Tuhinga 15: 27–41

Geographic variation in *Hebe macrantha* (Plantaginaceae): morphology and flavonoid chemistry

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ABSTRACT: This paper investigates geographic variation in *Hebe macrantha*, endemic to mountains of South Island, New Zealand. It assesses the attributes, distribution, and appropriate taxonomic status of its two previously described varieties, the validity and circumscriptions of which have been questioned by some taxonomists. Morphometric analyses support the existence of two distinguishable entities that equate with previous circumscriptions of these varieties, whose continued recognition is recommended. Variety *brachyphylla* occurs in the north of the species' geographic range, from the Anatoki Range, northwest Nelson, to the Hanmer Range, north Canterbury. Variety *macrantha* is geographically more widespread and morphologically more variable. It occurs in the south of the species' range, south and west from Mt Haast (southwest Nelson) and Lewis Pass (south Nelson/north Canterbury), as well as at Lake Tennyson (southeast Nelson), the only locality at which specimens assigned to both varieties occur. The two varieties are morphologically most similar at localities close to their geographic interface. Patterns of variation in leaf flavonoids neither strongly support nor contradict recognition of the two varieties. Analysed samples share a similar and, within *Hebe*, distinctive flavonoid profile, and the distribution of two flavonoid glycosides is partly correlated with the morphological circumscription of varieties (the correlation is incomplete in samples taken near the geographic interface of varieties). A distribution map and a table of key morphological differences between varieties are provided.

KEYWORDS: *Hebe macrantha*, Scrophulariaceae Plantaginaceae, flavonoids, New Zealand flora.

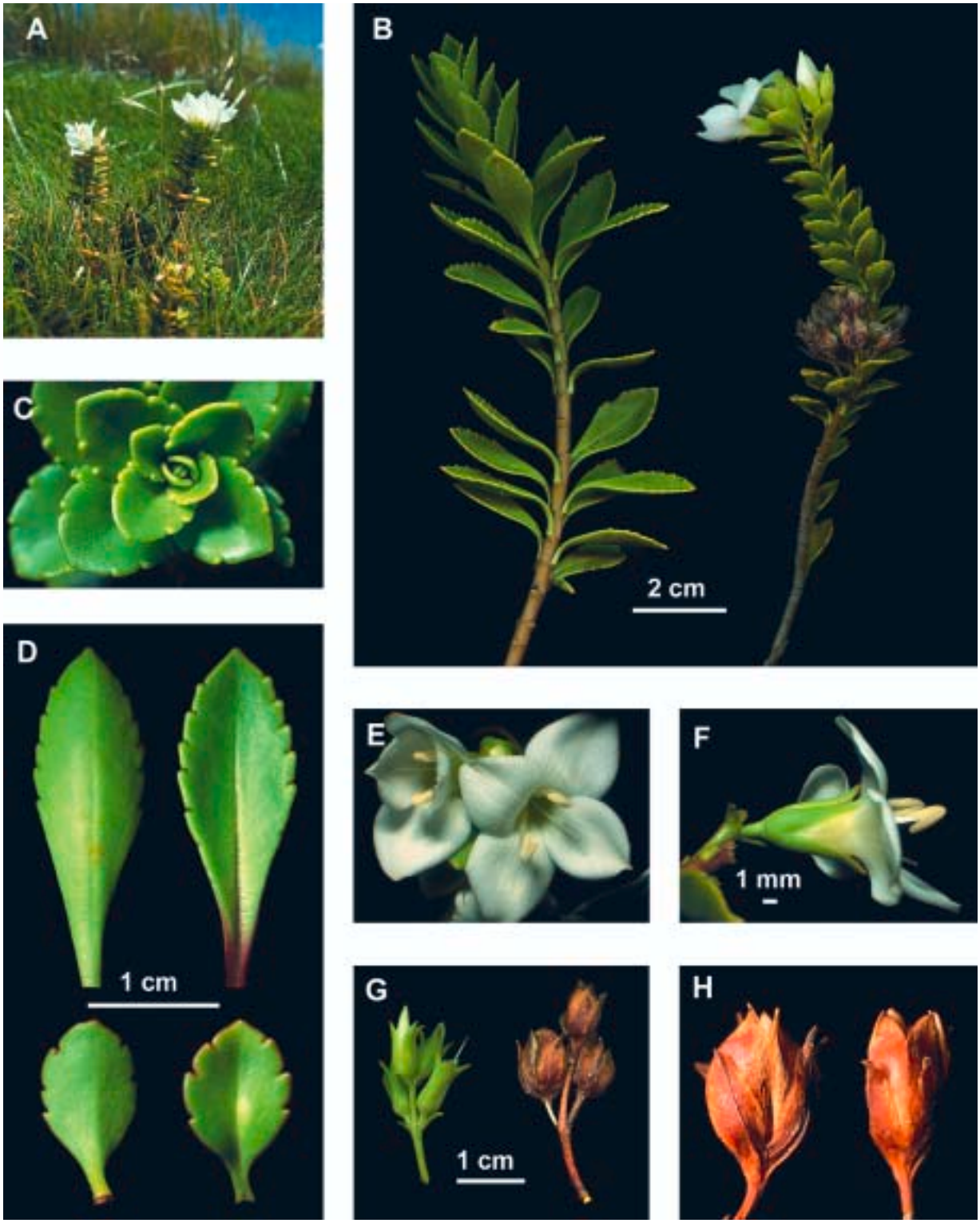

Fig. 1 Some morphological features of *Hebe macrantha*: (**A**) habit of a plant of var. *brachyphylla* on Mt Arthur; (**B**) sprigs of var. *macrantha* (left) and var. *brachyphylla*; (**C**) top view of shoot apex, showing that young leaves diverge early (i.e. there is no prominent 'lead bud' like that seen in many hebes); (**D**) lower and upper leaf surfaces of var. *macrantha* (top) and var. *brachyphylla*; (**E**) inflorescence showing frontal view of flower; (**F**) lateral view of flower; (**G**) inflorescence (left) and infructescence; (**H**) septicidal (left) and loculicidal views of capsule (voucher specimens: A, from same population as WELT 80740; B (left), D (upper), WELT 82429; B (right), E, F, G, WELT 83544; C, D (lower), WELT 82554; H, WELT 83545).

Introduction

Hebe macrantha (Hook.f.) Cockayne et Allan is a distinctive sub-shrub from alpine regions of South Island, New Zealand. It is readily distinguishable from other members of *Hebe* by its much larger flowers (*see* Figs. 1E and 1F), fruits that are laterally compressed (with the septum at right angles to the widest diameter; *see* Fig. 1H), and leaves that are prominently petiolate (*see* Fig. 1D), have toothed margins, and diverge early in bud (*see* Fig. 1C). Moore (in Allan 1961), in an informal infrageneric classification of *Hebe*, placed *H. macrantha* in the monotypic grouping "Grandiflorae", this name referring to the characteristically large flowers. Alternatively, Heads (1987), considered *H. macrantha* best removed from *Hebe* and placed in *Parahebe*, whose members it resembles in many morphological features. More recent analyses of nuclear ribosomal DNA sequences (Wagstaff & Garnock-Jones 1998, Wagstaff *et al.* 2002) group *H. macrantha* with other members of *Hebe*, sister to all other species of the genus (as defined by Wagstaff *et al.* 2002, and followed here).

Cheeseman (1906) reported that specimens of *Hebe macrantha* (as *Veronica macrantha*) 'from Mount Arthur and other parts of the Nelson District have shorter, broader leaves, more numerous racemes and smaller flowers than is usual in Canterbury and Otago …', and provided the variety name *brachyphylla* to distinguish these collections from more typical forms. Cockayne and Allan (1926) agreed with the presence of two varieties of *H. macrantha* (using the name var. *vera* for the typical form), and added that var. *brachyphylla* 'occurs not only in the North-western Botanical District, as given in the *Manual*, but also in the wetter part of the North-eastern District'. Moore (in Allan 1961) also recognised two varieties in *Hebe macrantha*, and further defined them, giving leaf dimensions of *c.* 1.5–2.5 x 0.5–1.0 cm for var. *macrantha* and *c.* 1.3–1.5 x 0.9–1.0 cm for var. *brachyphylla*. This classification, including two varieties, has been followed in subsequent, general works on the New Zealand flora (e.g. Eagle 1982, Druce 1993, Wilson & Galloway 1993, Mark & Adams 1995). Distribution maps for the two varieties are given by Heads (1994a) and Macdonald (1982; with the two maps labelled the wrong way around), with the former providing no data on morphological circumscription, and the latter largely repeating details given by Moore (in Allan 1961).

The study presented here is part of ongoing work toward a revised classification of *Hebe* (e.g. Bayly *et al.* 2000, 2001, 2002, 2003; Garnock-Jones *et al.* 2000; Kellow *et al.* 2003a, b). It aims to identify and describe patterns of geographic variation within *H. macrantha* using data on morphology and leaf flavonoids, and to reassess its infraspecific classification. In particular, it seeks to determine whether or not there are grounds for the recognition of two taxa, and if so, to identify clearly their distinguishing features, map their distributions, and assess their appropriate taxonomic rank.

This study was initiated primarily because an initial survey of specimens suggested that the leaf dimensions specified by Moore (in Allan 1961) were insufficient to identify reliably all specimens to variety rank. A further motivation was the opinion of Prof. P. Garnock-Jones (Victoria University of Wellington), based primarily on field observations of morphological variation in the area around Lake Tennyson, south Nelson Province (personal communication 1997), that there were probably insufficient grounds for recognition of two taxa, and that the classification of *H. macrantha* warranted thorough assessment. Heads (1994a) also suggested that 'the two varieties of the species and their distribution require revision'.

Materials and methods

Morphometric analysis

Fifty-one herbarium specimens from WELT and CHR (*see* Appendix 1; herbarium abbreviations follow Holmgren *et al.* (1990)), covering most of the geographic range of *Hebe macrantha*, were scored for 16 morphological characters (*see* Table 1). The geographic distribution of these specimens is shown in Fig. 4, although three specimens – WELT 13110 ('western Amuri District', presumably somewhere to the west of Hanmer Springs), WELT 13101 ('Ashburton mountains'), and WELT 13111 ('Otago') – have only vague locality information and could not be mapped. Unless each of the fragments on an herbarium specimen was known to be from a single individual (e.g. in the case of MJB collections), or fragments were very small or were uniform in appearance, only one fragment was scored per specimen. In one case, WELT 82420, two fragments on the one sheet were known to be from separate plants, and each was treated as a separate specimen (specimens 12a and 12b in Appendix 1). Vegetative characters were measured for each of 10 leaves and 10 internodes per specimen. Characters of flowers and inflorescences were measured for up to eight flowers or inflorescences per specimen (where available). Character

Table 1 Characters used in the morphometric analysis.

Internode length (INT) (mm)
Lamina length (LL) (mm)
Lamina width (LW) (mm)
Lamina length/lamina width (LL/LW)
Lamina length/total leaf length (LL/TLL)
Distance from leaf base (including petiole) to widest point (DWP) (mm)
Distance to widest point/total leaf length (including petiole) (DWP/TLL)
Petiole length (PET) (mm)
Number of teeth on one side of leaf (the bigger number if uneven)
Peduncle length (mm)
Rachis length (mm)
Rachis length/total inflorescence length
Number of flowers per inflorescence
Length of lowermost bracts on inflorescences (mm)
Pedicel length (mm)
Calyx lobe length (mm)

means were calculated for each specimen and used as input for multivariate and univariate analyses.

For multivariate analyses, data for each character were range-standardised, such that the range of all characters equalled one unit, giving all characters equal weight (recommended by Milligan & Cooper 1988). Pairwise distances between specimens were calculated using the Manhattan metric, and the distance matrix was subjected to clustering by the unweighted pair-group method using arithmetic averages (UPGMA; Sneath & Sokal 1973) and to ordination using non-metric multidimensional scaling (NMDS; Kruskal 1964a, b) in two dimensions, both implemented by NTSYSpc Version 2.11. The results of NMDS are dependent on starting conditions, being based on iterations from an initial configuration of points, and are sensitive to local minima. Here, the procedure was repeated at least 30 times with random starting conditions, and the best result taken as that with the lowest stress value – i.e. best fit to the distance matrix.

Univariate comparisons were made between the two major groups of specimens identified by UPGMA analysis. Prior to comparison, data for each character were subjected to the Kolmogorov-Smirnov test for normality (Sokal & Rohlf 1969) and Levene's median test for homogeneity of variance (Levene 1960). For characters that passed tests for normality and equal variance ($P > 0.05$), t-tests were used to compare groups. For characters that failed either test, the Mann-Whitney Rank Sum Test was used to compare groups. These analyses were performed using SigmaStat for Windows Version 2.0.

Examination of additional herbarium specimens

Results of the morphometric analysis were assessed by reference to further herbarium material. All specimens of *Hebe macrantha* at WELT and CHR (95 additional specimens) were assessed for the five most discriminating morphological characters, and on the basis of their geographic origin, to determine whether variation among all specimens was congruent with, and adequately reflected by, that shown in the morphometric study.

Analysis of leaf flavonoids

Leaf samples collected from wild populations were placed in press-seal plastic bags with silica gel and couriered to the laboratories of Industrial Research, Lower Hutt. Voucher specimens are listed in Table 3, and sampling localities are indicated on Fig. 4.

Flavonoids were extracted from dried samples, and were separated and identified using the methods of two-dimensional paper chromatography (2DPC) and high-performance liquid chromatography outlined by Bayly *et al.* (2002, 2003). For the purpose of this report, results are shown only for compounds definitely present in two or more samples. A number of additional compounds were found in only one sample, or could not be distinguished with certainty (in a range of samples). Details of these compounds, which do not influence conclusions presented here, will be published elsewhere in a more comprehensive summary of *Hebe* flavonoids (Markham *et al.* in preparation).

Results

Morphometric analysis

UPGMA analysis produced a single dendrogram, i.e. there were no 'ties' between groups at any stage in the tree-building process. The primary dichotomy on this tree distinguishes two clusters, groups A and B (*see* Fig. 2),

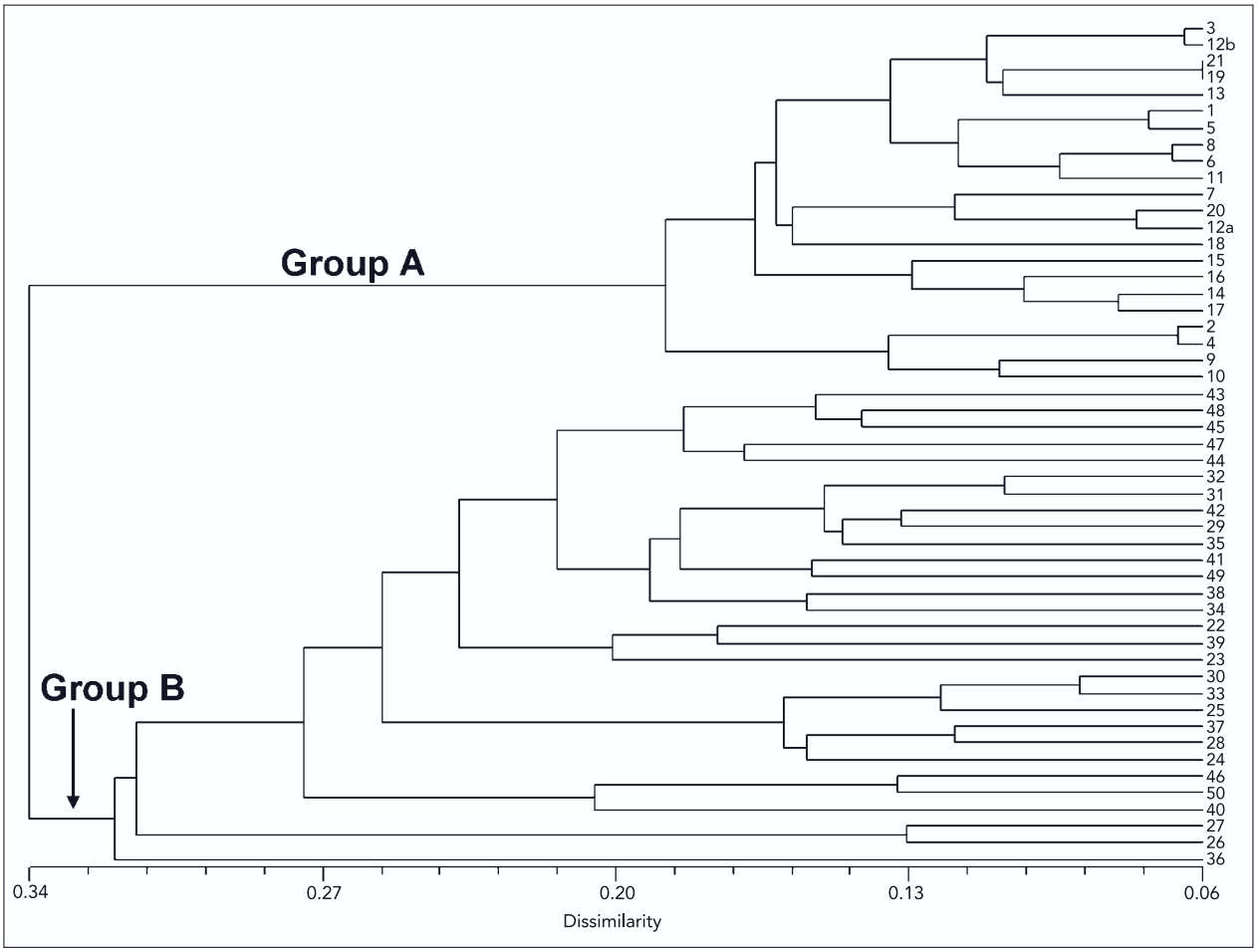

Fig. 2 UPGMA tree derived from analysis of morphometric characters. Specimen numbers are as given in Appendix 1. In the classification adopted here: Group A = *Hebe macrantha* var. *brachyphylla*; Group B = *H. macrantha* var. *macrantha*.

which are also separated in the NMDS ordination (*see* Fig. 3). Specimens of groups A and B overlap in their geographic distribution only slightly (*see* Fig. 4), and correspond broadly with previously accepted geographic limits of var. *brachyphylla* and var. *macrantha*, respectively. Group A includes specimens from localities between the Peel Range, northwest Nelson, and Mt St Patrick and Mt Percival, northeast Canterbury. Group B includes all specimens from localities south and west of Mt Haast and Lewis Pass, as well as one specimen from Lake Tennyson. Lake Tennyson is the only locality at which specimens of both groups occur. It is evident from both the UPGMA dendrogram and the NMDS ordination that specimens of Group A, which is geographically more restricted, are generally more similar to each other than are specimens of the more widespread, and more variable, Group B.

Variation in individual morphological characters within and between the two groups, together with the results of univariate statistical comparisons, are summarised in Fig. 5. All characters show some overlap in range between the two groups, but most comparisons, nonetheless, show statistically significant differences between groups (the only characters not significantly differing between the two groups are lamina width (*see* Fig. 5C), the ratio of lamina length to total leaf length (*see* Fig. 5E), and rachis length (*see* Fig. 5K)). The characters providing greatest differentiation between groups (the least amount of overlap, in terms of mean values for specimens) are the length of lowermost inflorescence bracts (*see* Fig. 5N), the number of teeth on leaf margins (*see* Fig. 5I), the ratio of leaf lamina length to width (*see* Fig. 5D), the distance from leaf bases to their widest points (DWP; *see* Fig. 5F), and peduncle length

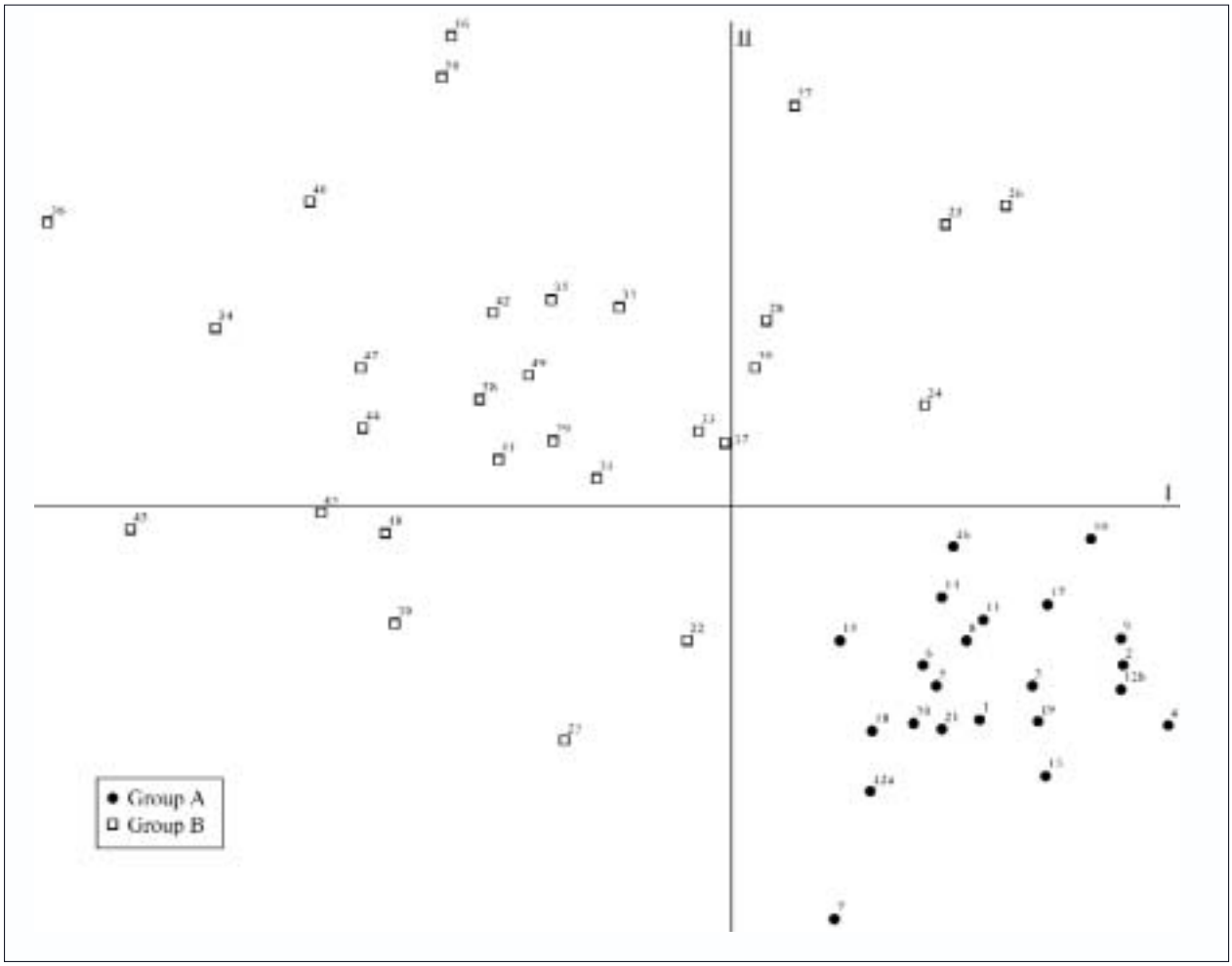

Fig. 3 Two-dimensional NMDS ordination derived from analysis of morphometric characters. Specimen numbers are as given in Appendix 1. Groups A and B are the same as shown in Fig. 2. In the classification adopted here: Group A = *Hebe macrantha* var. *brachyphylla*; Group B = *H. macrantha* var. *macrantha*.

(*see* Fig. 5J). In general, specimens of Group B frequently also have longer leaf laminae (*see* Fig. 5B), more obovate leaves (i.e. with a greater ratio of DWP to total leaf length; *see* Fig. 5G), longer petioles (*see* Fig. 5H), a lower ratio of rachis length to total inflorescence length (*see* Fig. 5L), longer pedicels (*see* Fig. 5O), and longer calyx lobes (*see* Fig. 5P). Group B specimens sometimes also have longer internodes (*see* Fig. 5A) and fewer flowers per inflorescence (*see* Fig. 5M), but there is substantial overlap between groups in these characters (the probability, or *p* value, that group means/medians are different is between 0.05 and 0.001).

Results of the NMDS show that specimens of Group A and Group B are most similar at localities close to the geographic interface between these groups. In particular, three Group B specimens – one from Mt Haast (specimen 24), one from Lake Tennyson (specimen 23), and one from 'western Amuri district' (specimen 22) – are placed in positions intermediate between Group A and remaining Group B specimens. Likewise, among the Group A specimens closest to those of Group B are one from Mt Mantell (specimen 14), one from Lake Tennyson (specimen 16), and one from Baldy (specimen 15); these three specimens, together with one other from Lake Tennyson, specimen 17, also form a group in the UPGMA dendrogram.

Within Group A, patterns of similarity among specimens, apart from the similarity of those specimens from near the southwest of the group's geographic range

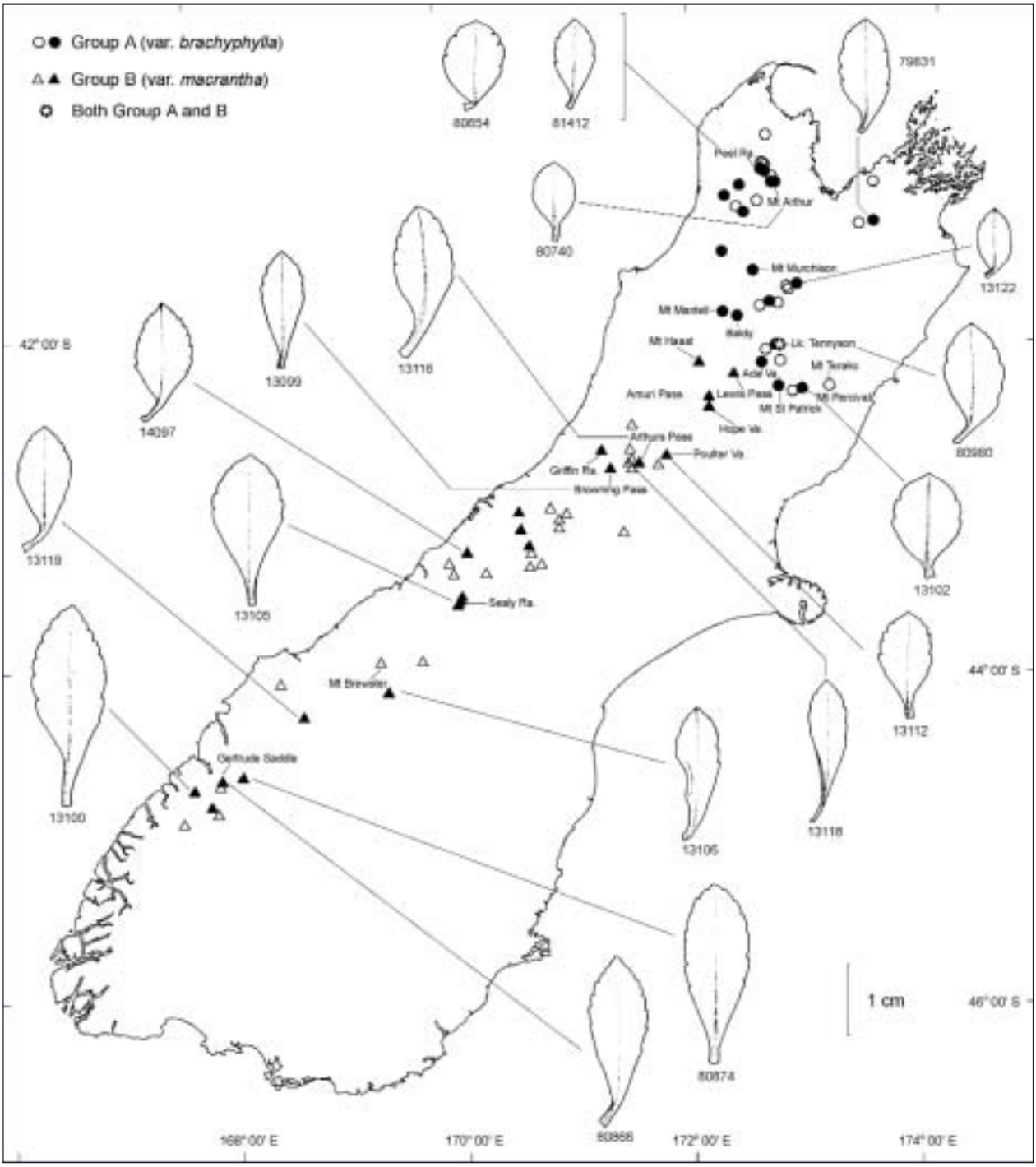

Fig. 4 Map of South Island, New Zealand, showing the distribution of *Hebe macrantha* and some examples of leaf shape and size. Closed symbols indicate localities represented by specimens in the morphometric analysis. Names are given only for localities mentioned in the text, and those from which flavonoid samples were collected. Numbers under leaf outlines are WELT numbers for the specimens from which they were drawn. Scale bar is for leaf outlines.

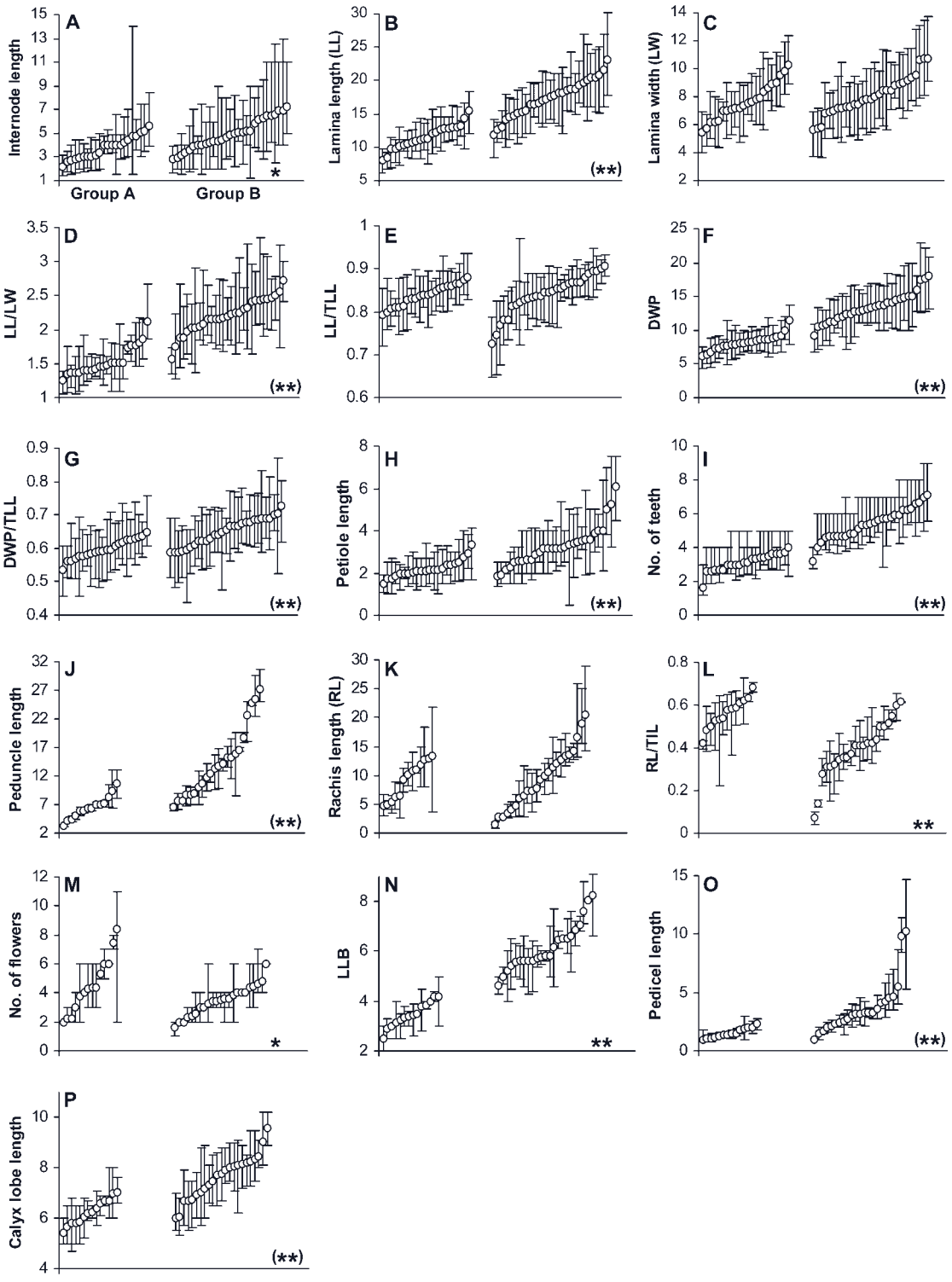

Fig. 5 Graphs showing variation in 16 morphological characters. Each data point represents one specimen (of those listed in Appendix 1), and shows the mean, maximum, and minimum measurement for the character. Specimens are sorted into the two groups (Groups A and B) recovered by UPGMA analysis (*see* Fig. 2), and arranged within these groups by mean value for each character. Asterisks at the bottom right of graphs indicate statistically significant differences between groups for that character (* = $p < 0.05$; ** = $p < 0.001$), based on a Mann-Whitney Rank Sum Test (asterisks in parentheses), or t-test (no parentheses). Units on graphs are millimetres, except for I and M (which are absolute numbers), and ratios given on D, E, G, and L (which are unitless). Character abbreviations are as given in Table 1. In the classification adopted here: Group A = *Hebe macrantha* var. *brachyphylla*; Group B = *H. macrantha* var. *macrantha*.

Table 2 Ranges of variation, based on all herbarium specimens at WELT and CHR, for the five morphological characters best discriminating Groups A and B.

Character	Group A (var. *brachyphylla*)	Group B (var. *macrantha*)
Lamina length/lamina width	(0.97–)1.1–2.2(–2.9)	1.2–3.3(–3.8)
Distance from leaf base (including petiole) to widest point (mm)	(4.4–)6–11(–13.8)	(5.1–)10–20(–23.2)
Number of teeth on one side of leaf	(0–)1–4(–5)*	(2–)3–7(–11)
Peduncle length (mm)	(1.5–)3.0–13.0	(6–)7.0–30.7
Length of lowermost bracts on inflorescence (mm)	2–4(–8)†	(4–)5–9.1

* Value = 0 on only a few leaves of WELT 80740 (Mt Arthur).

† Extreme value of 8 mm seen only on CHR 333979 (Mt Arthur), which has unusually large flowers. Lowermost bracts on all other specimens ≤ 5 mm.

(specimens 14, 16, and 15), show no strong geographic association. In contrast, within Group B, there is some additional, though partial, geographic correlation in patterns of similarity among specimens. For instance, specimens from Amuri Pass (specimens 26 and 27) are placed near that from near Lewis Pass (specimen 25) in the NMDS ordination. Together, these specimens are close to those from the Hope (specimen 28) and Poulter valleys (specimen 30), and all of these are close to those from Browning Pass (specimen 33), Arthurs Pass (specimens 31 and 32), and the Griffin Range (specimen 29). Also, five of the six Fiordland specimens (specimens 43, 44, 45, 47, and 48) cluster closely in both the NMDS ordination and the UPGMA dendrogram. There is, therefore, a general trend in the arrangement of specimens on axis I of the ordination that correlates roughly, though not absolutely, with latitude – i.e. south to north, moving from left to right on the axis.

Examination of additional herbarium specimens

Variation in additional herbarium specimens at WELT and CHR was generally consistent with that seen in the morphometric study. Specimens that would, on the basis of geographic origin, be placed in either Group A or Group B were generally also, in terms of the five most discriminating morphological features, morphologically consistent with these groups. Placing all specimens in groups in this way required only minor modification of the ranges of some morphological characters for each group. The morphological ranges of Group A and Group B for the five most discriminating characters (using all specimens at WELT and CHR) are shown in Table 2 (compare with Fig. 5 for minor differences from character ranges in the subset of specimens used in morphometric analyses).

Leaf flavonoid composition

Flavonoids identified in *Hebe macrantha* in general resemble those found in other *Hebe* species. Flavonoids with the basic apigenin and luteolin oxygenation patterns, and glycosylated at the 7-hydroxyl group (e.g. compounds **4** and **10**), are found throughout *H. macrantha,* as also is luteolin glycosylated at the 4-hydroxyl (**1a**). Luteolin glycosylated at the 3-hydroxyl (**1b**), however, is only conspicuously evident in the Group A samples and in one Group B sample (WELT 81716). Modification of the basic apigenin and luteolin aglycone types in *H. macrantha* includes *C*-glycosylation (in some Group B specimens only) and 6- and 8-oxygenation (in both groups). Further biosynthetic elaboration of the 6-hydroxyluteolin flavonoid nucleus, as evidenced by the accumulation of a 6-methoxyluteolin glycoside (**3**), is seen consistently only in Group B. Also confined to Group B, although not in all samples, is the unidentified flavonoid 'r', which possesses an absorption spectrum that suggests it is an 8-hydroxyluteolin-8-*O*-glycoside.

Table 3 Presence/absence of flavonoid compounds in each of the samples analysed. Key: +, conspicuous presence on 2DPC; w, weak presence on 2DPC; ?, possible or uncertain occurrence (after a structure name it indicates a tentative identification); L, luteolin; A, apigenin; OMe, methoxy; OH, hydroxy. Each compound is given a number/letter code that is part of a database (being developed at Industrial Research) of all major flavonoid compounds in *Hebe*. Asterisks (*) after voucher numbers indicate specimens also included in morphometric analysis.

Voucher (WELT no.)	Locality	**10** A-7-*O*-glucoside	**3e** 6OHA(like)-glycoside	**5e** 6OHA(like)-glycoside	**24** A-6,8-di-*C*-glucoside	**4** L-7-*O*-glucoside	**12a** L-7-*O*-[2-*O*-rhamnoglucoside]	**1b** L-3'-*O*-glucoside	**1a** L-4'-*O*-glucoside	**8b** 6OHL-7-*O*-[2-*O*-xyloglucoside]	**9** 6OHL-7-*O*-[2-*O*-glucoglucoside]	**3** 6OMeL-7-*O*-glucoside	**5a** 8OHL-7-*O*-glucoside	**r** Unidentified flavonoid
Group A	(**var. *brachyphylla***)													
80653[§]	Peel Range	+	+	+		+	+	+	+	+			+	
80653[§]	Peel Range	+	+			+	+	+	+	+			+	
82420*	Mt Murchison	w	+			+	w	+	+	+			+	
80980*	Lake Tennyson	+	+	+		+		+	+	+		+	+	
Group B	(**var. *macrantha***)													
81671*	Mt Haast	+	w		w	+			+	+	w	+	+	w
81716*	Amuri Pass	+	+	+	+	+		+	+	+		+	+	w
80507	Sealy Range	w		+	w	+		?	+	+	w	+	+	
81622	Sealy Range	+		+		+	?	w	+	+		+	+	
82429	Near Mt Brewster	+		?		+	+		+	+		+	+	w
82430	Near Mt Brewster	+	+	+		+		?	+	+		+	+	
80866*	Gertrude Saddle	+	+	+		+		w	+	+	+	+	+	
80867*	Gertrude Saddle	+	+	+		+		?	+	+	w	+	+	w

§ These are samples from two individuals in the same population (first row = M.J. Bayly 472; second row = M.J. Bayly 474).

These observations indicate some partial differences in the biosynthetic enzyme activities between the two groups. For example, luteolin-3'-*O*-glucosyltransferase (which produces compound **1b** from luteolin in Group A) is absent or largely ineffective in Group B. Conversely, 6-hydroxyluteolin-6-*O*-methyltransferase (which converts 6-hydroxyluteolin-7-*O*-glucoside into 6-methoxyluteolin-7-*O*-glucoside, **3**) is chiefly functional only in Group B plants. It is noteworthy that both of these differences between the two groups are least pronounced in samples from near their geographic interface, i.e. the only Group A sample producing compound **3** was from Lake Tennyson, while the only Group B sample producing a conspicuous amount of **1b** was from Amuri Pass.

A distinctive feature in the flavonoid constituents of *Hebe macrantha* (both groups) is the occurrence of compounds **3e** and **5e**. The aglycone moiety is the same for each compound and, although unidentified, is similar to, but not identical with, 6-hydroxyapigenin, based on the uv/visible absorption spectra. Glycosides of this aglycone are not found in quantities above trace levels in other hebes, except in the informal group "Semiflagriformes" of Moore (in Allan 1961), which could, on phylogenetic grounds (Wagstaff *et al.* 2002), be considered a distinct genus, *Leonohebe* Heads (but in a narrower circumscription than proposed by Heads 1987, 1994b, c).

Discussion

Appropriate classification

Analyses of morphological data differentiate two groups of specimens, with a small number of specimens (e.g. specimens 22, 23, and 24 of Group B) having somewhat intermediate characteristics. These groups have substantial, only narrowly sympatric, geographic ranges, indicating that patterns of morphological variation are far from random, and supporting the view that the groups are worthy of taxonomic recognition. Given that all specimens share distinctive characters of flowers, fruits, and leaves (*see* 'Introduction'), have similar flavonoid profiles, and that variation is mostly quantitative, with the ranges of all characters overlapping in the two morphological groups, recognition at infraspecific rank is most appropriate. The ranks of subspecies or variety could possibly equally be used (given the different ways in which they are used by different authors), but here we suggest the continued use of variety rank. This is chiefly because of the degree of morphological and geographic separation of the groups, and the presence of somewhat intermediate specimens. This choice also allows continued use of the existing variety names, var. *macrantha* and var. *brachyphylla*, avoiding the creation of new names or combinations.

Defining the morphological limits of var. *macrantha* and var. *brachyphylla* is not straightforward, given that some specimens are somewhat intermediate between the two main groups. Here, the two varieties are defined such that they correspond to the two groups identified in the UPGMA dendrogram, and have the key characteristics outlined in Table 2. The taxonomic placement of some intermediate specimens could be debated, and other, perhaps less mathematical methods, could possibly be used to define groups; if anything, the pattern of morphological variation might allow a slightly broader definition of var. *brachyphylla*, but not of var. *macrantha*. However the two varieties are separated, the fact would remain that most specimens could readily be placed under one variety or the other, but that a small number would be more problematic. For problematic specimens, understanding where they stand in relation to the pattern of variation in the species is probably more important than what name they are given. Further collecting could, of course, extend both the geographic and morphological ranges of the two varieties, and, particularly in south Nelson, could potentially affect interpretations of the boundaries between them.

Patterns of variation in leaf flavonoids neither strongly support nor contradict recognition of the two varieties. The similarity of the flavonoid profiles of all samples supports the view that members of the species are closely related. Partial correlation in the distribution of both compounds **3** and **1b** with the morphological circumscriptions of varieties is interesting, but further sampling would be required to judge the consistency and significance of these results. Lack of substantial flavonoid variation within species, including between infraspecific taxa, is not unusual (Bohm 1987), and is also seen in other *Hebe* species, e.g. *H. stenophylla* (Mitchell *et al.* 2001) and *H. stricta* (unpublished data).

Distribution of varieties

The distribution map presented here (*see* Fig. 4) shows some differences from those previously presented by Macdonald (1982) and Heads (1994a), particularly in southern Nelson (map of Macdonald) and in the northern part of the range of var. *macrantha* (map of Heads).

Differences partly reflect different sources of herbarium specimens (Macdonald used CHR and CANU; Heads used a range of herbarium specimens, as well as published and unpublished records, and personal field observations) and collecting subsequent to publication of the earlier maps. They also reflect different interpretations of the identity of some specimens, e.g. Heads (1994a) identified specimen(s) from Mt Haast as var. *brachyphylla*, and that/those from Mt Terako as var. *macrantha* (for which reverse identifications are accepted here).

Wilson (1991) provided a map of *Hebe macrantha*, not distinguishing or mentioning the different varieties, in the provinces of Canterbury and Westland. That map shows a similar distribution to that presented here. However, it was based not only on herbarium specimens, but also on published and unpublished reports and extensive field observation, and shows more detail of the species distribution in some areas.

Historical interpretation

Several explanations could be offered for the pattern of variation in *Hebe macrantha*, i.e. that there are two more or less well-defined groups, with some geographic overlap and some morphologically intermediate specimens. This pattern could result from ongoing, *in situ*, differentiation of forms from within a cline of variation. It could also result from the introgression of two previously differentiated forms, e.g. if the species' distribution was restricted in glacial periods to separated refugia (say one in Nelson and one further south), and separated populations differentiated from each other and then subsequently expanded their ranges with the coming of interglacial conditions. The data provided here cannot distinguish between these or other (possibly more complex) hypotheses. The partial geographic correlation of variation, especially in var. *macrantha*, is possibly suggestive of a north–south cline of variation, but these patterns are not clear-cut, and variation within var. *brachyphylla* is less strongly correlated with latitude. Use of further sources of data (e.g. DNA sequencing or fingerprinting) could provide further insight into the historical basis of observed variation.

Acknowledgements

David Glenny, Debra Wotton, Phil Garnock-Jones, Bill Malcolm, Barbara Brown, Ilse Breitwieser, and Rainer Vogt all provided assistance with fieldwork. Bill Malcolm provided the photographs for Figs 1C, 1D, 1E, 1F, and 1H. Patrick Brownsey, Phil Garnock-Jones, and Leon Perrie provided constructive comments on the draft manuscript. The Director and staff of CHR provided access to collections and a loan of herbarium specimens. The Department of Conservation provided permits to collect in reserves under their control. This research was funded by a grant from the Foundation for Research, Science and Technology (contract MNZX0201).

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Appendix 1: details of specimens used in morphometric analysis.

Asterisks (*) indicate whether specimens were scored for vegetative (Veg.) and/or inflorescence/flower (Infl.) characters.

CSpec. No.	Herb. No.	Locality	Latitude	Longitude	Collector(s)	Date	Veg.	Infl.
Var. *brachyphylla*								
1	WELT 80671	Peel Range, just east of Thoms Creek	41° 8'S	172° 35'E	M.J. Bayly 490, A.V. Kellow & D. Glenny	07.01.1997	*	*
2	WELT 80652	Peel Range, along track to Lake Peel from Myttons Hut	41° 9'S	172° 37'E	M.J. Bayly 471, D. Glenny & A.V. Kellow	07.01.1997	*	*
3	WELT 80654	Peel Range, along track to Lake Peel from Myttons Hut	41° 9'S	172° 37'E	M.J. Bayly 473, D. Glenny & A.V. Kellow	07.01.1997	*	
4	WELT 80740	Along track to Mt Arthur	41° 13'S	172° 42'E	M.J. Bayly 560, D. Glenny & I. Breitwieser	13.02.1997	*	*
5	WELT 13108	Arthur Range, Mt Arthur	41° 13'S	172° 41'E	T.F. Cheeseman	01.1886	*	*
6	WELT 13122	Arthur Range, Mt Arthur	41° 13'S	172° 41'E	T.F. Cheeseman	01.1886	*	*
7	CHR 358531	Garibaldi Ridge	41° 14'S	172° 25'E	A.P. Druce	01.03.1980	*	*
8	WELT 14905	Arthur Range, Cowin Spur	41° 18'S	172° 18'E	W.R.B. Oliver	24.01.1956	*	*
9	CHR 219913	North Branch Wangapeka River, ridge below Mt Luna	41° 24'S	172° 27'E	B.H. Macmillan 71/103	23.01.1971	*	*
10	WELT 79831	Richmond Range, Mt Fishtail	41° 27'S	173° 30'E	J. Hadfield	11.1932	*	
11	CHR 355250	North west Nelson, Matiri range	41° 38'S	172° 17'E	A.P. Druce	03.1979	*	*
12a&b	WELT 82420	Braeburn Range, Mt Murchison	41° 45'S	172° 31'E	M.J. Bayly 1467 & A.V. Kellow	12.01.2001	*	
13	CHR 198132	Nelson Lakes, Mt Misery	41° 56'S	172° 40'E	—	—	*	*
14	CHR 506839	North of Maruia Saddle, Mt Mantell	42° 0'S	172° 17'E	B.H. Macmillan 94/41	30.01.1994	*	*
15	CHR 401820	South-south-west of Mt Baldy [Baldy]	42° 2'S	172° 24'E	A.P. Druce	01.03.1984	*	*
16	CHR 280430	Lake Tennyson	42° 12'S	172° 44'E	P.J. Garnock-Jones 451	18.01.1976	*	
17	WELT 80980	Lake Tennyson, near south-west corner of lake	42° 13'S	172° 45'E	M.J. Bayly 763, P.J. Garnock-Jones & W. Malcolm	18.12.1997	*	
18	CHR 10743	Spencer Mountains, Ada Valley	42° 19'S	172° 36'E	R.M. Laing	14.01.1949	*	*
19	CHR 228691	Mt St Patrick	42° 27'S	172° 44'E	—	01.1972	*	
20	CHR 333978	Hanmer Range, Mt Percival	42° 28'S	172° 56'E	A. Wall	01.1919	*	
21	WELT 13102	Hanmer Range, Mt Percival	42° 28'S	172° 56'E	D. Petrie	10.02.1914	*	*

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22	WELT 13110	Western Amuri District	—	—	W.G. Morrison	—	*	*
23	CHR 280428	Hillside above Lake Tennyson	42° 12'S	172° 43'E	P.J. Garnock-Jones	18.01.1976	*	*
24	WELT 81671	Mt Haast, northeast slopes	42° 18'S	172° 5'E	M.J. Bayly & D. Wotton	12.12.1999	*	
25	CHR 323544	West of Lewis Pass	42° 23'S	172° 22'E	A.P. Druce	01.1978	*	
26	WELT 81715	Amuri Pass	42° 31'S	172° 45'E	M.J. Bayly 1287 & A.V. Kellow	30.12.1999	*	
27	WELT 81716	Amuri Pass	42° 31'S	172° 45'E	M.J. Bayly 1288 & A.V. Kellow	30.12.1999	*	*
28	CHR 479927	Upper Hope Valley, Top Hope Hut vicinity	42° 35'S	172° 10'E	D.R. Given 11216 & P. Douglass	03.1978	*	
29	CHR 63421	Griffen [Griffin] Range, south of Taramakau river	42° 50'S	171° 17'E	W. Mackay	20.01.1924	*	*
30	WELT 13112	Near Poulter River, Green Hill	42° 52'S	171° 49'E	L. Cockayne	22.01.1900	*	*
31	WELT 13116	Arthurs Pass, Blimit	42° 55'S	171° 35'E	W.R.B. Oliver	26.01.1928	*	*
32	WELT 14906	Arthurs Pass, Blimit	42° 55'S	171° 35'E	W.R.B. Oliver	26.01.1928	*	
33	WELT 13099	Main divide, Browning Pass	42° 57'S	171° 21'E	K. Thomas	—	*	*
34	CHR 499955	Mt Wilberg	43° 12'S	170° 35'E	P. Wardle, R.P. Buxton & K.A. Ford	27.04.1993	*	*
35	CHR 317876	Barlow River, south of south fork	43° 18'S	170° 36'E	A.D. Campbell, D. Prouting & W. Wooff	02.1978	*	*
36	CHR 469139	Two Thumb Range, Eric Stream	43° 24'S	170° 40'E	A.P. Druce 214	02.1991	*	*
37	WELT 14907	Franz Josef, Alex Knob	43° 26'S	170° 9'E	W.R.B. Oliver	22.01.1950	*	*
38	WELT 13123	Mt Cook, Hooker Valley	43° 42'S	170° 6'E	T.F. Cheeseman	—	*	*
39	WELT 13104	Mt Cook, near old Hermitage	43° 44'S	170° 5'E	Boyd	02.1891	*	*
40	WELT 13105	Mt Cook, Sealy Range	43° 45'S	170° 5'E	D. Petrie	02.1911	*	*
41	WELT 13106	Lake Hawea, Hunter River	44° 16'S	169° 27'E	R.A. Wilson	04.1920	*	*
42	WELT 13119	Mt Aspiring	44° 23'S	168° 44'E	—	—	*	*
43	WELT 80874	Lake Harris, near south edge of lake	44° 44'S	168° 11'E	M.J. Bayly 600, D. Glenny & B. Brown	28.02.1997	*	*
44	WELT 80866	Gertrude Saddle	44° 45'S	168° 1'E	M.J. Bayly 592, D. Glenny & B. Brown	25.02.1997	*	*
45	WELT 80867	Gertrude Saddle	44° 45'S	168° 1'E	M.J. Bayly 593, D. Glenny & B. Brown	25.02.1997	*	*
46	WELT 13103	Clinton Saddle	44° 48'S	167° 46'E	D. Petrie	01.1892	*	*
47	WELT 13113	Clinton Saddle	44° 48'S	167° 46'E	L. Cockayne	—	*	*
48	WELT 13109	Clinton Valley	44° 54'S	167° 55'E	J.W. Murdoch	1912	*	*
49	WELT 13101	Ashburton mountains	—	—	T.H. Potts	—	*	*
50	WELT 13111	Otago	—	—	—	—	*	*