Anal. Inst. Bot. Cavanilles 32 (2): 419-440 (1975)

THE ALPINE FLORA OF TIERRA DEL FUEGO

by

D. M. MOORE

This paper is dedicated to Prof. S. Rivas Goday on his 70th birthday.

INTRODUCTION

Since the first known collection of Fuegian plants, made along the NW coast of Tierra del Fuego by George Handisyd in 1690 (MORETON-MIDDLETON, 1909; GUNCKEL, 1971), more than 200 collectors have contributed to our knowledge of the flora of this region (Moore and Goodall, unpub.). Because of the importance of shipborne expeditions, most of the earlier studies were confined to coastal areas and fuller information on the interior did not become available until the expeditions of Nordenskjold (DUSÉN, 1900), SKOTTSBERG (1916) and ROIVAINEN (1954) during the late 19th and early 20th centuries. Since then there has, of course, been a continued accumulation of data on the flora and vegetation of Tierra del Fuego so that now, although many problems remain, the general characteristics are fairly clear.

The mountainous regions of Tierra del Fuego are generally difficult of access and have uncertain and inclement weather so that even today many parts have not been visited by botanists. However, the travels of ALBOFF (1896, 1897), DUSÉN (1900), GUSINDE (SKOTTSBERG, 1926) and SKOTTSBERG (1916) served to outline the general features of the alpine flora and these have been confirmed and amplified by more recent studies (GODLEY, 1960; MOORE, 1969, 1970, 1971, etc; MOORE and GOODALL, 1973, 1974, etc.). In consequence, despite the inevitable lacunae in our knowledge, it seems appropriate to summarize current information on the alpine flora of Tierra del Fuego and this paper represents the first such attempt since that of SKOTTSBERG (1916).

Geology and Structure

Virtually all the high ground of Tierra del Fuego lies in the south and west of the region (fig. 1), only parts of the Altos del Boquerón exceeding 500 m in the northern half of the Isla Grande. The line of the great depression occupied by Seno Almirantazgo, Rio Azopardo and Lago Fagnano serves to divide the Fuegian mountains into two geologically and topographically distinct groups. North of this line the mountains rise rather evenly to 6-700 m, with deep, densely wooded valleys between them; the slopes are comparatively gentle and sharp summits of alpine character are lacking. The climate is much drier than in the southern mountains and there is no permanent ice. This group, which has been termed the «Marginal Cordillera» (Kranck, 1932) or «Pre-Cordillera» (Bonarelli, 1917), is composed of Cretaceous

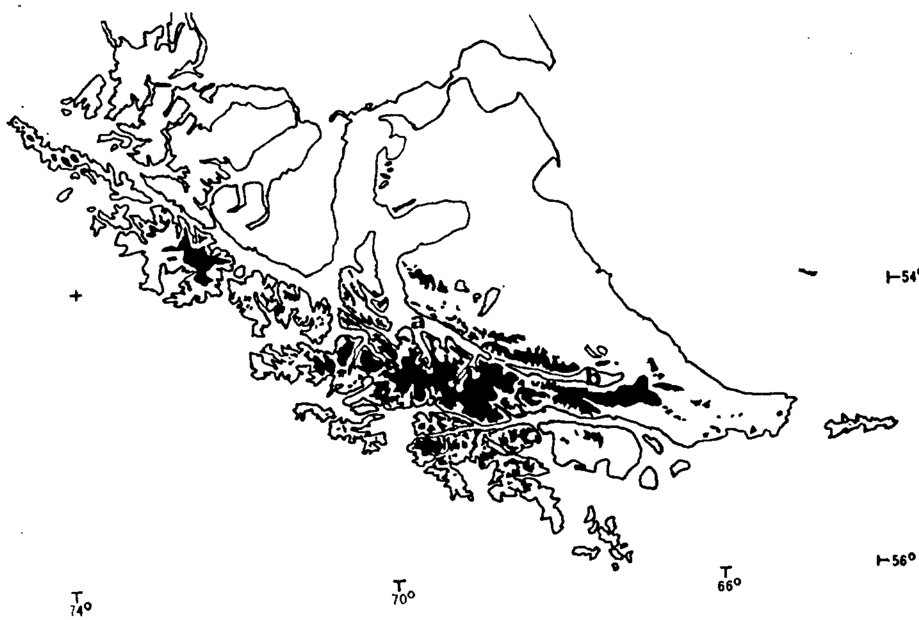


Fig. 1.—Outline map of Tierra del Fuego showing (in black) the occurrence of land over 500 m. altitude. Seno Almirantazgo (a) and Lago Fagnano (b) serve to indicate the line separating the Marginal Cordillera to the north from the more southerly Central Cordillera.

sediments —sandstones, clay-slates, marls and conglomerates—, which underly the Tertiary sediments forming the undulating plains of NE Tierra del Fuego but in the Marginal Cordillera they are strongly folded with the beds often almost vertical.

The main mass of the Fuegian mountains, lying south of the Almirantazgo-Fagnano depression, is composed of strongly deformed and metamorphosed Palaeozoic to Jurassic rocks. The core of this «Central Cordillera» is composed of strongly tectonized mica- and quartz-schists, together with greenstones, and is penetrated in many places by younger granites. The schists are flanked by dark slates (graywackies), marls and quartz-porphyries, while further south, in the outer Fuegian archipelago, the so-called Andean diorites of the Patagonian batholith (DALZIEL, et al., 1974) predominate; these mountains have sometimes been distinguished as the «Coast Cordillera» (QUENZEL, 1911; BONARELLI, 1917; KRANCK, 1932).

The main or Central Cordillera of Tierra del Fuego shows abundant signs of extensive glaciation, such as the acute, 'horn' peaks of, for example, Montes Alvear, Cornú and Olivia, and the numerous glacial cirques at higher elevations. Indeed, in several areas, notably the Cordillera Darwin, quite large glaciers still persist, although they appear to be retreating slowly. The glacial land-forms result from the Pleistocene glaciations and it is now generally agreed that there were three or four glacial periods correlated with the last three, or all four, European glaciations (BRÜGGEN, 1928; FERUGLIO, 1949; AUER, 1956, 1958, 1960). During these periods the whole of Tierra del Fuego was covered with ice, as was virtually all the land west of the Andes north to about lat. 44° S. (CALDENIUS, 1932; BRÜGGEN, 1950; VUILLEMIER, 1971). East of the Andes, however, in southern Patagonia there were almost ice-free areas, which extended over large parts of the continental shelf exposed by glacioeustatic lowering of the sea-level (AUER, 1958, 1960), and these probably acted as refuges for plants retreating before the ice (DUSÉN, 1905; SKOTTSBERG, 1916; DONAT, 1931; AUER, 1958; SIMPSON, 1973). It has been pointed out (VUILLEUMIER, 1971; SIMPSON, 1973) that the repeated drastic ecological alterations of the alpine habitats in the southern Andes during the various advances and retreats of the Pleistocene ice, which gave several cycles of expansion and contraction of the ranges of alpine plants, has been the most potent force for speciation since the habitats first became available after the final uplift of the southern Andes, probably in the upper Pliocene (BRÜGGEN, 1950; HARRINGTON, 1956).

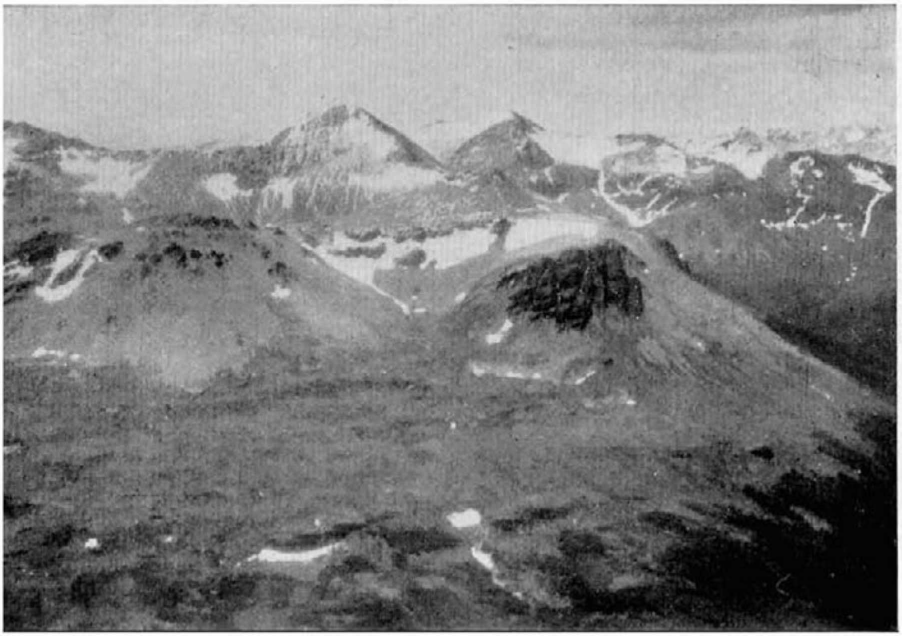
Since the end of the last ice age, about 12,000 years ago (AUER, 1970), and the severance of the final connections across the Strait of Magellan some 2,000 years later, there has been an alternation of wet and dry periods in Tierra del Fuego with which have been correlated advances and retreats of the forest (AUER, 1958). Local glaciations persisted well into postglacial times in parts of Tierra del Fuego, such as the Altos del Boquerón and the Cordillera Fueguina (AUER, 1970), but after various fluctuations they have mostly disappeared, apart from the glaciers still found today in the Cordillera Darwin, Isla Santa Inés, etc. There is still no detailed information either on the exact timing of the local ice movements during the postglacial period or as to when the alpine habitats, demarcated by a clear timberline, emerged with their present character.

ALPINE VEGETATION

In Tierra del Fuego the transition from forest to alpine vegetation is marked by a rather clear timberline, which almost everywhere comprises a dense belt of 'Krumholz' formed by *Nothofagus antarctica* (Plate 1 (c)). The timberline lies at an average altitude of about 550-600 m but, as pointed out by SKOTTSBERG (1916), this depends on the size of the mountain so that timberline is lower, for example, on the smaller, drier peaks towards the east end of the Sierra Lucio López and higher (up to 700 m) on the larger mountains such as those in the Sierra de Valdivieso and the Cordillera Darwin.

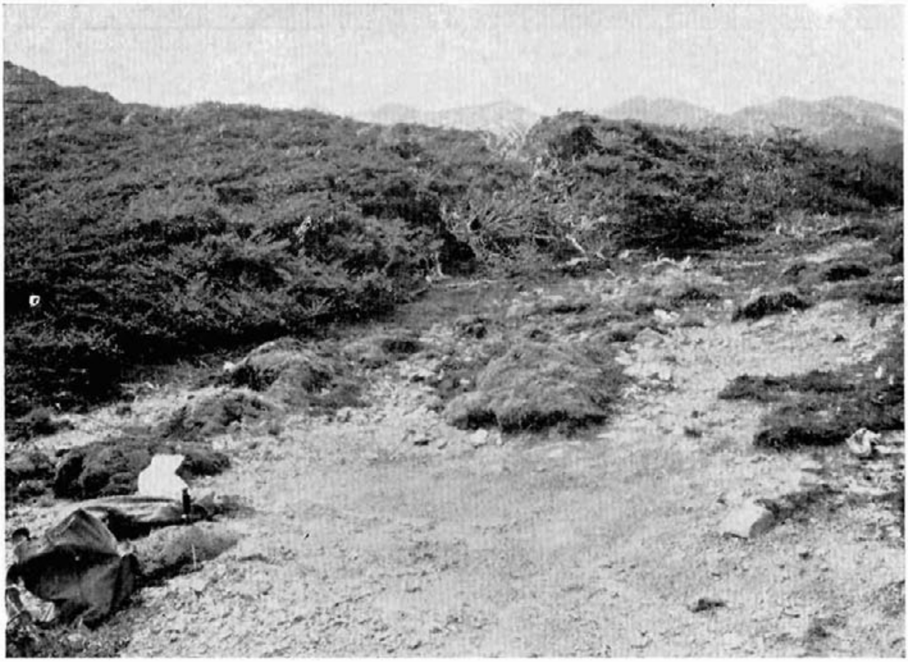
The vegetation of the alpine region seems to be governed by three principal factors — exposure to wind, the occurrence of water and the physical nature of the substrate. Depending upon these factors it is possible to recognize four major structural types of vegetation — cushion heath, dwarf shrub heath, alpine 'meadow' and feldmark.

CUSHION HEATH, which is widely distributed in suitable habitats at lower elevations in Tierra del Fuego, is well-developed at and just above timberline. Here, as elsewhere, *Bolax gummifera* forms pro-



(a) Alpine zone of Central Cordillera. Note timberline towards bottom right corner. Sierra Lucas Bridges with Cerro Cornú (1380 m.).

(b) General view in Central Cordillera showing prominent timberline. Sierra Alvear on west side of Laguna Escondida.



(c) Timberline showing 'krumholz' form of *Nothofagus antarctica* and cushion heath (*Bolax gummifera*) at lower margin of alpine zone. Cerro Moore, east end of Cordon No Top.

(d) Well-developed cushion heath dominated by *Bolax gummifera*, with *Festuca contracta* intermingled.
Cerro Heuheupen (704 m.) near SE corner of Lago Fagnano, Marginal Cordillera. Sierra Lucas Bridges behind.

minent cushions often up to 1 m or more high with which are usually closely associated a number of widespread cushion forming species such as *Abrotanella emarginata*, *Azorella lycopodioides*, *Colobanthus subulatus*, *Drapetes muscosus* and, under wetter conditions, *Caltha appendiculata*, *C. dioneifolia*, *Bolax caespitosa* and *Plantago barbata*. Upon and between the cushions are found many widespread species, such as *Acaena magellanica*, *Empetrum rubrum*, *Festuca contracta*, *Gamochaeta spiciformis*, *Luzula alopecurus*, *Lycopodium magellanicum*, *Pernettya pumila*, *Schizeilema ranunculus*, *Serpyllopsis caespitosa* and *Stipa rariflora*, as well as, for example, *Saxifragodes albowiana* and *Tetrachondra patagonica* subsp. *fuegina*, which are virtually restricted to this association.

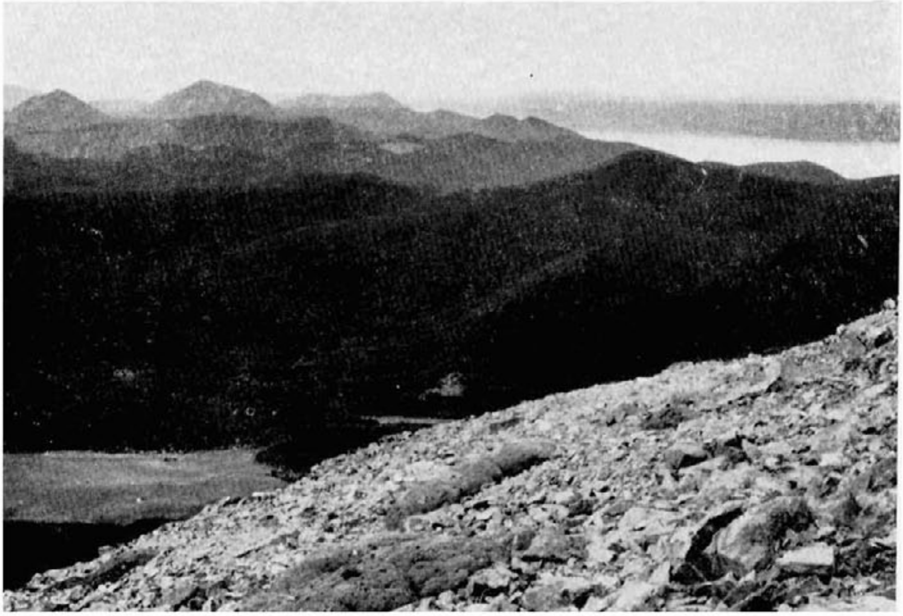
With increasing altitude and exposure *Bolax gummifera*, although still important, becomes a much less dominant member of the cushion heath, which has a more open aspect and is composed of smaller, lower cushions. Here *Armeria maritima* subsp. *andina*, *Azorella selago*, *Cerastium arvense*, *Draba magellanica*, *Leuceria hahnii*, *Onuris alismatifolia*, *Oxalis enneaphylla*, *Perezia magellanica*, *Poa alopecurus* subsp. *alopecurus*, *Saxifragella bicuspidata* and *Trisetum spicatum* become prominent. Towards its upper limit the cushion heath becomes increasingly open and impoverished until, at the point where vegetation ceases (800-1000 m), it is usually represented only by scattered cushions of *Saxifragella bicuspidata*, sometimes accompanied by *Azorella selago* and/or *Cerastium arvense*. The cushion heath also becomes much more open where periodic seepage water runs over the surface of the ground, which in such places is frequently gravelly, and here *Viola tridentata* is common, while the only known alpine occurrence of the rare *Koenigia islandica* is also in such places.

On steep slopes, particularly in the Marginal Cordillera, where the cushion heath is developed over a deep clay soil, the substrate can be rather unstable so that under conditions of exposure to wind or trampling by, for example, guanaco or sheep, an open soil-run develops. A few species of the open facies of the cushion heath, such as *Calandrinia fuegiana*, *Oxalis enneaphylla*, *Nassauvia pygmaea* and *Senecio alloeophyllus* are able to tolerate these conditions, while the higher elevation occurrences of *Phaiophleps lyckholmii* and *Tristagma nivalis* are restricted to these areas.

DWARF SHRUB HEATH shares most of its species with the cushion heath and, indeed, over large areas the associations intergrade so much in physiognomy that they can be considered extreme facies of one structural unit, as is implied by SKOTTSBERG's (1916) notes. However, along the margins of rock screes, as isolated islands of more stable ground within the screes and on some other well-drained sites, *Empetrum rubrum* and, to a lesser degree, *Pernettya pumila* and *Myrteola nummularia* dominate the structure of the vegetation to the extent that it must be considered dwarf shrub heath such as is found widely on better drained ground at lower elevations in Tierra del Fuego, southern Patagonia and the Falkland Islands (SKOTTSBERG, 1913; MOORE, 1968). Although, as noted above, most of the species present in this association are the same as those found in the cushion heath, a few species, e. g. *Cystopteris fragilis* and *Senecio darwinii,* have their principal alpine occurrences here. *Grammitis magellanica, Hymenophyllum falklandicum, H. peltatum, H. tortuosum* and *Polystichum mohrioides* var. *plicatum*, which occur on rock faces and in crevices in the screes, can become intermingled with the dwarf heath association and the *Hymenophyllum* species may even enter it on occasions.

FELDMARK. In addition to the rock screes already mentioned, at higher elevations on many Fuegian mountains there are extensive areas of undulating or gently sloping ground covered by tallus deposits (Plate 2 (c)). Although these tend to be largely devoid of plant life they provide the rather specialized habitat for *Nassauvia lagascae* var. *globosa* and *Nastanthus spathulatus* which, in Tierra del Fuego, occur nowhere else, while a dense community of *Usnea* is frequently developed (Plate 2 (d)). Towards the margins of such 'rock pavements' or where there is a degree of stabilization and moisture-retention because of intermingled clayey soil, such species as *Nassauvia latissima, N. pygmaea, Saxifraga magellanica* and *Senecio humifusus* indicate a transition to the cushion heath. Indeed, because of the often considerable areas of exposed, mineral soil and the importance of terrestrial cryptogams, some of the communities referred to open facies of the cushion heath association may with justice be considered to be feldmark, and in the present state of knowledge it is not possible to define a strict demarcation between the two,

ALPINE 'MEADOW'. The alpine regions of many mountains in the



(a) Upper limit of cushion heath showing scattered plants of *Bolax gummifera*. Note narrow alpine zones of other mountains of Marginal Cordillera (Sierra Beauvoir) in distance.
Cerro Atukoyak, Sierra de las Pinturas, north side of Lago Fagnano.

(b) Dwarf shrub heath dominated by *Empetrum rubrum* and *Pernettya pumila* (foreground). Cushion heath and timberline behind.
Monte Moore, Sierra Lucas Bridges, Central Cordillera.

(c) Feldmark showing exposed nature of tallus slopes. Tree-line visible on mountains in background.
Monte Lincoln Constance, Sierra Lucas Bridges, Central Cordillera.

(d) Feldmark community dominated by *Usnea*. Canal Beagle and Isla Navarino behind.
Cerro No Top (934 m.), Cordon No Top, Central Cordillera.

Marginal Cordillera and the eastern parts of the Central Cordillera have little or no persistent surface water. Elsewhere, however, there are frequent streams or seepage areas, derived in many cases from permanent glaciers or slow-melting snow patches, and these support a rather distinct and often rich vegetation to which the somewhat inappropriate name 'meadow' can be applied.

Along the margins of streams, where the soil is relatively fine, occur mats of *Abrotanella linearifolia, Caltha appendiculata* and *Plantago barbata*, amongst which grow such species as *Acaena antarctica, A. tenera, Caltha sagittata, Gunnera magellanica, Hierochloë redolens, Lagenophora nudicaulis, Ourisia fuegiana, Oxalis magellanica, Poa alopecurus* subsp. *fuegiana, Primula magellanica, Senecio acanthifolius, S. trifurcatus, Tapeinia obscura, Viola commersonii* and *V. tridentata*. Where the stream bank is rocky or composed of coarser soil, species such as *Cardamine glacialis, Epilobium australe, Hamadryas magellanica* and *Nassauvia magellanica* are also found; the occasional occurrence of the latter species along streams at lower elevations being the result of its accidental waterborne transport from such habitats.

The sheltered parts of many alpine streams are flanked by a broad belt of marshy ground which, together with seepage areas having impeded drainage, can support a community in which grassy leaved plants are prominent. *Agrostis magellanica, Carex banksii, C. magellanica, Carpha alpina, Cortaderia pilosa, Deschampsia atropurpurea, Phleum alpinum, Rostkovia magellanica, Schoenus antarcticus, Uncinia kingii* and *U. lechleri* can all be found in such areas, together with many of the streamside species noted above.

There are, of course, transitions to the wetter facies of the cushion heath described earlier and detailed studies of all environmental parameters will be necessary before the interrelationships of the vegetation types can be fully understood. However, the richness of the streamside and 'meadow' communities serves to emphasize the importance of available water and, to some extent, shelter in determining the composition and distribution of the alpine vegetation of Tierra del Fuego.

ALPINE FLORA

Of the 430 species of phanerogams and vascular cryptogams native to Tierra del Fuego (MOORE, 1974) no less than 120 are known to occur above timberline. Some of these are of only sporadic occurrence but in most instances the species are known from several localities and must be considered constant members of the alpine flora. Although most of these species also occur below timberline in suitable habitats elsewhere in Tierra del Fuego, about 20 per cent of them are truly alpine and are only found above timberline.

a) *Species of wide altitudinal amplitude*

Seven species occur only occasionally above timberline. Four of these — *Asplenium dareoides* Desv., *Dysopsis glechomoides* (Rich.) Mull. Arg., *Geum parviflorum* Comm. and *Rubus geoides* Sm., have obviously advanced slightly above their normal forest habitats in places where the cushion heath or dwarf shrub heath provides sufficient shelter and moisture. These factors are probably also important in permitting the occasional alpine occurrence of *Gentianella magellanica* (Gaudich.) Fabris ex D. M. Moore, *Hieracium antarcticum* D'Urv. and *Hypochoeris arenaria* Gaudich., which normally grow in lowland grassland communities.

Ninety-five species occur frequently in alpine habitats, most of them being indistinguishable from populations occurring elsewhere in Fuegia at lower elevations:

Abrotanella emarginata Cass.
Acaena antarctica Hook. f.
A. magellanica (Lam.) Vahl
A. pumila Vahl
Agropyron pubiflorum (Steudel) Parodi
Agrostis canina L.
A. magellanica Lam.
Alopecurus magellanicus Lam.
Armeria maritima L.
Astelia pumila (Forst. f.) Banks & Sol. ex R. Br.
Azorella caespitosa Cav.
A. lycopodioides Gaudich.
Bolax caespitosa Hombr. & Jacq.
B. gummifera (Lam.) Spreng.
Calandrinia fuegiana Gandoger
Callitriche antarctica Engelm. ex Hegelm.
Caltha appendiculata Pers.
C. dioneifolia Hook.
C. sagittata Cav.
Cardamine glacialis (Forst. f.) DC.
Carex banksii Boott
C. caduca Boott
C. decidua Boott
C. magellanica Lam.

Carpha alpina R. Br.
Colobanthus quitensis (Kunth) Bartl.
C. subulatus (D'Urv.) Hook. f.
Cortaderia pilosa (D'Urv.) Hack.
Cystopteris fragilis (L.) Bernh.
Deschampsia atropurpurea (Wahlenb.) Scheele
D. flexuosa (L.) Trin.
D. parvula (Hook. f.) Desv.
Draba funiculosa Hook. f.
D. magellanica Hook. f.
Drapetes muscosus Banks ex Lam.
Empetrum rubrum Vahl ex Willd.
Epilobium australe Poepp. & Hausskn.
Erigeron myosotis Pers.
Festuca contracta T. Kirk
F. magellanica Lam.
Gaimardia australis Gaudich.
Gamochaeta nivalis Cabrera
G. spiciformis (Sch. Bip.) Cabrera
Grammitis magellanica Desv.
Gunnera lobata Hook. f.
G. magellanica Lam.
Hamadryas magellanica Lam.
Hierochloë redolens (Vahl) Roem. & Schultes
Hymenophyllum falklandicum Baker
H. peltatum (Poir.) Desv.
H. tortuosum Hook. & Grev.
Koenigia islandica L.
Lagenophora nudicaulis (Comm. ex Lam.) Dusén
Leuceria hahnii Franchet
Luzula alopecurus Desv.
L. racemosa Desv.
Lycopodium magellanicum (P. Beauv.) Swartz
Marsippospermum grandiflorum (L. f.) Hook.
Myrteola nummularia (Poir.) Berg
Nanodea muscosa Banks ex C. F. Gaertn.
Oreobolus obtusangulus Gaudich.
Ourisia breviflora Benth.
Oxalis enneaphylla Cav.
O. magellanica Forst.
Perezia lactucoides (Vahl) Less.
P. magellanica (L. f.) Less.
P. pilifera (Don) Hook. & Arn.
Pernettya pumila (L. f.) Hook.
Phleum alpinum L.
Pinguicula antarctica Vahl
Poa alopecurus (Gaudich.) Kunth
subsp. *alopecurus*
subsp. *fuegianus* (Hook. f.) Moore & Doggett
Ranunculus sericeocephalus Hook. f.
Saxifraga magellanica Poir.
Schizeilema ranunculus (D'Urv.) Domin
Schoenus antarcticus (Hook. f.) Dusén
Serpyllopsis caespitosa (Gaudich.) C. Chr.
Senecio acanthifolius Hombr. & Jacq.

S. eightsii Hook. & Arn.
S. humifusus (Hook. f.) Cabrera
S. kingii Hook. f.
S. magellanicus Hook. & Arn.
S. patagonicus Hook. & Arn.
S. trifurcatus (Forst. f.) Less.
Stipa rariflora (Hook. f.) Benth.
Taraxacum gilliesii Hook. & Arn.
Tribeles australis Phil.
Trisetum spicatum (L.) Richt.
Tristagma nivale Poeppig
Uncinia kingii Boott
U. lechleriana Steudel
Viola commersonii DC.
V. tridentata Menz. ex DC.

All of these species occur in grassland, dwarf shrub and cushion heath, bogs or saxicolous communities in lowland Tierra del Fuego and elsewhere. None of the species is restricted to Fuegia and many of them have a wide distribution and show a similar altitudinal amplitude north of the Strait of Magellan, in the Falkland Islands and, in some cases, on the sub-Antarctic oceanic islands. It is clear that these taxa have a relatively wide tolerance of cool temperate conditions and are thus able to occupy non-forested habitats at low and higher elevations so long as water and some shelter are available. In view of the superficial similarities in the habitats, several species, such as *Phyllachne uliginosa* Forst. and *Tapeinia pumila* (Forst. f.) Baillon, at present known only in Tierra del Fuego from exposed coastal areas, might be expected to occur in the alpine zone. If their absence is substantiated in the future it is likely that they require much more oceanic conditions and a longer growing season than are encountered on the upper parts of the Fuegian mountains; only detailed autecological studies will clarify this problem further.

Although the widespread species listed above frequently exhibit significant morphological variation, this does not seem to be obviously associated with their occurrence in alpine habitats. In *Leuceria hahnii*, for example, alpine populations comprise densely villous plants of reduced stature and with relatively large capitula, thus differing significantly from plants lower on the mountain slopes; these differences are maintained in cultivation. However, populations from the dry lowland steppe of NE. Tierra del Fuego closely resemble the alpine forms so that exposure, and perhaps available moisture, would seem to be important in selection and it is inappropriate at this stage to consider that alpine 'ecotypes' can be delimited. A comparable situation has been found in *Armeria maritima*, but there are few relevant experimental data for the other species listed.

Three further species belonging to this group of widespread taxa show marked morphological differences between alpine and lower elevation populations. *Polystichum mohrioides* Bory has two distinct varieties in Fuegia — var. *plicatum* (Poepp.) C. Chr., which is virtually restricted to the alpine zone, and var. *elegans* (Remy) C. Chr., which rarely grows outside the forests and never occurs at higher elevations. Similarly, the alpine forms of *Cerastium arvense* L. are sufficiently distinct to be recognized as a variety, which has even been given specific status (*C. nervosum* Naud.). Finally, the widespread and very variable *Plantago barbata* Forst. f. always occurs in alpine areas as one of the densely caespitose forms of var. *monanthos* (D'Urv.) Pilger. In all these species, therefore, the alpine plants can be readily distinguished from those occurring below timberline. However, it should be noted that these alpine forms are not restricted to Tierra del Fuego but are also known from the Andes north of the Strait of Magellan. The implications of this will be mentioned later (p. 436) in connection with the origins of the flora.

b) *Species only found above timberline in Tierra del Fuego*

Twenty-one species are restricted to the alpine regions of Tierra del Fuego. On present evidence 6 of these seem to be Fuegian endemics, the remainder occurring elsewhere, principally above timberline in the southern Andes north of the Strait of Magellan.

i) *Endemic alpine species.*

These taxa and their affinities are as follows:

Abrotanella linearifolia A. Gray — v. close to *A. trichoachenia* Cabrera (S. Andes).

Nassauvia latissima Skottsb. — close to *N. serpens* D'Urv. (Falkland Islands).

Onuris alismatifolia Gilg — close to *O. oligosperma* (Speg.) Gilg & Muschler (S. Andes).

Ourisia fuegiana Skottsb. — close to *O. breviflora* Benth. (Fuegia) and *O. pygmaea* Phil. (S. Andes).

Senecio darwinii Hock. & Arn. — close to *S. littoralis* Gaudich. (Falkland Islands).

Tetrachondra patagonica Skottsb.
subsp. *fuegiana* D. M. Moore — close to subsp. *patagonica* (S. Andes).

It should be noted that *Onuris alismatifolia* exceptionally occurs in open conditions at lower elevations in Tierra del Fuego (near Cabo Domingo). As might be expected, four of these species have their closest relatives in the southern Andes, where they usually occur above timberline; *Tetrachondra patagonica* subsp. *patagonica* is an exception in that it occurs at lower elevations. The two species having their closest relatives in the Falkland Islands may, at first sight, appear anomalous but it should be noted that, apart from Fuegia, the whole Falkland Islands flora has its closest affinities with the southern Andes (SKOTTSBERG, 1913; MOORE, 1968) and the three regions undoubtedly largely derived their present floras from a common source.

ii) *Non-endemic alpine species.*

Of the 15 species belonging to this group the majority also occur in the southern Andes:

Agrostis araucana Phil.
Azorella selago Hook. f.
Calamagrostis erythrostachya (Desv.) Macloskie
Epilobium conjungens Skottsb.
Nassauvia magellanica J. F. Gmel.
N. lagascae (Don) F. Meige var. *globosa* Skottsb.
N. pygmaea (Cass.) Hook. f.
Nastanthus spathulatus (Phil.) Miers
Phaiophleps lyckholmii (Dusén) R. C. Foster
Saxifragella bicuspidata (Hook. f.) Engler
Saxifragodes albowiana (Kurtz) D. M. Moore
Senecio alloeophyllus O. Hoffm.
Tapeinia obscura (Cav.) D. M. Moore

Phaiophleps lyckholmii also occurs on the lower mesetas (up to c. 300 m) of NE. Tierra del Fuego, which rise from the unforested steppe and do not have a recognizable alpine zone. However, like *Tristagma nivale* (see sect. a), it does not extend south of the Marginal Cordillera and both species are important in suggesting the affinities of these drier Fuegian mountains with comparable parts of the Patagonian Cordillera. *Nastanthus spathulatus* is perhaps intermediate between i) and ii) since the Fuegian populations show a number of differences from Patagonian plants (MOORE, 1970) which, although not recognized formally, nevertheless indicate a degree of divergence during recent evolution.

Of the two remaining species which belong to this group, *Acaena tenera* Alboff occurs on the Central Cordillera of Tierra del Fuego and the sub-Antarctic island of South Georgia, where it reaches sea-level. Its reported occurrence near Lago Nahuel Huapi (SKOTTSBERG, 1916) suggests that this species also may show the link with the southern Andes where, following further collecting, its occurrence will probably be confirmed. *Luzula pumila* Hook. f., whose only Fuegian locality is on Isla de los Estados, is otherwise known from New Zealand and it is thus an alpine representative of the group of southern South American species having amphi-Antarctic affinities.

ORIGINS OF THE FLORA

As noted earlier, Tierra del Fuego appears to have been completely covered with ice during the Pleistocene glaciations, after which recolonisation took place from the refugia generally considered to have existed in southern Patagonia and the adjacent continental shelf. It is quite likely that this could have taken place in the c. 2,000 years between the retreat of the ice and the final opening of the Strait of Magellan but even if this was not, or only partly, so the narrower parts of the Strait would not constitute a major obstacle to most species. The persistence of montane glaciers well into post-glacial times means that the alpine habitats as we know them today are of relatively recent origin and it is consequently not surprising that the alpine flora, with a very low level of endemism, displays every evidence of youth.

Over eighty per cent of the species present in the alpine zone are widespread at lower elevations and, as noted earlier, they have a rather wide tolerance which has permitted them to invade the open areas above timberline from their normal unforested habitats at lower elevations. In only a few cases is there evidence of ecotypic differentiation, but this is a generalised response to exposure not restricted to the alpine populations. Further investigations will undoubtedly reveal some altitudinal pattern, as in the different chemical composition of lowland and montane examples of *Carex microglochin* (Aye, unpub.), but there is no indication that the alpine environment has as yet significantly modified the invaders from the lowlands.

As mentioned previously, the rather distinct alpine varieties of *Polystichum mohrioides* and *Cerastium arvense* are also known outside Tierra del Fuego and they should consequently be considered along with the group of taxa confined to alpine habitats in Fuegia. These taxa comprise only 18 % of the total alpine flora of Tierra del Fuego and over two thirds of them are known from alpine regions north of the Strait of Magellan. These may be considered to have envolved during or prior to the last glaciation and to have followed closely after the retreating ice as it left suitable open, cold habitats both north and south of the Strait of Magellan. In some instances it is clearly possible to envisage distance dispersal in more recent post-glacial times since, for example, *Epilobium conjungens* and *Senecio alloeophyllus* have fruits obviously capable of such dispersal, while *Azorella selago* almost certainly crossed sizeable oceanic gaps to reach Macquarie Island and perhaps other sub-Antarctic islands where it now occurs. Among the species less obviously capable of such dispersal it is interesting that there are differences between Fuegian and Patagonian populations of *Nastanthus spathulatus*, which probably result from their isolation subsequent to the retreat of the ice sheets, and it is likely that the divergence of the related *N. falklandicus* in the Falkland Islands (MOORE, 1967) was due to speciation consequent upon the same events. Almost certainly the origin of *Acaena tenera* resulted from similar processes in the southern Andes or Tierra del Fuego and it has spread to South Georgia more recently, probably by distance dispersal, for which it is ideally suited. The otherwise New Zealand species *Luzula pumila* must owe its presence on Isla de los Estados to long-distance dispersal within a circum-Antarctic pattern shown by many species (e. g. MOORE, 1972) and emphasizes the importance of chance colonization of the open habitats such as those at high levels in Tierra del Fuego.

The six alpine taxa apparently endemic to Tierra del Fuego have their closest relatives either in the southern Andes or in the Falkland Islands. Whilst further collection north of the Strait of Magellan may well show that they occur more widely, their present distribution and affinities are consistent with the idea that they originated by fragmentation of the ancestral stock due to geographical isolation following their post-, or inter-, glacial advance from the ice-free refugia of SE. Patagonia to the areas they now occupy, in a manner analogous to that postulated by SIMPSON (1973) for the differentiation of the *Perezia magellanica* group.

In conclusions, therefore, the youth of the alpine flora of Tierra del Fuego is demonstrated by its low level of differentiation. The small number of apparently endemic taxa appear to have evolved by gradual speciation as they followed the ice from perglacial refugia to attain their present distribution with or without noticeable divergence subsequent to their separation, but in some instances distance dispersal between isolated alpine regions is quite feasible. Indeed, the open habitats and low species pressure here mean that chance colonization by long distance dispersal has been a constant possibility. Most of the alpine flora is composed of widespread species of unforested habitats in southernmost South America, which show generally broad ecological tolerance and which, in view of the relatively small amount of differentiation in response to the high altitude conditions, represent the most recent phase in the colonization of the developing Fuegian alpine zone.

Acknowledgements

The data reported here arise as part of a programme on the flora of Tierra del Fuego supported by a grant from the Natural Environment Research Council, whose support is gratefully acknowleged. The extensive collections from the Fuegian mountains made by Mrs. R. N. Prosser de Goodall, Estancia Harberton, Tierra del Fuego, have been of considerable value and I am indebted to her for her continued interest and co-operation.

RESUMEN

De las 430 especies de plantas vasculares naturales de la Tierra del Fuego, 120 se encuentran por encima del nivel de bosques en las montañas fueguinas. La mayoría de ellas (82 %) se encuentran ampliamente distribuidas a menores altitudes en habitats no forestales a ambos lados del Estrecho de Magallanes, muestran una amplia tolerancia ecológica, y parecen ser colonizadoras relativamente recientes de los habitats alpinos. El 20 % restante, formado por especies restringidas al piso alpino, muestra por lo general claras afinidades con los Andes meridionales, de los que en algunos casos podrían haberse derivado por dipersión geográfica reciente. Este grupo de especies, en especial los escasos (5 %) endemismos fueguinos alpinos, apuntan a un origen debido al aislamiento en la Tierra del Fuego, los Andes australes y las islas Malvinas (I. Falkland), consecutivo a un avance postglaciar a partir de refugios periglaciares en el SE. de Patagonia. En la colonización de los hábitats alpinos abiertos juega también un papel la dispersión a larga distancia.

La exposición, la disponibilidad de agua y el sustrato son los factores determinantes de la vegetación del piso alpino fueguino. Se reconocen cuatro unidades estructurales de vegetación —brezal pulvinular, brezal enano, feldmark y pastizal alpino— y se describen sus características fundamentales y su presencia y composición florística.

Se considera que los habitats alpinos fueguinos son de origen relativamente reciente y su flora es evidentemente joven. Las diferencias geológicas y estructurales entre las Cordilleras Marginal y Central de la Tierra del Fuego se reflejan en la estrecha banda alpina de la primera, que muestra cierta evidencia de afinidades florísticas con las

SUMMARY

120 of the 430 vascular plants native to Tierra del Fuego occur above timberline in the Fuegian mountains. Most of these (82 %) are widespread in non-forested habitats at lower elevations on both sides of the Strait of Magellan, are of wide ecological tolerance and appear to be relatively recent colonisers of the alpine habitats. The 20 % of species restricted to the alpine zone generally show close affinities with the southern Andes, from which in some cases they could have been derived by recent distance dispersal. This group of species, particularly the few (5 %) Fuegian alpine endemics, suggest an origin due to isolation in Tierra del Fuego, the southern Andes and the Falkland Islands following postglacial advance from perglacial refugia in SE. Patagonia. Long distance dispersal has also been involved in colonizing the open alpine habitats.

Exposure, water-availability and substrate are important in determining the vegetation of the Fuegian alpine zone. Four structural vegetation units — cushion heath, dwarf shrub heath, feldmark and alpine 'meadow' — are recognized and their salient features, species-composition and occurrence described.

The Fuegian alpine habitats are thought to be of relatively recent origin and their flora is evidently young. The geological and structural differences between the Marginal and Central Cordillera of Tierra del Fuego are reflected in the narrow alpine zone of the former, which shows some evidence of floristic affinities with the drier mountains and mesetas of S. Patagonia and NE. Tierra del Fuego.

montañas y mesetas más secas del S. de Patagonia y NE. de Tierra del Fuego.

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