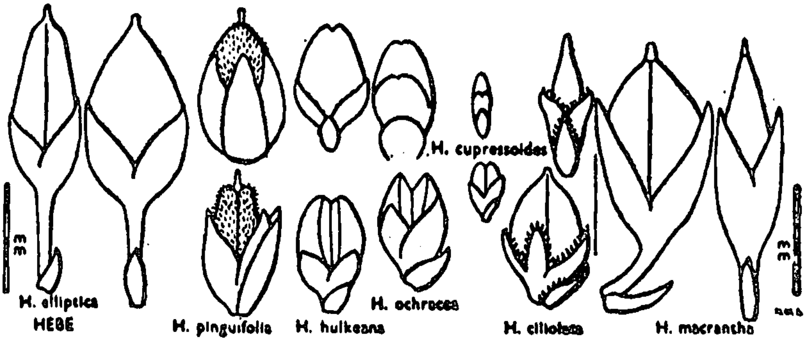


Fig. 6.7.b. Examples of types of capsules with calyces and bracts. (After Moore (Allan 1961)).

Fig. 6.8. Mature seeds of (from left) H. salicifolia, H. elliptica, H. lavaudiana *and* H. raoulii. *(Modified after Simpson 1976).*

6.5. Hybridization in nature and culture

Hybrids are very common in *Hebe* (in example, Cockayne et Allan 1934, Moore in Allan 1961 who cites Hooker (1854), Metcalf 1987, Rooney 1987, Chalk 1988, A.P. Druce pers. comm., P. Garnock-Jones pers. comm.)

Hybridization in nature is limited because distribution of most taxa is localized, but fertile and sterile hybrids are to be found in many habitats. The chromosome number varies from monoploid (n=20, n=21) to diploid (n=40, n=42), triploid (n=59, n=60, n=61, n=62, n=63) groups (Appendix 1 and Chapter 4). Cockayne and Allan (1934) list for example 43 wild hybrids, while Moore (Allan 1961) lists 13 wild hybrids and 15 horticultural forms.

Man has been involved in breeding since the first species came to Europe in 1776 and now more cultivars than species are present in Europe (mainly Britain) while the opposite is the case in New Zealand (Chalk 1988). An updated "*Hebe* International Check List of Cultivars" is in preparation (Chalk 1988, L.J. Metcalf pers. comm.) and about 500 cultivar names are being examined for validity (L.J. Metcalf pers. comm.). *Hebe* species and cultivars make very nice evergreen shrubs in gardens and parks, and I will assert that the potential for further use as ornamentals in temperate to subtropical climates is almost unlimited.

Different ways to establish new cultivars are:

1) a breeding program,
2) collection and selection of types from the wild,
3) casual crosses happening within a collection.

Breeding programs are not very common. *Hebe* breeding at Auckland Regional Botanic Gardens is an example. The first crossing was made in 1979 (Hobbs 1986), and the program started in 1982. The main object is "to produce attractive cultivars which perform well in Auckland gardens. Pest and disease resistance is a particularly important requirement" (Hobbs 1988).

The first crosses included *H. speciosa* crossed with some of the more disease resistant varieties in the Auckland collection. Out of 232 seedlings raised, 5 proved improvements at various positions within the Gardens and were selected and named in 1988:

H. 'Wiri Joy', rose pink flowers on a plant with assemblance to *H.* 'Inspiration',

H. 'Wiri Splash', mauve flowers, attractive goldengreen foliage

H. 'Wiri Jewel', magenta flowers, texture and undulating margins of foliage and pointed tips

H. 'Wiri Spears', long spear shaped spike, mauve flowers, quick growing

H. 'Wiri Grace', mauve flowers, compact growth, with *H. stricta, H. speciosa* and *H. bollonsii* in its parentage

The large variation within *Hebe* species led some plantspeople to select and name cultivars from wild grown species. An example is the British nurseryman Graham Hutchins, County Park Nursery. During expeditions into the native bush of New Zealand he collected and selected forms of different species of *Hebe* and other plant species. The forms are grown on at Hutchins' nursery near London, England. If the forms maintain their differences in shape and behaviour, they are given cultivar names. Crossings are made in the nursery as well, and a number of cultivars has been released (G. Hutchins pers. comm.).

Many people find seedlings in their garden. Seedlings that look a bit different from their possible parents; and an unknown number of these seedlings are named and find their way into commercial production both in Europe and New Zealand (L.J. Metcalf pers. comm., pers. obs.).

6.6. Discussion

Monoploids, n=20 and n=21, have evolved to diploids and triploids. At present new forms, either species (stable from seed) or hybrids (mostly unstable from seed) occur both in nature and in cultivation. From which origin the monoploids arrived is not known, but suggestions have been made (Chapter 3). Evidence of phylogeny would give important information for understanding the characteristics of the *Hebe* genus.

Fertility is high, and plants have a high proportion of gender dimorphism. Most species are self-compatible but mechanisms which avoid self-pollination have evolved and flies and native bees seem to be the most important pollinators in alpine and subalpine habitats. These three recognized features must correspond in their functions. Firstly, it does not seem logical that plants are self-fertile and have evolved dimorphism at the same time. But because the populations of plants often are local, the flowering time short and the weather cool and humid (for example in a wet subalpine habitat in the South Island), the plants must be advantaged by developing mechanisms which secure the highest degree of cross-pollination. Then, if the climate conditions are poor, the flower longevity increases and pollination is delayed until the weather improves and pollinators are available. Therefore, I hypothesize that the ability to be self-pollinated is only used if cross-pollination can not be carried out.

How pollination takes place in *Hebe* taxa growing in montane and lowland habitats has not been studied but birds might be involved. Flower colours also indicate pollination by flies and native bees in higher altitudes (white and pale colours). Other pollinators might be attracted at low altitudes (blue, purple and red colours). The bright coloured species have long tubed corollas which in other plant species are found to be more likely to have bird-pollination. Further studies are required.

Patterns of inheritance in the genus *Hebe* have not been studied, but casual hybridization in nature and cultivation happens frequently. The genus is still under development, adaptations to climates and ecological systems are improved by natural selection of genotypes. If breeding systems became known, the hybridization within the genus would be understood and would be valuable for controlled breeding programs.

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Appendix 1

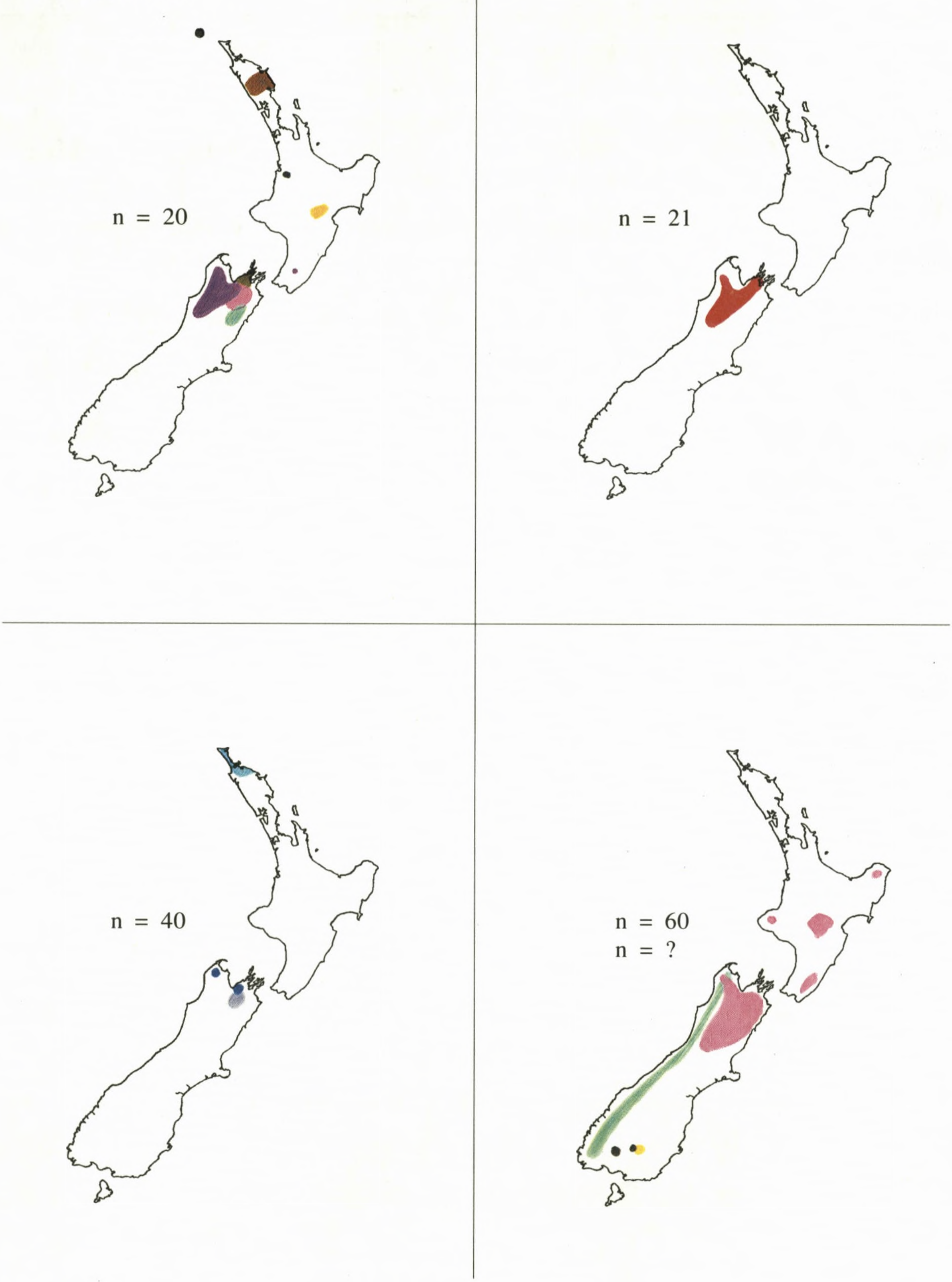
Habitat and distribution of New Zealand *Hebe* taxa

Characteristics and specifications on New Zealand *Hebe* species and varieties: Names (Allan 1961), tagnames for unnamed species (A. P. Druce pers. comm.), botanical sections (Moore in Allan 1961 and A. P. Druce pers. comm.), chromosome numbers (Hair 1967, A. P. Druce pers. comm.), original habitat (A. P. Druce pers. comm. and Eagle 1986) and distribution (A. P. Druce pers. comm. and Eagle 1986).

A. Subdistichae, leaf bud with narrow pointed sinus; dorsally compressed capsule; inflorescences lateral, shrubs with smallish leaves tending to distichous arrangement.

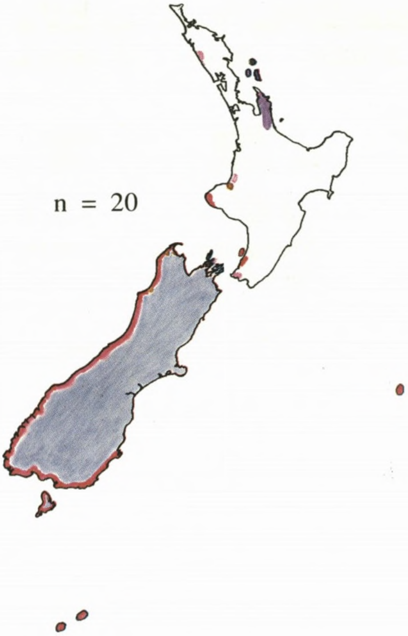
Name	Habitat altitudinal zone	Hydrology	Landform	Growth-form	Plant-height (m)
Chromosome number: n = 20					
▨ *H. diosmifolia* (spring flow.) (A. Cunn.) Ckn. et Allan	montane-lowland	wet	forest margin, cliff	bushy shrub	2
▨ *H. insularis* (Cheesem.) Ckn. et Allan	montane-lowland	wet	maritime cliff	erect or sprawling shrub	1
▨ *H. colensoi* (Hook. f.) Ckn., incl. *H. c.* var. *colensoi* and *H. c.* var. *hillii* (Col.) L.B. Moore	montane-lowland	dry	cliff	spreading bushy shrub	1
▨ *H. rupicola* (Cheesem.) Ckn. et Allan	subalpine-lowland	dry	cliff, rock	erect shrub	1.5
▨ *H. rigidula* (Cheesem.) Ckn. et Allan, incl. form (II) (A. Eagle)	subalpine-lowland	dry	forest margin, rock	small shrub	0.6
☐ *H. rigidula* form (I) (A. Eagle) tagname "H. Lady" A.P. Druce	montane-lowland	wet	calcareous cliff	small shrub	0.6
▨ *H. sp. (q)* Eagle, tagname "H. aff. rigidula" A.P. Druce	alpine-subalpine	dry	tussockland,rock	dome-shaped shrub	1.5
☐ *H. canterburiensis* (J.B. Armst.) L.B. Moore	alpine-subalpine	wet	tussockland	straggling or rounded shrub	1
Chromosome number: n = 21					
☐ *H. vernicosa* (Hook. f.) Ckn. et Allan	subalpine-lowland	wet-dry	forest	spreading shrub	1
Chromosome number: n = 40					
☐ *H. divaricata* (Cheesem.) Ckn. et Allan	montane-lowland	wet	forest margin	erect shrub	3
▨ *H. diosmifolia* (summer flow.) (A. Cunn.) Ckn et Allan	montane-lowland	wet	forest margin	erect tall shrub	6
▨ *H. carnosula* (Hook. f.) Ckn.	alpine-subalpine	dry	rock	shrub	0.5
Chromosome number: n = 60					
▨ *H. venustula* (Col.) L.B. Moore (syn. *H. brachysiphon* Summerhayes)	alpine-lowland	wet-dry	tussockland, rock	erect bushy shrub	1.5
▨ *H. cockayniana* (Cheesem.) Ckn. et Allan	alpine	wet	tussockland, rock	erect shrub	1
Chromosome number: n = ?					
▨ *H. dilatata* Simpson et Thomson ▨ and *H. crawii* M. Heads	alpine	wet	rock	prostrate spreading shrub	?

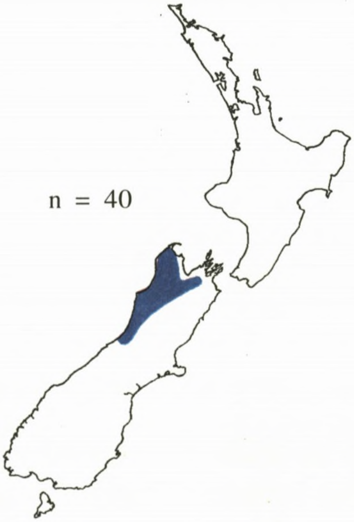
A. *Subdistichae*



Name	Habitat altitudinal zone	Hydrology	Landform	Growth-form	Plant-height (m)
B. Apertae, leaf bud with broad, + square sinus; dorsally compressed capsule; inflorescences lateral; many-branched shrubs; leaves medium-large.					
Chromosome number: n = 20					
☐ *H. elliptica* (Forst. f.) Pennell incl. *H. e.* var. *elliptica* and *H. e.* var. *crassifolia* Ckn. et Allan	montane-lowland	wet	maritime cliff	bushy shrub	2
▨ *H. speciosa* (A. Cunn.) Ckn. et Allan	montane-lowland	wet	maritime cliff	rounded bushy shrub	2
▨ *H. townsonii* (Cheesem.) Ckn. et Allan	montane-lowland	wet	calcareous cliff	upright shrub	2.5
☐ *H. pubescens* (Banks et Sol. ex Benth.) Ckn et Allan incl. form (I), tagname *H. p.* var. "Barrier" A. P. Druce	montane-lowland	wet	forest margin	many branched shrub	2
▨ *H. salicifolia* (Forst. f.) Pennell	montane-lowland	wet-dry	forets margin, cliff	erect shrub	5
■ *H. sp. (v)* Eagle tagname "H. mokohinau" A. P. Druce	montane-lowland	wet	cliff	shrub	2
Chromosome number: n = 40					
⬚ *H. gracillima* (Kirk) Ckn. et Allan *H. corriganii* Carse (see *Occlusae*)	montane-lowland	wet-dry	forest margin	spreading shrub	2
Chromosome number: n = ?					
▨ *H. sp.*, tagname "H. Unuwhao" A. P. Druce	montane-lowland	wet	rock	erect multibranched shrub	?

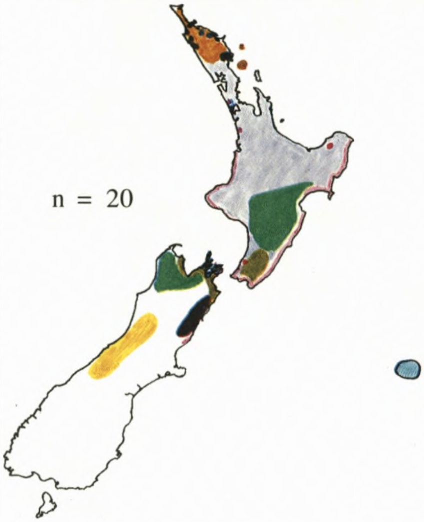
B. Apertae

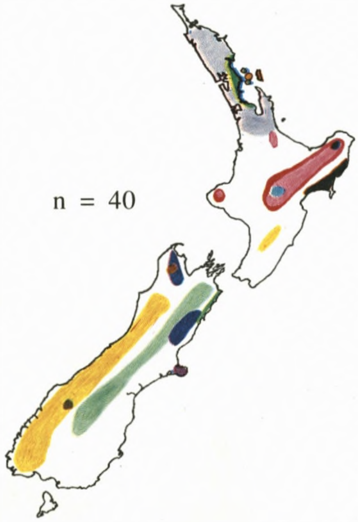




	Name	Habitat altitudinal zone	Hydrology	Landform	Growth-form	Plant-height (m)
	C. Occlusae, leaf bud without sinus; dorsally compressed capsule; inflorescences lateral; bracts not opposit, mostly small; flowers pedicellate; many-branched shrubs, occasionally small trees.					
	Chromosome number: n = 20					
░	*H. ligustrifolia*	montane-lowland	wet	forest margin	shrub	3
	(A. Cunn.) Ckn. et Allan					
░	*H. acutiflora* Ckn.	montane-lowland	wet	forest margin	erect shrub	1
▓	*H. stricta* var. *stricta*	subalpine-lowland	wet	forest margin	shrub	1
	(Benth.) L. B. Moore	montane-lowland	wet-dry	maritima cliff	shrub	2
▓	var. *macroura*					
	(Benth.) L. B. Moore					
▓	var. *atkinsonii*	subalpine-lowland	wet-dry	forest margin,scrub,	tall robust shrub	3
	(Ckn.) L.B. Moore	rock				
□	form (I) A. Eagle,	montane-lowland	wet	cliff	shrub	1
	tagname "H. angustissima" A.P. Druce					
□	*H. obtusata*	montane-lowland	wet	maritime cliff	spreading prostrate	0.5
	(Cheesem.) Ckn. et Allan				shrub	
▓	*H. bollonsii*	montane-lowland	wet	cliff?	erect shrub	1
	(Ckn.) Ckn. et Allan					
▒	*H. dieffenbachii*	montane-lowland	wet	maritime cliff	low spreading shrub	1
	(Benth.) Ckn. et Allan					
░	*H. barkeri*	montane-lowland	wet	forest	large shrub to	7
	(Ckn.) Ckn.	small tree				
░	*H. chathamica*	montane-lowland	wet	maritime cliff	small trailing	1
	(Buchan.) Ckn. et Allan	shrub				
█	*H. traversii*	subalpine-lowland	dry	forest margin, scrub,	compact ball-like	2
	(Hook. f.) Ckn. et Allan			cliff	shrub	
░	*H. treadwellii* Ckn. et Allan	alpine-subalpine	wet	rock	small low shrub	0.5
	incl. *H. brockiei* Simpson et Thomson					
▓	*H. sp. (x)* A. Eagle,	montane-lowland	wet	cliff	shrub	2.5
	tagname "H. Bartlett" A. P. Druce					
□	*H. parviflora* var. *angustifolia**	montane-lowland	wet	cliff	lowgrowing or	2
	(Hook. f.) L.B. Moore				bushing shrub	
	(syn. *Veronica squalida* Kirk), tagname "H. squalida" A. P. Druce					
□	*H. sp (h),*					
	(syn. *Veronica x bishopiane)*	montane-lowland	wet	cliff		
▓	*H. sp (m),* tagname					
	"H. Whangarei" A.P. Druce	montane-lowland	wet	forest, cliff?		
	Chromosome number: n = 40					
▒	*H. macrocarpa* var. *macrocarpa*,	montane-lowland	wet	forest	erect stiffly	2.5
	(Vahl) Ckn. et Allan	branched shrub				
	tagname "H. macrocarpa" A.P. Druce					
▓	*H. corriganii* Carse**	subalpine	wet	forest	shrub	3
	tagname "H. macrocarpa var. corriganii" A. P. Druce					
□	*H. parviflora* var. *arborea**,	montane-lowland	wet-dry	forest margin, scrub,	small tree	7
	(Buchan) L.B. Moore	rock				
	tagname "H. arborea" A. P. Druce					
□	*H. stricta* var. *egmontiana****	subalpine-lowland wet		forest margin, scrub	closely branched	3
	L. B. Moore			bog	shrub	
	tagname "H. egmontiana" A. P. Druce					

C. Occlusae





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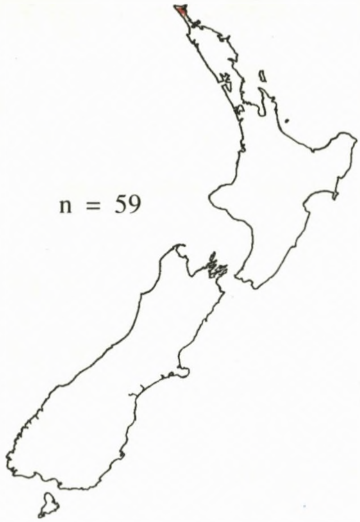
*) The two varieties are regarded as two distinct species by A. P. Druce (pers. comm.)

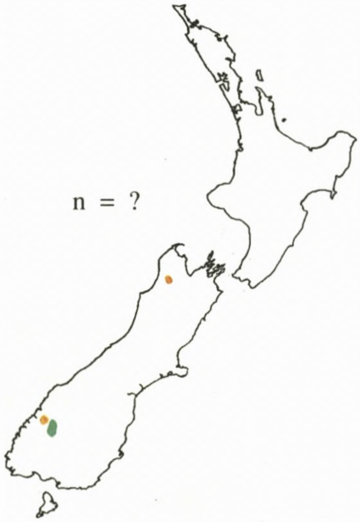
**) This species is considered to be a variety of *H. macrocarpa* by A. P. Druce (pers. comm.)

***) These two varieties of *H. stricta* are regarded as belonging to a separate species by A. P. Druce (pers. comm.)

Name	Habitat altitudinal zone	Hydrology	Landform	Growth-form	Plant-height (m)
C. Occlusae					
Chromosome number: n = 40 continued					
▨ *H. stricta* var. *lata*** L.B. Moore tagname "H. egmontiana var. lata" A.P. Druce	alpine-lowland	wet	rock	low growing shrub	1
▨ *H. subalpina* (Ckn.) Ckn. et Allan incl. *H. truncatula* (Col.) L. B. Moore	subalpine-lowland	wet	forest margin, scrub	rounded bushy shrub	2.5
▨ *H. fruticeti* Simpson et Thomson	subalpine	wet	scrub	bushy shrub	1
▨ *H. strictissima* (Kirk) L. B. Moore	montane-lowland	dry	cliff	erect shrub	2
▨ *H. rakaiensis* (J. B. Armst.) Ckn.	subalpine-lowland	dry	scrub, rock	bushy shrub	2
☐ *H. glaucophylla* (Ckn.) Ckn.****	alpine-lowland	wet-dry	cliff, rock	low to tall shrub	3
▨ *H. sp. (n)* A. Eagle, tagname "H. Wairoa" A.P.Druce	montane-lowland	wet	cliff, rock	tall shrub	4
▨ *H. sp. (o)* A. Eagle, tagname "H. marble" A.P. Druce	subalpine-lowland	wet	calcareous cliff	shrub	1
▨ *H. sp.*, tagname "H. Great Barrier" A.P. Druce	montane-lowland	?	forest, scrub?	bushy shrub	?
Chromosome number: n = 59					
☐ *H. macrocarpa* var. *brevifolia* (Cheesem.) L.B. Moore*****, tagname "H. brevifolia" A. P. Druce	montane-lowland	wet	rock (ultra mafic)	low clump-growing shrub	2
Chromosome number: n = 60					
▨ *H. macrocarpa* var. *latisepala* (Kirk) Ckn. et Allan tagname "H. latisepala" A. P. Druce	montane-lowland	wet	forest, cliff	erect sparingly branched shrub	2
▨ *H. evenosa* (Petrie) Ckn. et Allan	subalpine	wet	scrub	bushy shrub	2
▨ *H. urvilleana* W. R. B. Oliver	subalpine-lowland	dry	scrub (ultra mafic)	openly branched shrub	1.5
Chromosome number: n = 61					
▨ *H. topiaria* L. B. Moore	alpine-lowland	wet	tussockland, scrub, rock	rounded compact shrub	2
Chromosome number: n = ?					
☐ *H. breviracemosa* (W.R.B. Oliver) Ckn. et Allan	montane-lowland	wet	cliff	laxly branched shrub	2
▨ *H. matthewsii* (Cheesem.) Ckn.******	alpine-subalpine	wet	tussockland	erect shrub	1.5
☐ *H. sp.*, tagname "H. takahe" A. P. Druce	subalpine	wet	scrub?	bushy shrub	?

C. Occlusae





****) There are numerous forms/geographic races of *H. glaucophylla* in NW Nelson, South Island, some almost indistinguishable from *H. albicans* except by chromosome number. These two species should belong to same botanical section (A. P. Druce pers. comm.)

*****) These variety is suggested to be given specific status (Druce et al. 1979)

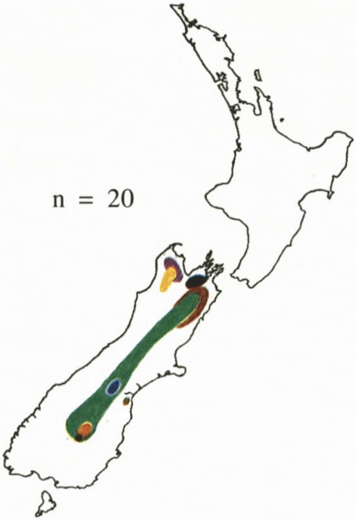
******) *H. matthewsii* is re-discovered by A. P. Druce 1989, from not being seen in nature since first discovery in 1906 by Cheeseman (A. P. Druce pers. comm., Allan 1961). The species is suggested by A. P. Druce to belong to *''Occlusae''* not *''Subcarnosae''*, because it has no sinus (pers. comm.)

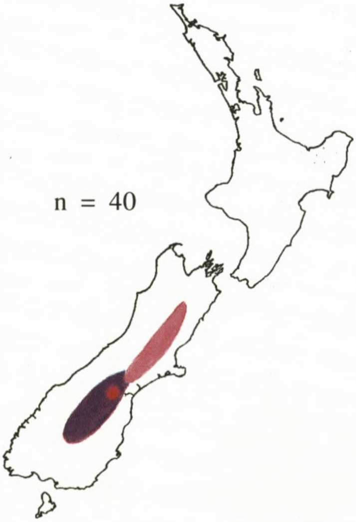
Name	Habitat altitudinal zone	Hydrology	Landform	Growth-form	Plant-height (m)
D. Subcarnosae, leaf bud with out sinus; dorsally compressed capsule; inflorescences lateral; bracts often opposite; flowers mostly +decumbent rather woody shrubs with leaves +fleshy and/or glaucous.					
Chromosome number: n = 20					
▨ *H. decumbens* (J.B. Armst.) Ckn. et Allan	alpine-subalpine	dry	cliff, rock	prostrate shrub	1
▨ *H. albicans* (Petrie) Ckn.*	subalpine-lowland	wet	cliff, rock, bog	spreading shrub	1
☐ *H. recurva* Simpson et Thomson*	montane-lowland	wet	cliff, rock	shrub	1
▨ *H. amplexicaulis* (J.B. Armst.) Ckn. et Allan (incl. *H. a.* var. *erecta* Ckn. et Allan and *H. allanii* Ckn.)	alpine-subalpine	dry	cliff, rock		
▓ *H. gibbsii* (Kirk) Ckn. et Allan	alpine-lowland	dry	rock	spreading shrub	0.3
▨ *H. sp.* tagname "H. aff. pinguifolia" A.P. Druce	alpine	dry	rock	shrub	?
☐ *H. pimeleoides* var. *pimeleoides* (Hook. f.) Ckn. et Allan (syn. *H. p.* var. *minor* (Hook. f.) Ckn. et Allan)	subalpine-lowland	dry	rock	small shrub	0.3
░ *H. pimeleoides* var. *rupestris*** Ckn. et Allan	montane-lowland	dry	rock	straggling shrub	0.5
▨ *H. pareora* Garnock-Jones et Molloy	montane-lowland	dry	calcareous cliff	large shrub	1.5
■ *H. biggarii* Ckn.	subalpine	dry	cliff, rock	small shrub	0.3
Chromosome number: n = 40					
░ *H. pinguifolia* (Hook. f.) Ckn. et Allan	alpine-subalpine	dry	rock	low or erect shrub	1
☐ *H. buchananii* (Hook. f.) Ckn. et Allan	alpine-subalpine	dry	rock, cliff	sprawling shrub	0.2
☐ *H. sp.* tagname "H. aff. pimeleoides" A.P. Druce	montane-lowland	dry	rock	small shrub	0.2

*) regarded as one species with two varieties, *H. albicans* var. *recurva* and *H. albicans* var. *albicans* by A. P. Druce (pers. comm.) (Druce et al. 1987)

**) regarded as a species distinct from *H. pimeleoides* by A. P. Druce (pers. comm.) *H. pimelioides* var. *glauca-caerulea* is based on a hybrid (A. P. Druce pers. comm.)

D. Subcarnosae





E. Buxifoliatae, leaf bud with +heart-shaped sinus; dorsally compressed capsule; inflorescences lateral or terminal or both; bracts opposite, the lowest large and + leaflike in texture; flowers sessile; small shrubs with small stiff leaves and strict usually erect twigs.

Chromosome number: n = 21

Name	Habitat altitudinal zone	Hydrology	Landform	Growth-form	Plant-height (m)
☐ *H. odora* (Hook f.) Ckn.*	alpine-subalpine	wet	bog, tussock, scrub	shrub	1.5
▨ *H. pauciramosa* var. *pauciramosa* (Ckn. et Allan) L. B. Moore	alpine-subalpine	wet	bog, tussock	shrub	0.5
☐ *H. pauciflora* Simpson et Thomson	alpine-subalpine	wet	bog?, rock?	small shrub	0.2

Chromosome number: n = 42

Name	Habitat altitudinal zone	Hydrology	Landform	Growth-form	Plant-height (m)
▨ *H. sp. (u)* form (I) A. Eagle tagname "*H. anomala*" A. P. Druce	alpine-subalpine	wet-dry	scrub, tussock	shrub	1.5

Chromosome number: n = 59

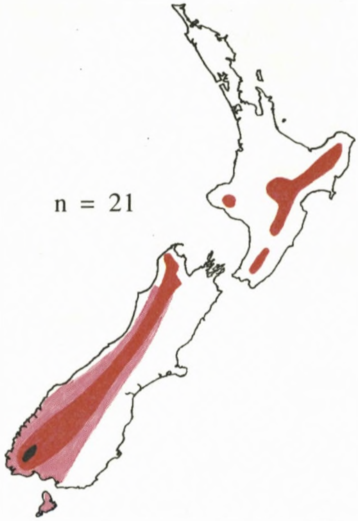
Name	Habitat altitudinal zone	Hydrology	Landform	Growth-form	Plant-height (m)
▨ *H. pauciramosa* var. *masonae* L. B. Moore (*Leonohebe masoniae* M. Heads)	alpine-subalpine	wet	bog, tussock	robust shrub	1

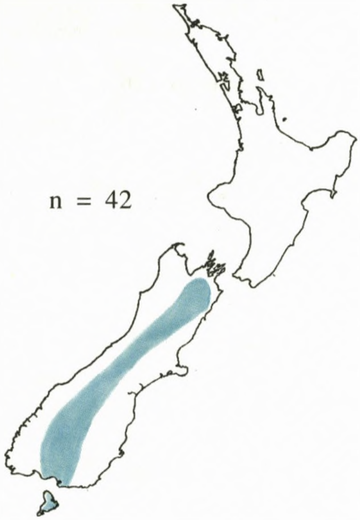
Chromosome number: n = 63

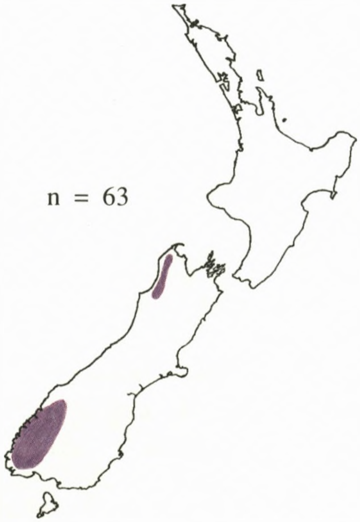
Name	Habitat altitudinal zone	Hydrology	Landform	Growth-form	Plant-height (m)
☐ *H. sp. (i)* A. Eagle (*Leonohebe mooreae* M. Heads)	subalpine	wet	bog, tussock	shrub	1.5

*) This species is stated by Hair (1967) to probably include more than one good species. Hair recorded the chromosome numbers n=21,42 and 63. Further a variety, *H. odora* var. *prostrata*, was recorded to have the chromosome number 2n=84.

E. Buxifoliatae







Name	Habitat altitudinal zone	Hydrology	Landform	Growth-form	Plant-height (m)
F. Flagriformes, leaf bases connate; dorsally or laterally compressed capsules; inflorescences terminal, simple; bracts opposite, often slightly > leaves; flowers sessile; shrubs, usually low growing, with twigs of whipcord form.					
Chromosome number: n = 20					
▨ *H. tetragona* (Hook.) Ckn. et Allan	alpine-subalpine	wet	tussock	stout erect shrub	1
▨ *H. subsimilis* (Col.) M.B. Ashwin var. *subsimilis**	alpine-subalpine	wet	tussock	shrub	1
▨ *H. subsimilis* var. *astonii* (Petrie) M. B. Ashwin*	alpine-subalpine	wet	tussock	small shrub	0.3
▨ *H. coarctata* (Cheesem.) Ckn. et Allan*	alpine-subalpine	wet	tussock	spreading shrub	1
▨ *H. hectori* (Hook. f.) Ckn. et Allan var. *hectori** incl. *H. subulata* Simpson	alpine-subalpine	wet	tussock, bog	small, erect shrub	0.8 0.8
▨ *H. hectori* var. *demissa* (Simpson) M. B. Ashwin*	alpine or subalpine?	wet	?		
☐ *H. laingii* (Ckn.) Ckn. et Allan*	alpine-subalpine	wet	tussock, bog?	small shrub	0.3
▨ *H. propinqua* (Cheesem.) Ckn. et Allan	alpine-subalpine	wet-dry	tussock	shrub	1
▨ *H. lycopodioides* (Hook. f.) Ckn. et Allan var. *lycopodioides*	alpine-subalpine	dry	tussock	stout shrub	1
☐ *H. lycopodioides* var. *patula* Simpson et Thomson**	alpine-subalpine	dry	tussock	decumbent shrub	0.2
■ *H. poppelwellii* (Ckn.) Ckn. et Allan**	alpine-subalpine	dry	tussock	slender shrub	0.2
■ *H. imbricata**** Ckn. et Allan	subalpine	wet	?	many branched shr.	0.6
Chromosome number n = 21					
▨ *H. salicornioides* (Hook. f.) Ckn. et Allan	alpine-subalpine	wet-dry	bog	erect shrub	1
☐ *H. annulata* (Petrie) Ckn. et Allan****	subalpine	dry	tussock	small shrub	0.2
▨ *H. cupressoides* (Hook. f.) Ckn. et Allan	subalpine	dry	scrub	rounded shrub	2
Chromosome number n = 42					
☐ *H. armstrongii* (J. B. Armst.) Ckn. et Allan	alpine-subalpine	dry	scrub	spreading shrub	1
Chromosome number n = 62					
▨ *H. ochracea* M. B. Ashwin	alpine-subalpine	wet	tussock, rock	spreading shrub	0.7

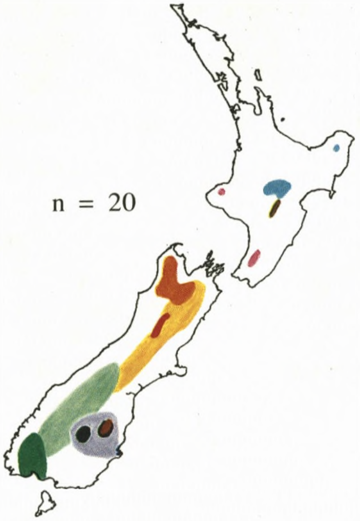
*) These six species and varieties are considered to be part of the wide spread species *H. tetragona* by A. P. Druce (Druce et al. 1987)

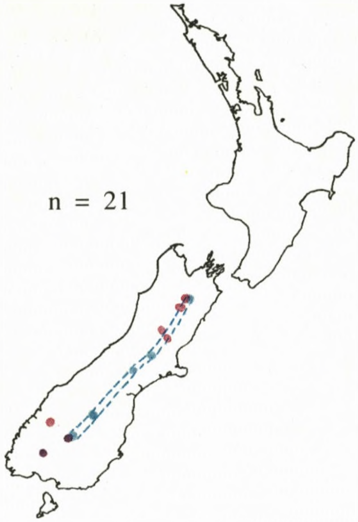
**) This variety and species are considered to be part of the species *H. lycopodioides* by A. P. Druce (pers. comm.)

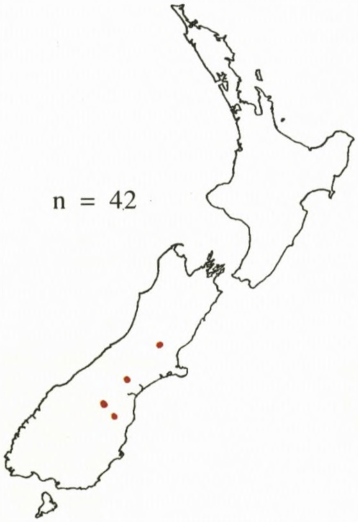
***) This species is considered to be part of the species *H. lycopodioides* by A. P. Druce (pers. comm.)

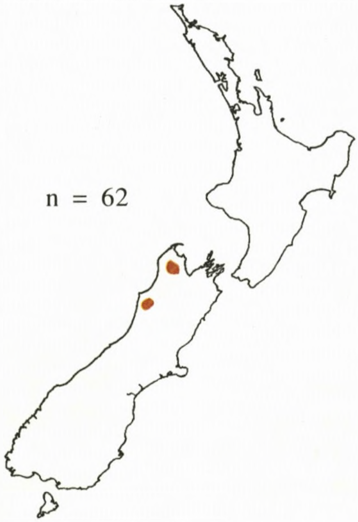
****) This species is considered to be a variety of *H. salicornioides* by A. P. Druce (pers comm.)

F. Flagriformes









Name	Habitat altitudinal zone	Hydrology	Landform	Growth-form	Plant-height (m)

G. Connatae, leaf bases connate; dorsally compressed capsules; inflorescences terminal, sometimes lateral also, forming compact head; bracts opposite and + leaf like; low growing to decumbent shrubs with ascending tips, leaves usually imbricate.

Chromosome number n = 20

Name	Habitat altitudinal zone	Hydrology	Landform	Growth-form	Plant-height (m)
☐ *H. benthamii* (Hook. f.) Ckn. et Allan	montane-lowland	wet	rock	small erect shrub	0.5

Chromosome number n = 21

Name	Habitat altitudinal zone	Hydrology	Landform	Growth-form	Plant-height (m)
▨ *H. epacridea* (Hook. f.) Ckn. et Allan	alpine-subalpine	wet-dry	rock	low-growing shrub	0.2
▨ *H. haastii* var. *haastii* (Hook. f.) Ckn. et Allan	alpine	dry	rock	low-growing shrub	0.3
▨ *H. haastii* var. *humilis* (Simpson) L. B. Moore	alpine	dry	rock	low-growing shrub	0.2
▨ *H. haastii* var. *macrocalyx* (J.B. Armst.) Ckn. et Allan	alpine	wet	rock	low-growing shrub	0.3
☐ *H. ramossisima* Simpson et Thomson*	alpine	dry	rock	prostrate shrub	0.2
▨ *H. petriei* var. *petriei* (Buchan.) Ckn. et Allan	alpine	dry	rock	low-growing shrub	0.2
☐ *H. petriei* var. *murrellii* (Simpson et Thomson) L. B. Moore	alpine	wet	rock	low-growing shrub	0.2

*) This species is considered to be a variety of *H. haastii* by A. P. Druce (pers. comm.)

Name	Habitat altitudinal zone	Hydrology	Landform	Growth-form	Plant-height (m)

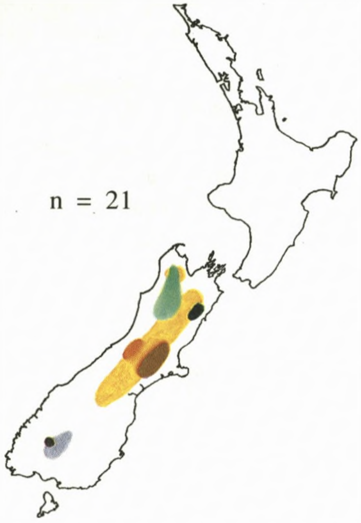
H. Paniculatae, leaf petiolate, members of a pair diverging early in bud; dorsally compressed capsules, turgid, +didymous; inflorescences terminal and usually compound; flowers mostly sessile; seed narrow, spindle shaped; low growing shrubs, leaves regularly toothed.

Chromosome number n = 21

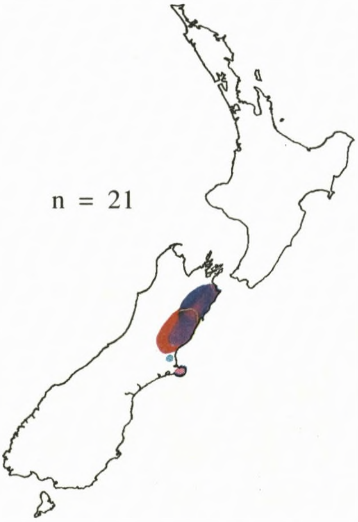
Name	Habitat altitudinal zone	Hydrology	Landform	Growth-form	Plant-height (m)
☐ *H. raoulii* var. *raoulii* (Hook. f.) Ckn. et Allan	subalpine-lowland	dry	rock	small shrub	0.3
▨ *H. raoulii* var. *maccaskillii** Allan	montane-lowland	dry	calcareous cliff	small shrub	0.2
☐ *H. raoulii* var. *pentasepala** L. B. Moore	subalpine	dry	rock	slender erect shr.	0.2
▨ *H. lavaudiana* (Raoul) Ckn. et Allan	montane-lowland	dry	rock	small shrub	0.4
☐ *H. hulkeana* (F. Muell.) Ckn. et Allan	montane-lowland	dry	cliff	slender laxly branched shrub	1

*) These two varieties are regarded as species separate from *H. raoulii* by A. P. Druce (pers. comm.)

G. Connatae



H. Paniculatae



Name	Habitat altitudinal zone	Hydrology	Landform	Growth-form	Plant-height (m)

I. Grandiflorae, leaf large, toothed, petiolate, members of a pair diverging early in bud; laterally compressed capsules, especially towards tip; septum across narrow diameter; inflorescences lateral, few flowered; flowers very large; short woody shrub with leafy twig.

Chromosome number n = 21

Name	Habitat altitudinal zone	Hydrology	Landform	Growth-form	Plant-height (m)
▥ *H. macrantha* var. *macrantha* (Hook. f.) Ckn. et Allan	alpine-subalpine	wet	scrub, tussock	straggling shrub	0.6
▨ *H. macrantha* var. *brachyphylla* (Cheesem.) Ckn. et Allan	alpine-subalpine	wet	scrub, tussock	straggling shrub	0.6

Name	Habitat altitudinal zone	Hydrology	Landform	Growth-form	Plant-height (m)

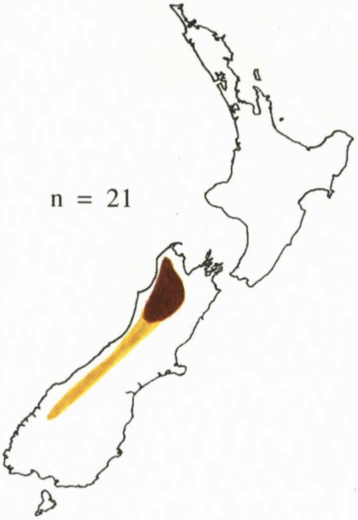
J. Semiflagriformes, leaf small, margins ciliate, bases connate; laterally compressed capsules, especially towards tip; septum across narrow diameter; inflorescences lateral, few flowered; flowers small, unisexual, plants usually dioecious; much branched very low shrubs from stout woody base, twigs of semi whipcord form with close set leaves almost or quite hiding very slender stem.

Chromosome number n = 21

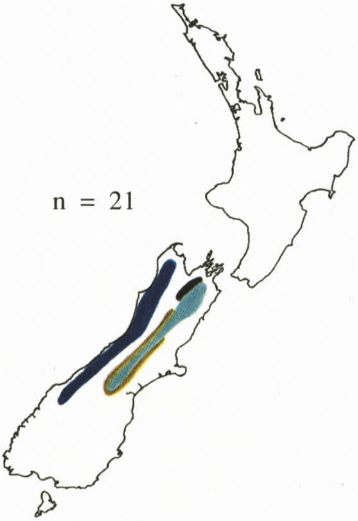
Name	Habitat altitudinal zone	Hydrology	Landform	Growth-form	Plant-height (m)
▓ *H. ciliolata** (Hook. f.) Ckn. et Allan	alpine-subalpine	wet	rock	straggling shrub	0.3
▒ *H. tetrasticha** (Hook. f.) Ckn. et Allan	alpine-subalpine	dry	rock	small shrub	0.2
░ *H. cheesemanii* (Buchan.) Ckn. et Allan	alpine-subalpine	dry	rock	small round shrub	0.3
■ *H. tumida* (Kirk) Ckn. et Allan	alpine-subalpine	dry	rock	prostrate shrub	0.2

*) These two species are suggested to be only one species by Wilson (1976)

I. Grandiflorae



J. Semiflagriformes



Appendix 2

Notes about the climate and geological history of New Zealand

The land masses of New Zealand have been isolated from all other land masses at least since the Mesozoic (200 million years ago). Until then they were part of the Gondwana Supercontinent (Stevens 1985, Anderson 1977). The changing patterns of land and sea in the Southern Hemisphere (Fig. A2.1) show in present day land shapes how the land masses are concidered to have moved apart from Gondwana and how the New Zealand land masses are concidered to have been in the Northern Hemisphere 520 million years ago, to have passed the equator and have moved close to the South Pole 120-100 million years ago. The New Zealand we know today is young in the geological history, perhaps only 80 million years old. Eruptions and earth quakes happen frequently on land and in the surrounding seas, and the land raises a few millimetres per year.

The present land area is 268,704 km^2, divided in the North Island, 114,453 km^2, the South Island, 150,718 km^2, and Stewart Island, 1,746 km^2. New Zealand lies in the Southern Hemisphere between the Tasman Sea and the Pacific Ocean at the parallels 34° 166' and 48° 178' S. Hills and mountains occupy 75% of the land, and a wide range of rocks are present. The soils are largely diverse and mostly of low fertility.

Ice has covered the New Zealand land masses a number of times; the latest ice age were 10,000 years ago, Fig. A2.2. The vegetation at that time was dramatically disturbed, and the land and vegetation is still marked. During the last 1000 years the vegetation has again changed dramatically, this time because of man (Fig. A2.3). The polynesians settled from about 1000 years ago and they have started the burning of forests (partly because of moa-hunting), a feature that was increased with the settlement of Europeans about 150 years ago. Today, the proportion of grass-, tussock- and scrubland is 500.000 hectares larger than before human settlements because of converting the natural bush into farmland (Anderson 1977).

The climate of New Zealand is mostly a maritime warm temperate climate. Positioned in the South Pacific, New Zealand has a place between two world pressure/wind zones; to the North the subtropical high-pressure belt and to the south, the belt of southern "westerlies" (Anderson 1977). The two belts interact, with the northern dominating in summer and the southern in winter.

The western winds prevail, with local modifications (Fig. A2.4). Annual rainfall varies from 250 to more than 6000 mm per year, Fig. A2.4. Mean annual temperature varies from 9°C to 15°C depending on latitude (Fig. A2.4). Frost and snow occur frequently in higher altitudes (Fig. A2.4), and it should be noticed that night frost mostly is replaced with temperatures above 0°C in the day. Annual sunshine hours number about 2000, and day length vary from 8.5 to 15.5 (south of South Island) and 9.5 to 14.5 (north of the North Island) (Fig. A2.4).

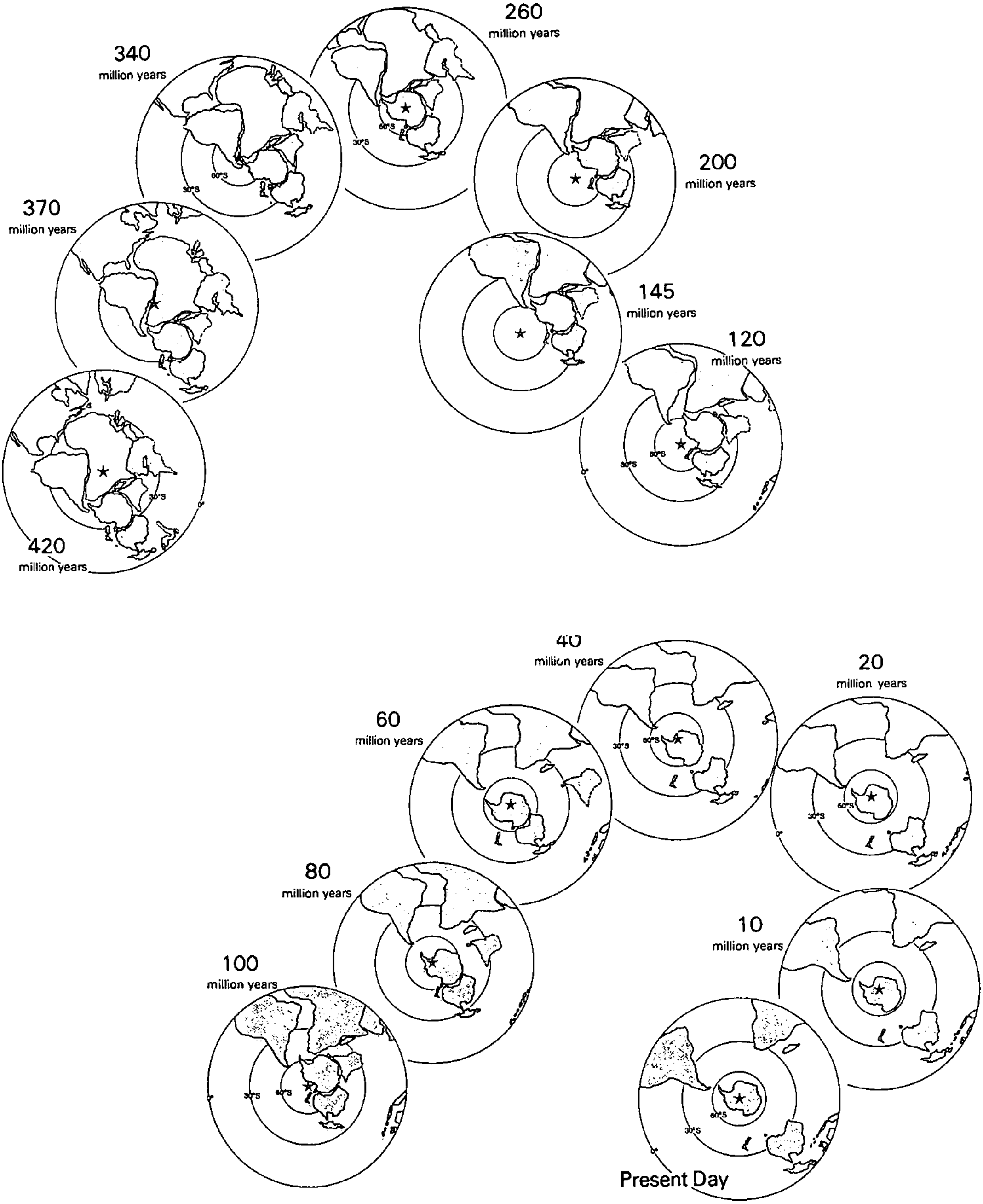


Fig. A2.1. Changing patterns of land and sea in the Southern Hemisphere 420 million years ago to present day. Note that land shapes used are the present land shapes, which are concidered to have changed largely during geological time. (After Stevens 1985).

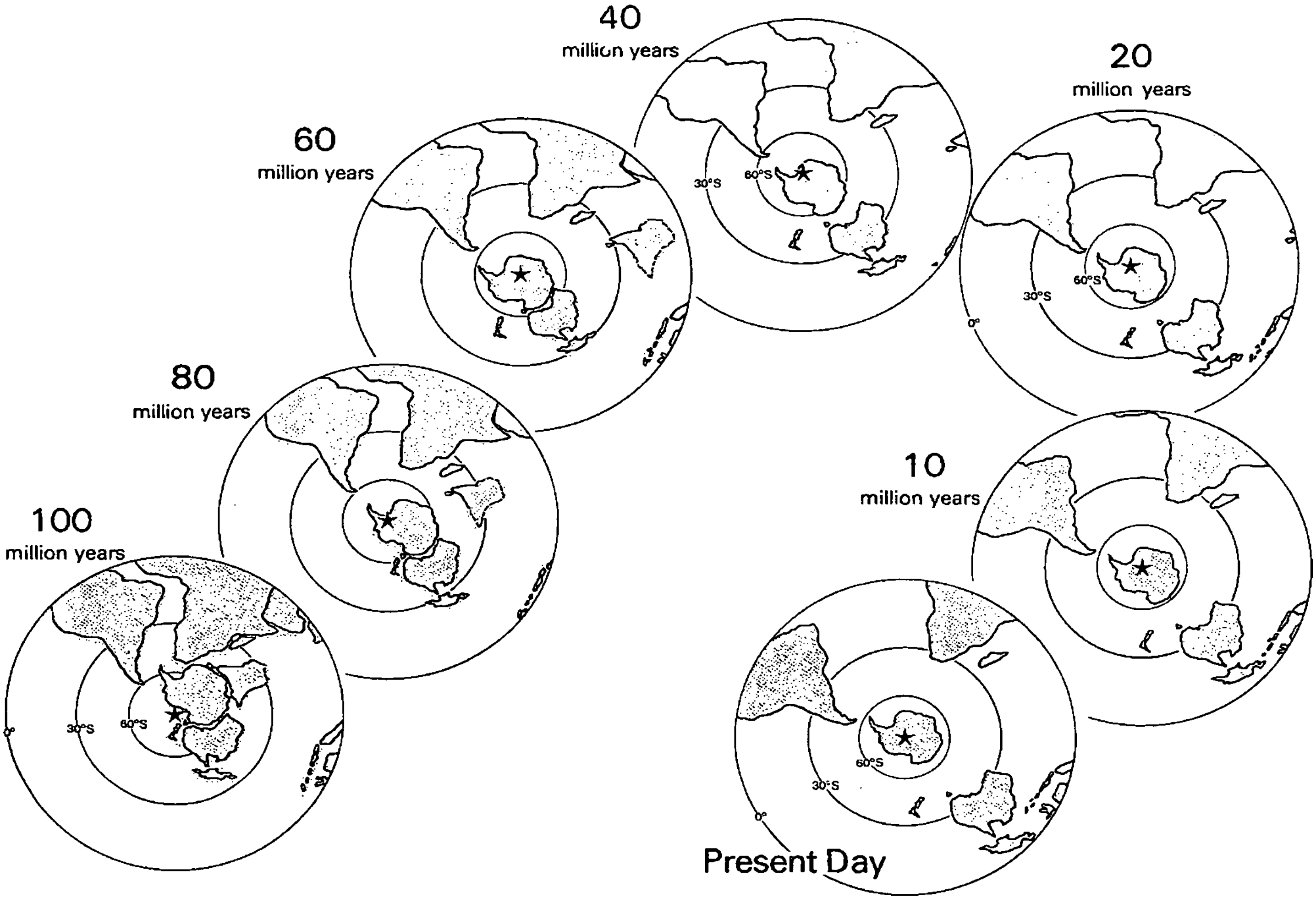


Fig. A2.2. Distribution of vegetation at the last ice age, about 10,000 years ago. (After Wardle 1963A).

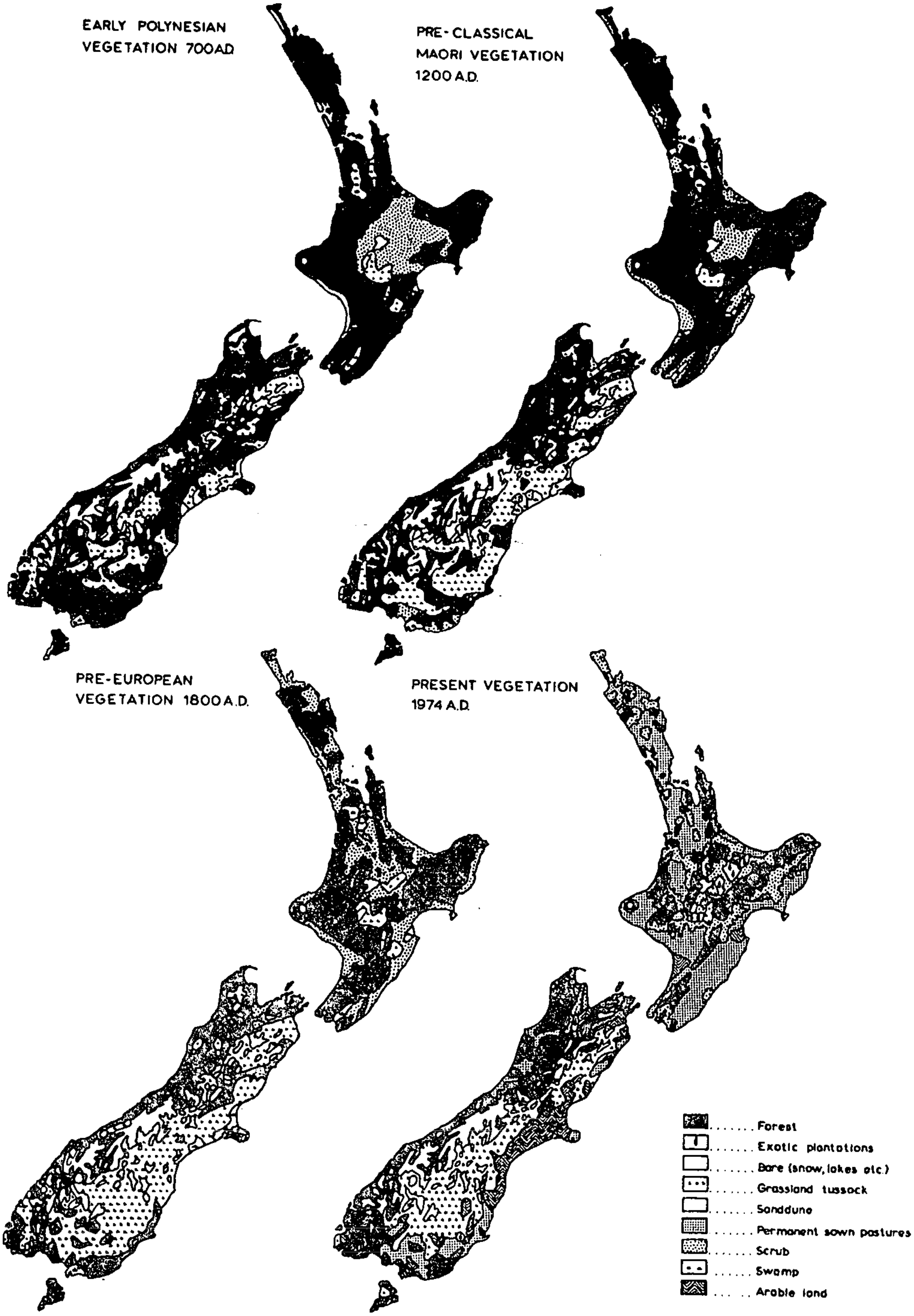
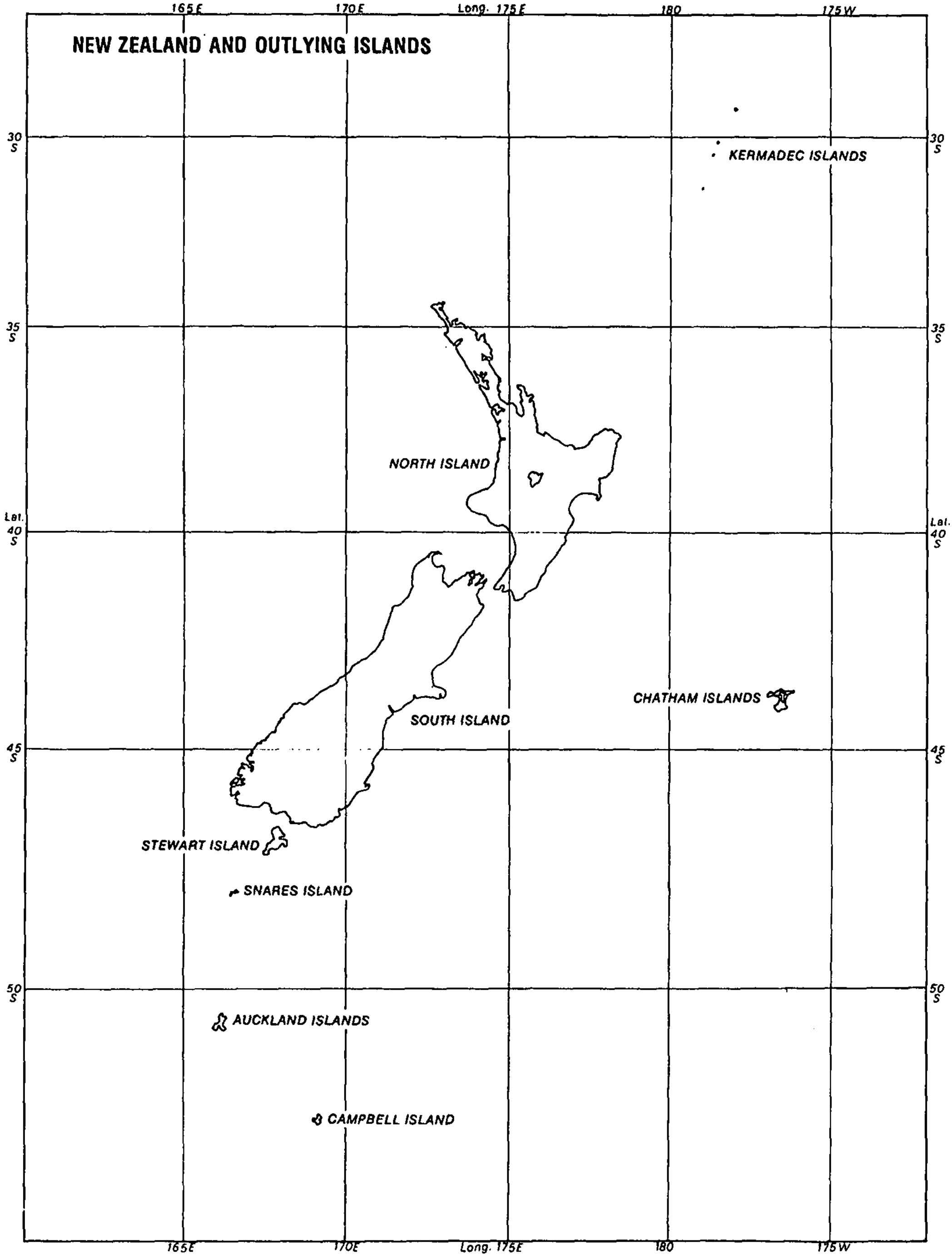


Fig. A2.3. Vegetation cover patterns from before the first settlement of polynesians. (After Anderson 1977).

Fig. A2.4. Climatical characteristics of New Zealand: hours of sunshine, surface temperatures, rainfall, wind frequences and frost season. (After Macaulay and Beavis 1983).


NEW ZEALAND AND OUTLYING ISLANDS

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