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ASPECTS OF THE GROWTH AND CLIMATE OF TUSSOCK GRASSLANDS IN MONTANE NEWGUINEA AND SUB-ANTARCTIC ISLANDS

by

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Thesis submitted for the degree
of Doctor of Philosophy at the
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'In the Paramo there is no spring, no autumn, no summer, and no winter there is only eternal sameness. Two-thirds of the leaves of the grass are always dry and of a brownish-yellow color which, with the new blue-green leaves, forms that olive-green garment which covers all the mountains and is termed pajonal. Complete desert does not give the traveller so sad and melancholy an impression as the wastes of the Pajonales.'

(Wolf, 1890, ex Troll, p. 19, 1959)

'... the gloomy aspect of the Pajonales (bunch grass meadows) of the Paramos, in which withered plants defy destruction and with their dismal remains dim and deform the splendour of the new generation.'

(Sodiro, 1874, ex Troll, p.19, 1959)

'... a banquet of beauty, a glory
Of fair mountain pasture, a glory of grasses

From the bed of the stream to the fringe of the shingle,
Stretching mile upon mile in a splendour unbroken,
Where the golds and the greys and grey-green commingle
In a beauty immaculate, mystic, unspoken.'

(A.Wall, ex Connor & Macrae, p.168, 1969)

I believe we know only a little about tussock grasslands, and what we feel about them is not a common emotion.

CHAPTER 1

INTRODUCTION

On the cool, misty slopes of high mountains that rise out of the hot equatorial lowland, there are places that bear surprising resemblances of climate and vegetation to the remote islands of the vast southern ocean. Why such disparate regions should look alike can be found in the three-dimensional (longitudinal, latitudinal, and altitudinal) view of climate and vegetation of the earth expressed by Troll (1961). He used the ideas of the great 19th century geographer Humboldt as a basis for his exposition. They noted that similar sequences of climate and vegetation are to be found in going from lowlands to highlands at one latitude as are found in moving from low latitudes to high latitudes at the same altitude. Tussock grasslands, because of their great extent, are one of the most conspicuous features common to the equatorial high montane and sub-Antarctic regions. It is with these grasslands that this thesis is concerned.

Before beginning the detailed description of the work carried out, it is useful to consider the question, 'What are tussock grasses and where are they found?'. A sixteenth century lady might have worn her hair in 'Thussocks' but not until 1832 is the use of the word 'Tussick' recorded and then, appropriately for this thesis, to describe the grasses of the 'bird' islands of the southern oceans (Oxford English Dictionary, 1933). The essence of a tussock is a clumping of hairlike or grassy objects. Tussock grasses are those graminoids that grow in tufts or bunches. At their most luxuriant they have a pedestal composed of a dense mass of living and dead roots, stems, and leaf bases up to a metre in diameter and one and a half times as high. The pedestal is topped by a crown of long arching leaves that commonly interlace with those of neighbouring tussocks. In places the canopy of tussock leaves is so dense that few if any other plants can grow beneath it. However, not all tussocks are pedestalled, and irregular spacing and seral change permit other plants, like small or giant herbs, and sometimes shrubs, ferns, and other cryptophytes, to grow amongst the tussocks.

Tussocks appear to arise by several modes of growth or combinations of these. For example, one individual plant with abundant vertical shoots with short internodes produces a tussock (*e.g. Eriophorum vaginatum*, Hopkins and Sigafoos, 1951; Phillips, 1954). Alternatively, several have not found cause to emphasize plant structure nor, consequently, to recognize the similarity of the austral and boreal tussock grasslands. More recently, some North Americans have begun to emphasize growth form as an important attribute of plant communities and have recognized 'tussock' vegetation there (Hopkins and Sigafoss,1950; Johnson *et al.*,1966; Wein and Bliss, 1971).

In Table 1.1 I have documented the occurrence of the tussock form throughout the world. I have grouped occurrences under headings of humid, mesic, and arid using the index of de Martonne which Lauer (1952) used to indicate the number of humid and arid months of the year. Whilst the index is a crude indicator of climate based on precipitation and temperature, it adequately serves to show the vast range of climatic conditions under which the tussock form dominates vegetation.

Table 1.1. Survey of the world distribution of tussock dominated vegetation.

Humid for 10 to 12 months:

a) Melanesian high mountain tussock grasslands (Wade and McVean 1969; personal observation);
b) Afroalpine tussock grassland (Hedberg,1964,1968; Coe,1967; personal observation);
c) tussock grasslands of the paramos of the Andes, 'pajonales' (Cuatrecasas,1968; Troll,1959);
d) Hawaiian islands high mountain tussock grassland (Fosberg,1961);
e) High altitude tussock grasslands of Australia (equivalent to Wimbush and Costin's (1973) '*Chionochloa* tall alpine herbfield'; personal observation);
f) low altitude, low tussock grassland of New Zealand (Cockayne,1958; Connor and Macrae,1969; personal observation);
g) low altitude, tall tussock grassland of New Zealand (Cockayne,1958; Connor and Macrae,1969; personal observation);
h) high altitude, low tussock grassland of New Zealand (Cockayne,1958; Connor and Macrae,1969; Burrows,1969; personal observation);
i) high altitude, tall tussock grassland of New Zealand (Cockayne,1958; Connor and Macrae,1968; Burrows,1969; personal observation);
j) sub-Antarctic tussock grasslands (Hooker,1847, Taylor,1955; Troll, 1960; Wace,1965; personal observation);
k) British and north-European *Molinia* and *Nardus* tussock grasslands (Tansley,1949);
l) British *Eriophorum* tussock vegetation (Conway,1949; Phillips,1954);
m) tussock grasslands of the pampas of Argentina and Uruguay (Eyre, 1963);

Mesic: 6 to 9 humid months:

n) tropical atoll tussock grasslands (Cremers,1972; personal observation);
o) large, tufted, *Stipa* steppe of Eurasia (Eyre,1963);
p) Palouse prairie, western North America (Eyre,1963);
q) bunch grass of the 'upland prairie' ,United States of America(*Andropogon scoparius, Sporobolus heterolepis*) (Weaver,1968);

Arid: 0 to 5 humid months:

r) arctic, sub-arctic *Eriophorum* tussock vegetation, Alaska (Hopkins and Sigafoss,1951; Johnson *et al.*,1966; Wein and Bliss,1971);
s) high altitude Mexican tussock grasslands:'zacontales' (Troll, 1973, personal communication);
t) high Andean puna and 'Ichu' tussock grasslands (Troll,1959);
u) Mitchell tussock grasslands of northern Australia (Moore and Perry,1970).

In the high tropical Andes, the cool, ever-humid tussock grasslands of the paramos and 'pajonales' grade imperceptibly into the increasingly dry tussock grasslands of the puna and 'Ichu' (Troll, 1959). In the Australian - New Zealand sector, the genus *Chionochloa* forms the dominant tussock vegetation from the uniformly cool, ever-humid sub-Antarctic Islands to the ~~drier, warmer Canterbury Plain, and into the~~ seasonally cold mountains of New Zealand (Burrows, 1969; Cockayne, 1958; Connor and Macrae, 1969).

Tussock grasslands pose an enigma in phytogeographical studies. No one appears to have attempted a comprehensive study of the world distribution of this life form, although numerous persons have written about particular tussock grasslands (see below), nor is there a general hypothesis to account for its distribution or selective advantage. However, the value of recognizing the common occurrence of a life-form as an approach to the understanding of vegetation on a world and a local scale has been remarked for a long time (Humboldt (ex Troll, 1959); Raunkaier, 1934). Troll (1959, p.49) writes:

> So sind uns die Lebensformen der Gewächse im Vergleich zu den ökologischen Bedingungen ein sicherer Wegweiser, um verwandte Vegetationstypen auch in anderen Gegenden mit anderer floristischer Ausstattung immer wieder zu erkennen.
>
> (Thus the life-forms of the plants, when considered in the light of their ecological conditions, provide a sure way of recognizing related vegetation types in regions with different floristic compositions.)

In searching for the common ecological conditions that have resulted in the development of the tussock life form, we find that neither temperature nor moisture nor nutrients alone can be held responsible. But it may be that when some combination of these factors is strongly limiting in a locality of non-arborescent vegetation, the dominant herbaceous growth form is a tussock.

This thesis is concerned only with tussock grasslands of the cool, moist regions. I shall examine, and compare in detail, examples from only two regions where tussock grasslands are dominant in an attempt to show where and to what extent similarities of life-form represent similarities on a finer scale. In particular, the work is directed towards determining the degree of similarity of growth characteristics of tussock grasses as revealed in daily above-ground growth rates, leaf area, biomass, structure, and carbohydrate content. It also examines rainfall, humidity, temperature, wind, and radiation in the two regions.

Many genera make up the tussock vegetation of the equatorial montane and sub-Antarctic regions. On the circum-Antarctic islands there are six

(1959) would segregate the humid, tropical, high mountain vegetation, which he proposes be called 'paramos' ,from the temperate, seasonally cold, high mountain vegetation called 'alpine'. For the same above-tree-line vegetation on Mt Wilhelm we have the terms 'oro-sub antarctic' and 'oro-antarctic' proposed by Wade and McVean (1969) and 'gras maunten' and 'ais' proposed by Smith (1974). It is perhaps better in the context of this thesis to use the geographically descriptive but otherwise neutral phrases , equatorial high montane ,and sub-Antarctic to describe the places in which I am working.

In order to make the study described in this thesis it was initially decided to study sites on Mt Wilhelm, New Guinea and on Macquarie Island, Australia. It was intended to build on the existing work of Wade and McVean (1969) for Mt Wilhelm, and of Jenkin (1972) who was known to be working on Macquarie Island. However, fate had other plans and, just as I returned from Mt Wilhelm to go to Macquarie Island, the Australian Department of Supply notified me that it was impossible. Immediate return to New Guinea and a change of the primary objective of the work was not feasible. An attempt was made to study tussock grasslands in the Snowy Mountains of Australia but a grasshopper infestation wiped out my growth samples. When the opportunity arose to join the 1971 New Zealand Wildlife

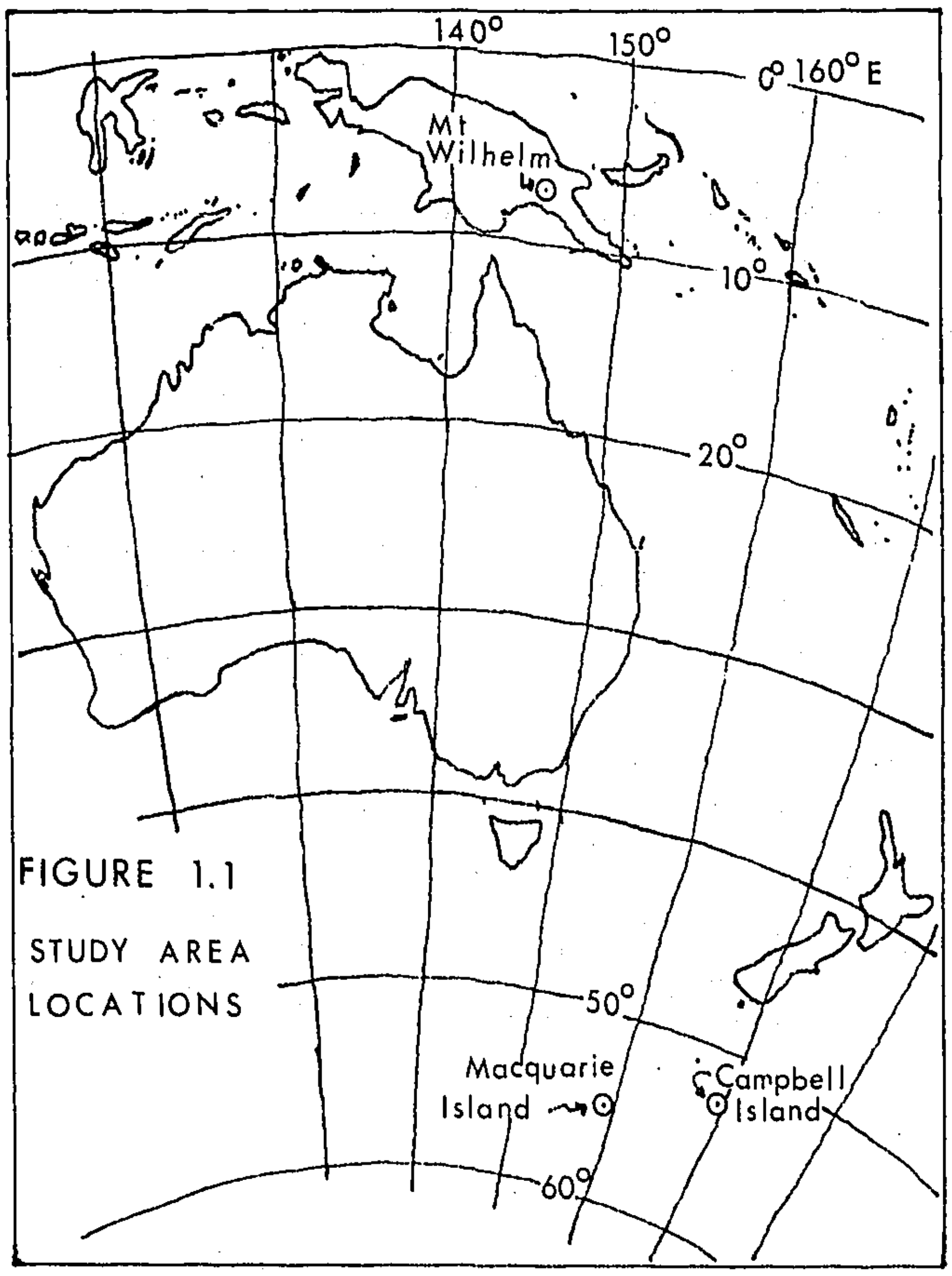


FIGURE 1.1

STUDY AREA LOCATIONS

taken from map NMP/ 68/ 025 Division of National Mapping Australia

Service Expedition to Campbell Island, I took advantage of the offer of a six week period on that island. Finally, following a very arduous and often exasperating period of complex negotiations, the way was cleared for me to visit Macquarie Island in the summer of 1972. The locations of the regions finally studied are shown in Figure 1.1.

Although the projected work on Macquarie Island was greatly curtailed, it was still possible to obtain useful information on which to base a comparison of the two regions originally selected.

The main growth measure used for comparison was the rate of net, aerial production of the tussock population. Because sites were selected as far as possible in places where the tussock grass was the sole species of any importance in terms of cover, variation due to interspecific competition was avoided. With site locations in rugged and remote areas, it was impossible to use sophisticated equipment, such as for gas exchange analysis, to monitor what appeared to be continuous growth. Instead, a highly portable, but simple method was developed, using rulers to measure extension rates of marked leaves and relating this to leaf weight and leaf density so as to estimate rates of net, aerial production. Where previous estimates of biomass were not available, oven-dry weights of plant material clipped from quadrats and soil cores were used to make them.

Particular use was made of the partition of aerial biomass amongst plant parts and their spatial distribution to describe variation in tussock form from place to place. Although very detailed studies of entire tussocks were not possible, the information concerning size and number of tussock parts helps to illustrate the ways in which the plants react to their environment and also to give clues to the environmental factors dominant in controlling morphology. To obtain some insight into the degree of physiological adaptation of the tussock grasses to their equatorial high montane, and sub-Antarctic environments, some observations were made of sugar and starch production and storage.

The climates in which the tussock grasses live also needed documentation. The general similarities of the thermal aspects of the equatorial high montane and sub-Antarctic were already clear from the work of DeLisle (1965), McVean (1968), and others, and were strengthened for Mt Wilhelm by new observations on precipitation, temperature, and radiation. These data, in conjunction with Jenkin's (1972) microclimatic observations from Macquarie Island, permitted the identification of similarities and

CHAPTER 2

I. SITE DESCRIPTIONS

Study areas were selected on the basis of the occurrence of tussock-grass dominated vegetation in equatorial montane and sub-Antarctic regions. The choice of Mt Wilhelm was governed largely by the presence there of the high altitude Field Station of the Australian National University and also by the availability of a detailed vegetation analysis of the mountain by Wade (1968). Campbell Island presented itself as a study area when I was able to join a New Zealand Wildlife Service Expedition to it. Macquarie Island was an important site because of the existing studies on its tussock grasses by Jenkin and Ashton (1970) from the University of Melbourne's Botany School; a visit to it was made possible by transport to and from the island and material supplies provided by the Department of Supply, Commonwealth of Australia.

Criteria for site selection within an area were as follow:

a) The tussock grass was to be completely dominant over as large an area as could be found. In only two instances was it necessary to use an area of less than 0.1 hectares.
b) The site was to represent optimal tussock development for the area (*i.e.* tussocks had to look healthy, vigorous, luxuriant, and large in relation to the range seen to be available in the area).
c) The tussocks actually measured for growth rate were to be completely surrounded only by other tussocks so that variability due to inter-specific competition could be eliminated.

A. MT WILHELM

Mt Wilhelm is an equatorial high mountain (4510 m) formed from a granodioritic body intruded into Paleozoic metamorphics (Haantjens, 1970). The age of the granodiorite is uncertain; Dow and Dekker (1964) propose Triassic or early Jurassic ages, while Peterson (1970) opts for the Miocene.

Several, deep, U-shaped valleys have been cut into the mountain by Pleistocene glaciers, the last of which retreated from the lower valleys about 12,500 years B.P. (Peterson and Hope, 1972), and about 10,000 years B.P. from the summit areas (G. Hope, Australian National University, pers. comm., Hope, 1974).

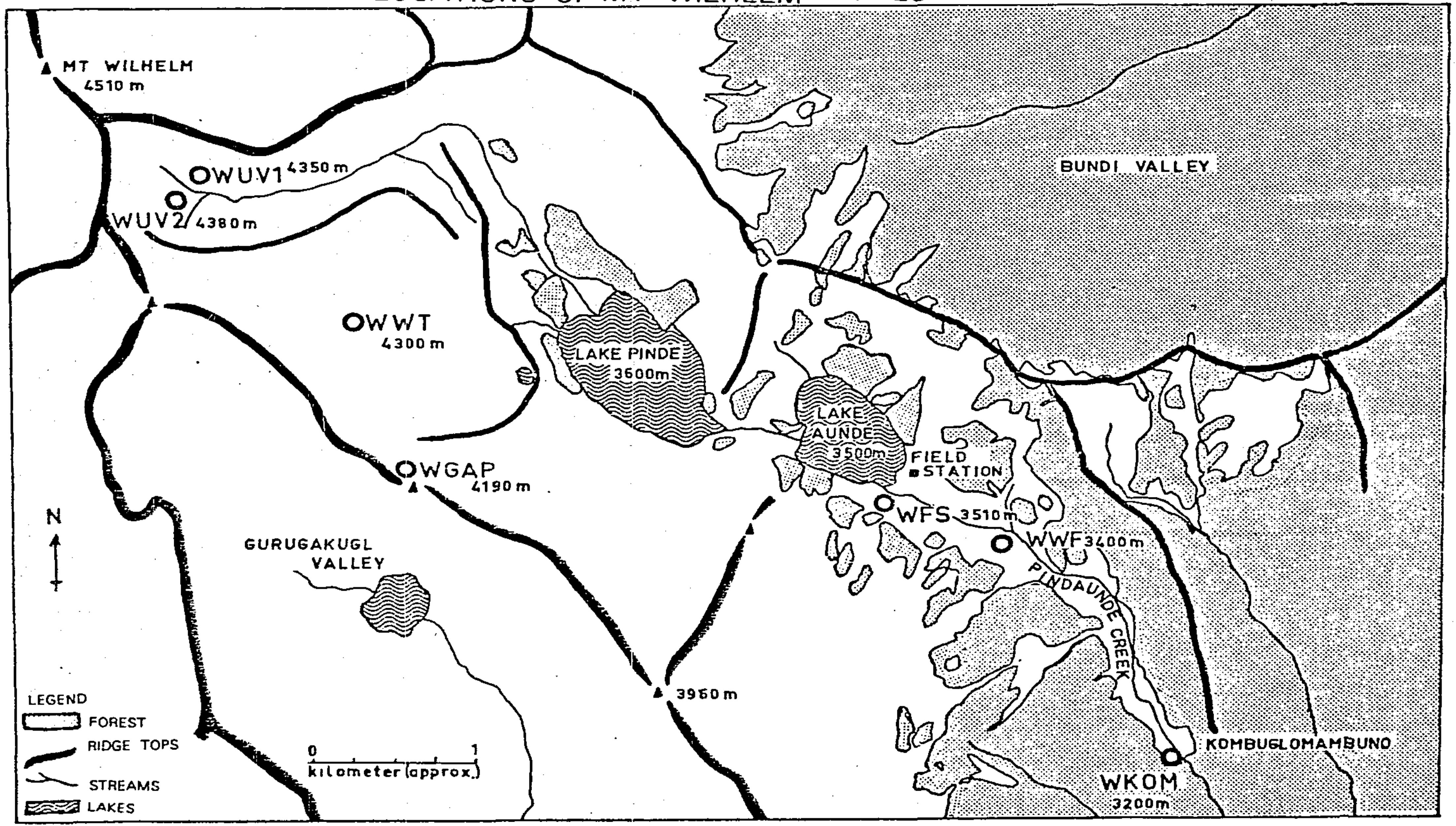
The vegetation of Mt Wilhelm (Pindaunde Valley and adjacent summit areas) has been comprehensively described by Wade and McVean (1969). In the current study, seven sites were selected in *Deschampsia klossii* dominated, tussock grassland. Four of the sites may be referred to Wade's and McVean's subalpine '*Deschampsia klossii - Danthonia penicilata* (tussock grassland) association' (p. 82). The remaining three sites were part of their 'alpine tussock grassland (*Deschampsia klossii - Hierochloe redolens*) association' (p. 182). The floristic compositions of the four major sites (Waterfall, WWF; Field Station, WFS; Upper Valley 1, WUV1; and Upper Valley 2, WUV2) are compared in Table 2.1 with the two Wade and McVean (1969) tussock grassland associations. All sites, except Kombuglomambuno (WKOM), consisted of closed-canopy populations of *Deschampsia klossii* which, in every respect, overwhelmingly dominated all other species. At the Kombuglomambuno site, the tussocks were more widely spaced and the inter-tussock species correspondingly more common.

The location of sites can be seen in Figure 2.1 and the general habitat conditions in Tables 2.2 and 2.3. Further details of the individual sites are given below.

a. Waterfall (WWF)

The site was a small, shallow (3-4 m deep), east facing valley. The bottom of the valley was much wetter than the sides and occasionally had a small stream flowing through it, although no definite stream bed had formed. The soil was 1-1.2 m deep. There appeared to be more organic matter in the valley bottom soils than in those on the sides. Charcoal and charred logs occurred in the top 0.3 m. Coarse, angular rock fragments up to 0.3 m in diameter were present at all depths in variable, but small quantities. Living roots were concentrated in the upper 0.3 m but occurred down to at least 1 m. The soil was mottled red, particularly in the lower portions, indicating a fluctuating water table. The depth of the water table was observed to vary from the surface during very wet weather to at least 0.8 m below the surface during dry spells. Shrubby species occurred throughout the site but were very

LOCATIONS OF MT WILHELM SITES



map revised from Wade, 1968

FIGURE 2.1

Table 2.2: Details of site descriptions for Macquarie Island, Campbell Island, and Mt Wilhelm.

Site	Latitude S	Longitude E	Altitude above sea level (m)	Aspect	Slope angle°	Drainage	Organic soil depth (cm)
Macquarie Island:	54°30'	158°57'					
Garden Cove (MGC)			30	210°(SSW)	41	v.good	0-100
Wireless Hill exposed (MWE)			60	246°(SW)	35	v.good	15-100+
Wireless Hill sheltered (MWS)			60	210°(SSW)	33	good	80
Razorback Hill (MRB)			12	360°(N)	11	v.good	50
Perseverance Bluff (MPB)			222	31°(NNE)	11	v.good	100+
Campbell Island:	52°33'	169°08'					
Beeman Hill (CBH)			105	ca 40°(NE)	38	v.good	ca 75
Mt Wilhelm:	5°47'	145°01'					
Upper Valley No.2 (WUV2)			4380	35°(NE)	ca 22	good	75
Upper Valley No.1 (WUV1)			4350	180°(S)	ca 16	good	50
Wilhelm Track (WWT)			4300	90°(E)	28	good	100
Bivouac Gap (WGAP)			4190	0°(N)	ca 26	v.good	?
Field Station (WFS)			3510	90°(E)	5	good	150
Waterfall (WWF)			3400	90°(E)	15	fair-moderate	100+
Kombuglomambuno (WKOM)			3200		ca 5	poor-fair	?

Table 2.3: Soil profiles at Mt Wilhelm sites

	Depth (m)	Colour		Water-table	Roots	Notes
		Matrix	Mottles			
WWF (slope)	0-0.3	5YR 2/2	(few)		>85% of total	
	0.3-1.1	5YR 3/3	5YR 3/6 10R 3/4			numerous mottles 0.3-0.6 m
(valley bottom)	0-0.3	7.5YR 2/2	2.5YR 3/3		>90%	charcoal present high organic content
	0.3-0.7	5YR 3/2	2.5YR 3/3		few	gravel lenses silt and clay content higher
	0.7-1.2	5YR 2/2	2.5YR 3/3	0.8m	few	some large rocks mottles associated with roots
WFS	0-0.43	75YR 2/2	-	-	> 90% in top 0.4 m	
	0.43-0.7	10YR 2/3	-	0.6m	few	
	0.7-1.0	10YR 3/4	-		few	
	1.0-1.05		-			fine gravel
	1.05-1.35	10YR 3/4	5YR 3/6		few	reticulate mottling
WWT	0-0.3	5YR 3/1	-	-	> 80%	wet but no free running water
	0.3-1.3	5YR 3/3	-	-	few	
	bedrock					mat of roots on top of rock
WUV2	0-0.75	5YR 3/2	-	-	numerous large roots	30-40% of soil volume composed of sharp angled rock
	0.75-1.1	7.5YR 3/3	-	-	fine roots	soil moist but no free running water

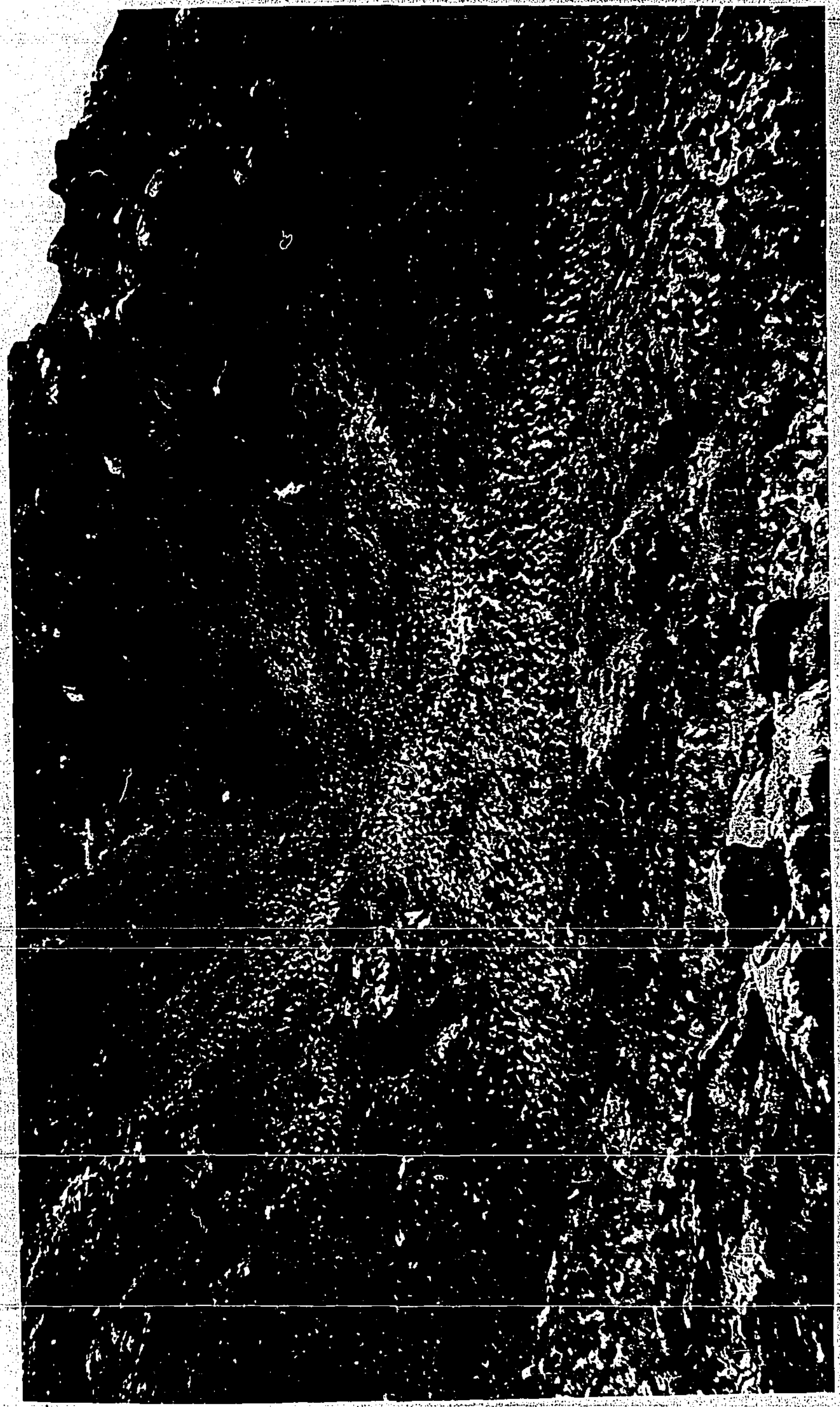
* Colour code from Oyama and Takehora, 1967.

from direct morning sunlight until 0930-1000 hr and was subject to cold air ponding.

The *Deschampsia klossii* tussock population continued upslope above the alluvial fan but became broken there by solifluction and land slip. On wetter, steeper areas, the tussocks gave way to vegetation of lower stature dominated by *Ranunculus pseudolowii, Oreomyrrhis pumila, Drapetes*

FIGURE 2.2 WFS tussock grassland, 3510 m, Mt Wilhelm. Outfall of Lake Aunde is from centre right to lower left. Study area is just right of centre.

FIGURE 2.3 WUV1 tussock grassland, 4350 m, Mt Wilhelm. Study area is central in Figure. WUV2 is located just beyond the upper left margin.



ericoides, and bryophytes. On lower, flatter areas the tussock vegetation slowly graded into a hard cushion bog dominated by *Astelia papuana*.

d. Upper Valley 2 (WUV2)

This site was situated in the same valley as WUV1, but was on a bench 30 m higher and on the opposite wall from the latter site (Figure 2.4). As at the other sites described, following heavy rain, streams often flowed over the surface through the site. The soil was deep (1 m) but very coarse, with 30-40% of the volume occupied by sharply angular rocks up to 0.5 m in diameter (Table 2.3). Rooting occurred throughout the soil; large grass roots were seen to a depth of 0.75 m and fine roots to 1.1 m.

The site had very sharp boundaries with adjacent vegetation. Where soil became shallower, short alpine grassland dominated, and *Papuapteris linearis* was common closer to the precipitous rock wall to the west.

The other sites were studied in less detail than the four above.

e. Kombuglomambuno (WKOM)

The site was located on the slopes of one of the ridges of the terminal moraine complex at the lower end of the Pindaunde Valley. The soil was deep (at least 0.8 m) and wet. An intermittent stream flowed through boggy ground nearby. The ground below the site was dominated by low-stature, bog vegetation, while the better-drained ground above the site had an abundance of the large tree fern, *Cyathea atrox*. The ground between the widely spaced tussocks was completely covered by a dense, short growth of many bog species.

f. Bivouac Gap (WGAP)

The site was at an intermediate altitude in the tussock grasslands. It lay at the upper limits of the subalpine tussock grassland as evidenced by the several large (1.2 m high) *Drimys piperita* and *Coprosma divergens* shrubs nearby (Figure 2.5). The area of study was a closed-canopy, tussock grassland free from shrubs within 10 to 15 m of it. The soil was presumably deep and received run-off water from the steep, rocky slopes above. Because of the aspect and small water catchment area above it, the site was drier and warmer than might otherwise have been expected.

g. Wilhelm Track (WWT)

This site was at a similar altitude (4300 m) to the two Upper Valley sites but was not located in a narrow valley. Situated on the broad,

FIGURE 2.4 WUV2 tussock grassland, 4380 m, Mt Wilhelm. Study area is just above the left half of the horizontal centreline of Figure. WUV1 is in valley bottom beyond the lower right margin of Figure.

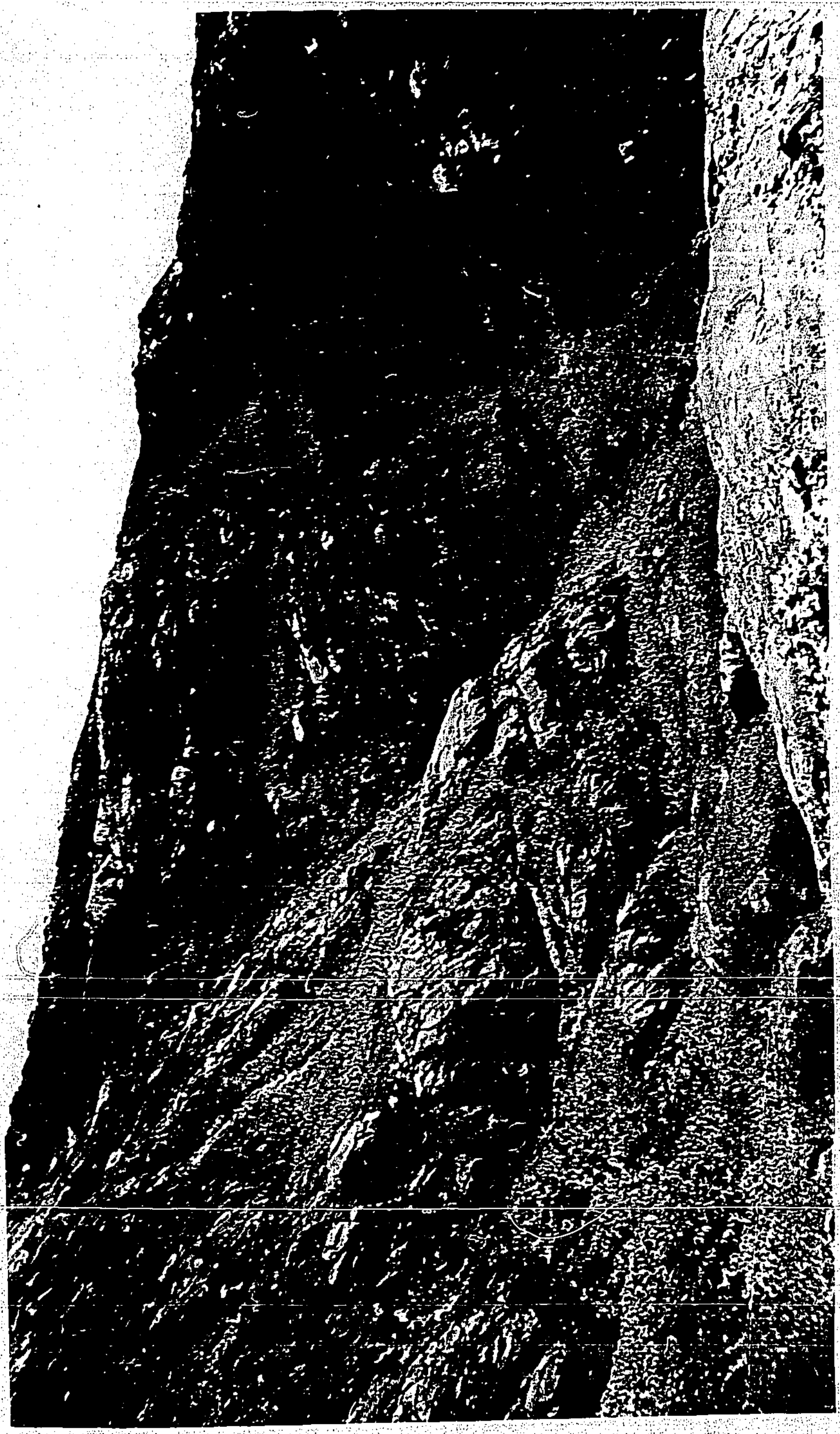
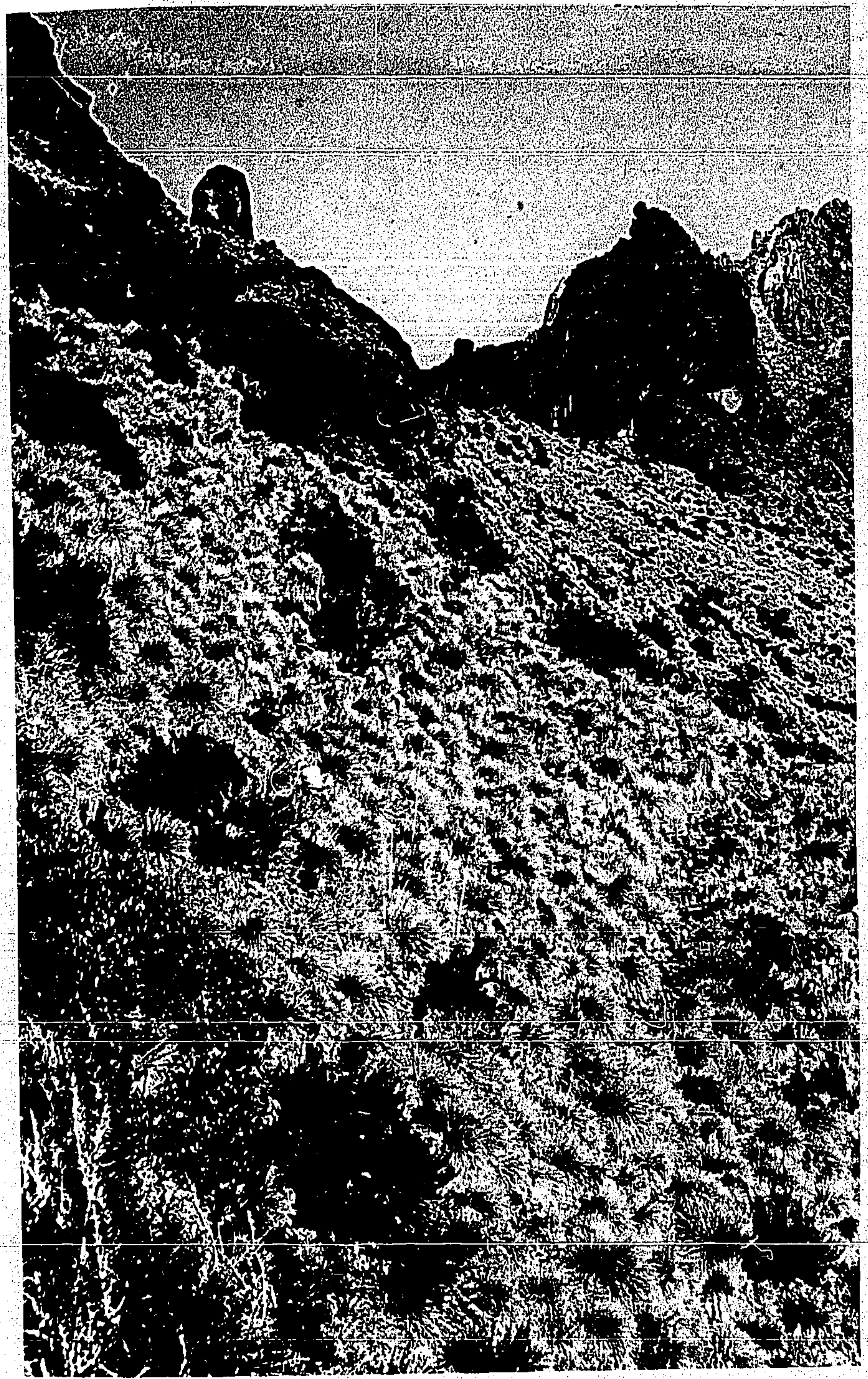


FIGURE 2.5 WGAP tussock grassland, 4190 m, Mt Wilhelm. Study area is central in Figure. The large shrubs are *Coprosma divergens* and *Drimys piperita*.



easterly facing flank below the Summit Ridge (Figure 2.6) it was in a glacially scoured depression in the granodiorite, 10 m wide, 1 m deep, and 40-50 m long, with its long axis parallel to the slope. The soil was high in organic matter (Table 2.3) and kept constantly wet by a small stream, which periodically overflowed into the depression. Roots occurred throughout the soil with a tendency for concentration in the top 0.3 m, and were immediately adjacent to the bed rock base of the depression in the form of a mat. No mottling was observed so that periodic waterlogging was probably not common though the soil was constantly moist.

The surrounding vegetation boundaries were sharp and coincided with the limits of the rock depression. Where the soil became abruptly shallow, short, alpine grassland occurred, dominated by *Danthonia vestita, Astelia papuana, Detzneria tubata,* and occasionally *Coprosma divergens* also occurred in the vicinity.

B. MACQUARIE ISLAND

Macquarie Island ($54^{\circ}30'$S.Lat., $158^{\circ}57'$E.Long.) lies in the vast Southern Ocean, midway between the Australian and Antarctic continents. The island is probably composed of Pliocene, oceanic, crustal rocks intruded into by ultramafic and mafic bodies and finally by doleritic dikes. The mass of the island appears to have been fault-lifted on the Macquarie Ridge between the Indian and Pacific plates (Varne *et al.*, 1968). The island is small, being only 31 km long (north-south) and 5 km wide (east-west), and rises to a maximum altitude of 433 m above the sea. The island is elongated and rises abruptly from very narrow beaches to an undulating plateau, 300m high, with numerous lakes. The north-south orientation of the long axis exposes much of the island to the full force of the strong, westerly gales.

The vegetation and soils of Macquarie have been well described by Taylor (1955). Briefly summarizing Taylor's description, five major vegetation formations are recognizable: grassland, herbfield, fen, bog, and feldmark. The soils, classified under the systems of Glinka (1928) with modifications by Hallsworth and Costin (1950), are grouped into four classes: highmoor peats, fen peats, bog peats, and dry tundra soils.

All of the sites chosen in the current study of primary productivity were on highmoor peat in Taylor's '*Poa foliosa:Cardamine corymbosa* subassociation'. The occasional occurrence of *Stilbocarpa* plants in the

FIGURE 2.6 WWT tussock grassland, 4300 m, Mt Wilhelm, east facing flank with strips of alpine tussock grassland, short alpine grassland, and bare rock surfaces. Study area is immediately left and below centre of photograph.

vicinity of the study areas (MWE and MRB) was not thought to warrant classifying these sites in the '*Poa:Stilbocarpa* association'. *Poa foliosa* was the sole dominant at each site and the subordinate species did not differ significantly between the two associations.

Five sites were selected at the northern end of Macquarie Island. Selection criteria, in addition to those already given, were:

a) a relatively steep slope angle assuring good drainage, and
b) the representation of the altitudinal range, aspect, and wind exposure under which the formation occurred.

The objective in choosing the five sites was to provide data to evaluate the relative importance to the growth of the *Poa* of the degree of wind exposure, slope, and aspect in relation to energy receipt and altitude above sea level. Summaries of the physical descriptions of the sites are presented in Table 2.2 and site locations in Figure 2.7. The floristic composition of each site is given in Table 2.4, together with those of two of Taylor's (1955) tussock grassland associations.

Differences are evident in the comparison of floristic composition (Table 2.4) of the current study sites with Taylor's (1955) lists for the '*Poa foliosa* association' and the '*Poa foliosa:Stilbocarpa polaris* association'. These differences, however, are actually minor given the simplicity of the vegetation and the fact that these associations are defined by the overwhelming dominance of *Poa foliosa*. The occurrence and abundance of other species is very much dependent upon the chance seeding of the species into the occasional breaks in the *Poa* canopy (*cf*. Ashton, 1965).

a. Garden Cove (MGC, 30 m)

The site was on the lower third of a steep, south-south-west facing slope and was only moderately exposed to winds, being partially sheltered by Hut Hill to the south and by a ridge of Wireless Hill to the west. Twenty metres above the site, bed rock was exposed. Sharply angular rock fragments up to boulder size were scattered throughout the site and in the soil.

The site had a mature population of tussocks which were 1-1.5 m high and formed a nearly continuous canopy of interlacing crowns (0.6-1.2 m in diameter). Tussock pedestals were large (0.3-0.5 m in diameter) and often decumbent. Tussock roots appeared primarily confined to the pedestal peat. The older parts of the pedestals were decaying and whole

LOCATIONS OF MACQUARIE ISLAND SITES

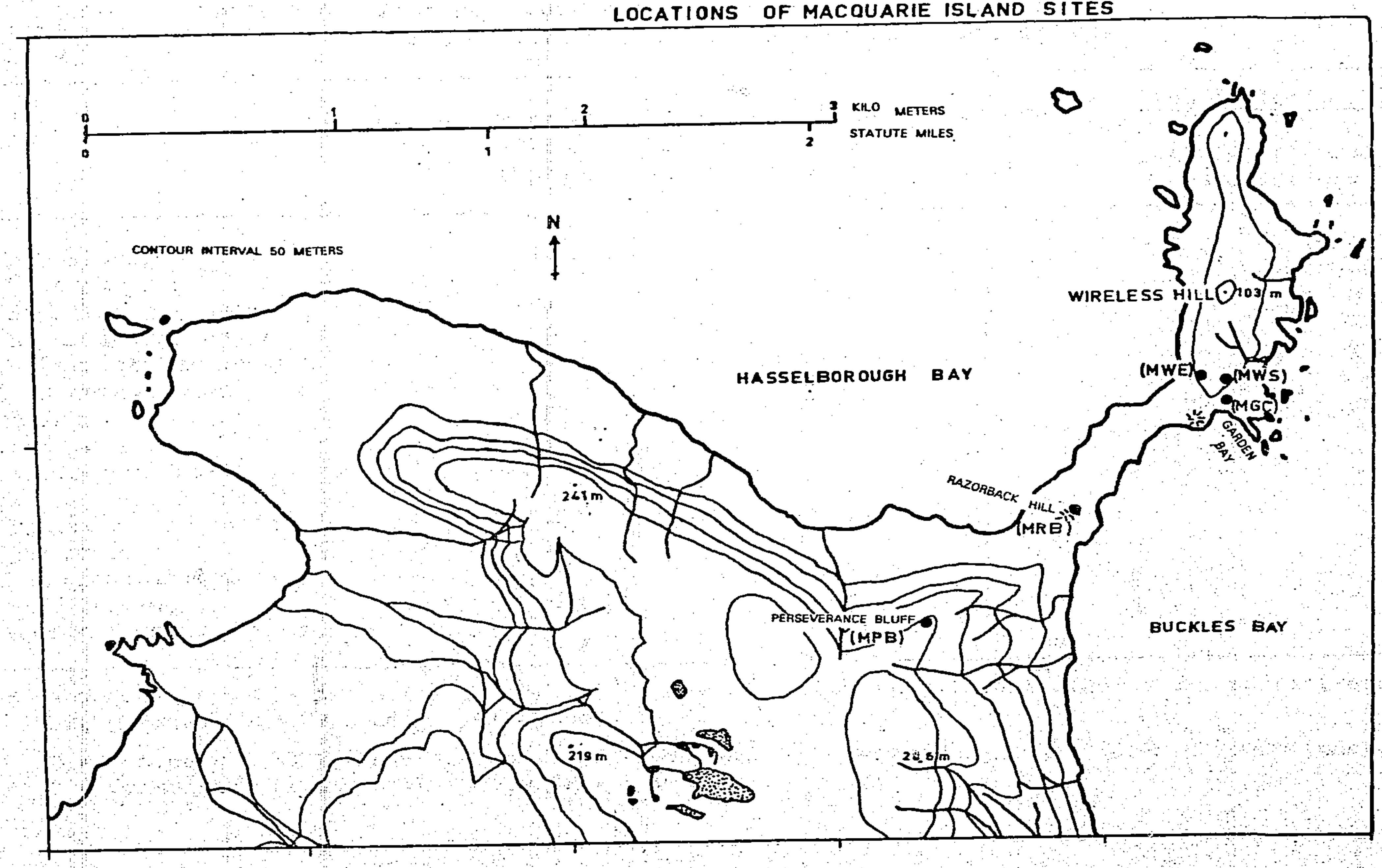


FIGURE 2.7

Table 2.4: Floristic composition of Macquarie Island sites, compared with two of Taylor's (1955) associations

	Garden Cove	Wireless Hill - exposed	Wireless Hill - sheltered	Razor-back Hill	Perseve-rance Bluff	From Taylor's 1955 associations		
						Poa foliosa	*Poa/ Stilbocarpa*	
Poa foliosa	D*	D	D	D	D	D	Co-D	tall plants forming canopy
Stilbocarpa polaris	VR	O	VR	O	R	–	Co-D	
Cardamine corymbosa	VR	VR	VR	VR	VR	O	C	low understorey plants occasionally in openings of canopy but always near the ground
Ranunculus biternatus	–	VR	VR	–	VR	–	–	
Callitriche antarctica	VR	VR	VR	–	–	–	R	
Colobanthus muscoides	VR	VR	–	VR	–	–	–	
Acaena sp.	–	R	–	VR	VR	VR	VR	
Uncinia sp.	–	–	VR	–	–	–	–	
Luzula compestris	–	–	–	–	VR	–	–	
Colobanthus crassifolius	–	–	–	–	VR	–	–	
Epilobium nerteroides	–	–	–	–	VR	–	–	
Poa annua	–	–	–	–	VR	–	–	
Stellaria decipiens	–	–	–	–	–	O	C	
Stellaria media	–	–	–	–	–	(L) O	(L) O	
Blechnum penna-marina	–	–	–	–	–	(L) A	–	

* Abundance symbols are after Taylor 1955. Percent cover equivalent used in the current study are given in brackets after the symbol.

D = Dominant (80%), A - Abundant, C = Common, R = Rare (0.5-1.0%), Co-D = Co-Dominant, O = Occasional (1.5%), VR - Very Rare (0.5%).

tussocks were easily broken off. Vascular plants other than *Poa foliosa* were rare. A few mosses and one lichen occurred commonly as a thin layer over the pedestal bases and between pedestals where there were canopy breaks.

b. Wireless Hill exposed (MWE, 60 m)

MWE was essentially like the MGC site, consisting of a mature community dominated by *Poa foliosa*. The site was south-west facing, steeply sloping, and completely exposed to winds from the east, south, and west. It was about 15 m below the hill crest with large areas of bare soil actively eroding above the site. The tussocks were not so large as at MGC. Many pedestals were decumbent and rooting was primarily confined to the pedestal. The soil was somewhat deeper (*ca.* 1.5 m) and freer from rocks than at MGC site.

c. Wireless Hill sheltered (MWS, 60 m)

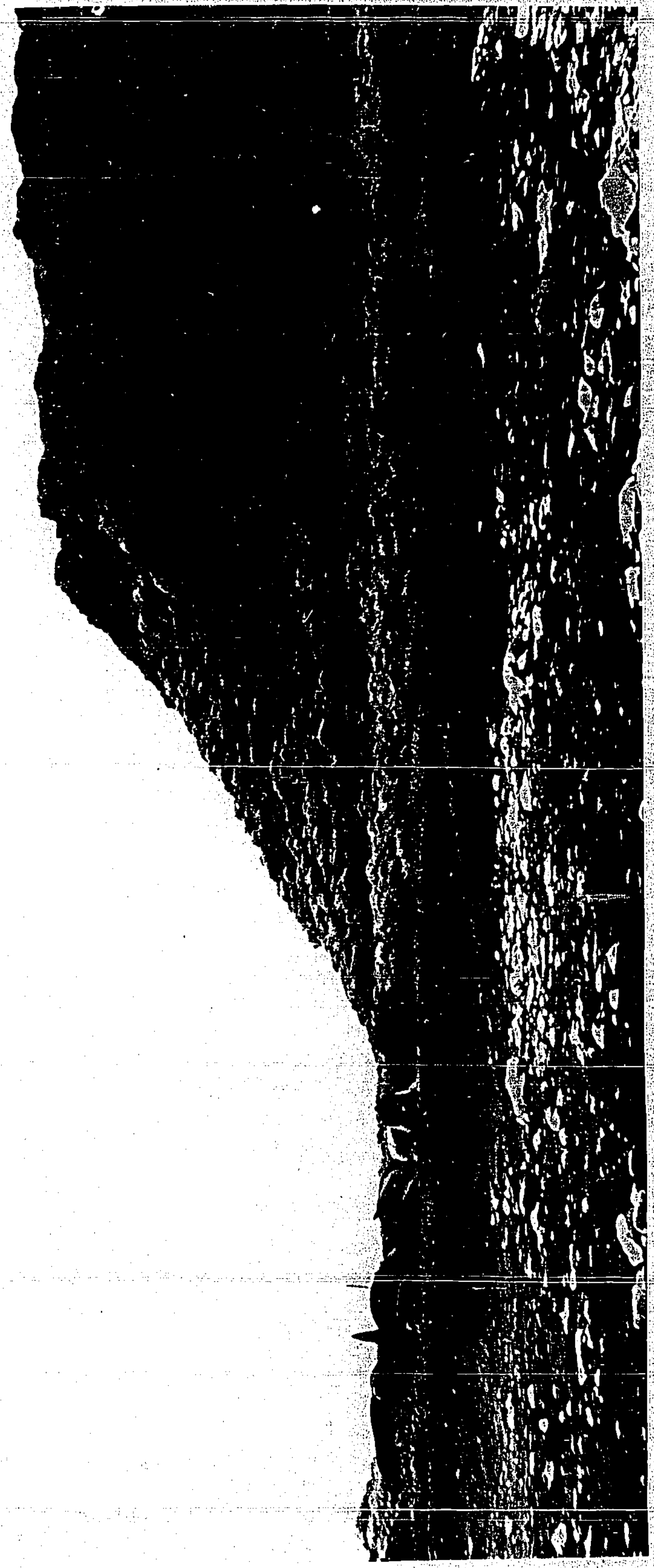
The MWS site was only marginally acceptable on the basis of the size and slope criteria. Only a small portion of the total community was on a slope of desired aspect and steepness. The remainder of the community lay primarily on nearly flat ground or on other than southerly facing slopes. However, the site was selected because it was protected from most winds by being in a shallow valley and was of comparable slope, aspect, and altitude to the MWE site, thus providing a means for monitoring the effect of wind exposure on growth.

Tussocks were mostly mature, having well developed pedestals, but most were completely erect rather than partially decumbent. Approximately 0.8 m of nearly rock free, very peaty soil overlay weathered bed rock on the site. (Tussocks growing on the adjacent valley bottom were not included in the site although they appeared to be more robust and to have broader leaves than those on the valley sides.)

d. Razorback Ridge (MRB, 12 m)

The site was situated 2-3 m below the crest and at the northern extremity of a sharp ridge extending out from the main island plateau onto the Isthmus (Figure 2.8). The tussocks were large and had decumbent bases. *Stilbocarpa* occurred in the vicinity but tussocks selected for study were completely surrounded by other tussocks, thus reducing interspecific effects. The soil was very rocky with sharply angular pieces up to 0.3 m in diameter common. Fine soil averaged only 0.3 m deep between tussocks, but pockets as much as 0.6 m deep occurred.

FIGURE 2.8 MRB tussock grassland, 12 m, Macquarie Island. Study area is on slope at end of ridge. Elephant seal wallows are in middle ground and beach sands and gravels are in fore of Figure.



The site was exposed to winds from the north to west to south-west, but protected from all southerly and easterly winds.

e. Perseverance Bluff (MPB, 222 m)

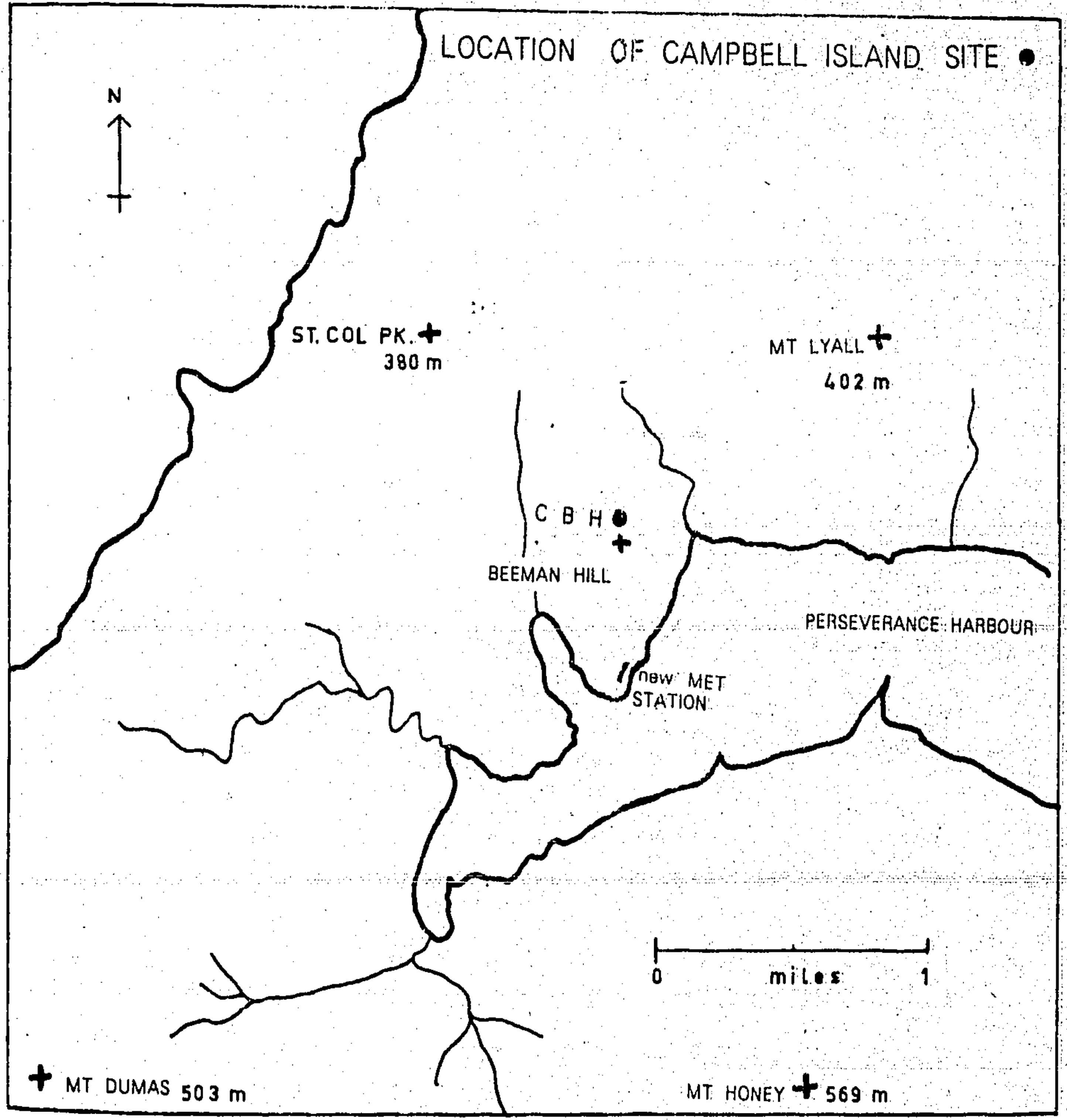
This site was located just below the northern crest of the main island plateau (Figure 2.9). It was exposed to all winds from northeast to north to northwest but protected from all others. The tussocks were mature, having well developed crowns and pedestals, the latter mostly erect. Plants other than *Poa foliosa* were rare and primarily occurred in the openings of the tussock canopy. There was more than one metre of fine soil, rich in organic matter, in which rock fragments were rare.

C. CAMPBELL ISLAND

Campbell Island (52°33'S.Lat., 169°08'E.Long.), like Macquarie Island, is a sub-Antarctic island with an extremely oceanic climate. Campbell Island represents the remnants of an ancient caldera, its amoeboid shape and precipitous cliffs marking the edges of old craters. Most of the rocks of Campbell are volcanic although a limestone stratum also occurs. Surficial glacial deposits are common and the conspicuous U-shaped valleys attest to extensive past glaciation (Oliver *et al.*, 1950). On Campbell, as on Macquarie Island, there is no permanent snow and only light falls, which melt either immediately or at most in a few days, occur at any time of the year (DeLisle, 1965).

To avoid the effects of sheep grazing, a site had to be chosen amongst inaccessible rocks and steeps. A small ravine on the upper, northern slopes of Beeman Hill (Figure 2.11) provided a small area of 40 m^2 in which 20 *Chionochloa antarctica* tussocks formed a nearly closed-canopy community. The ground covering species of this area are listed in Table 2.5, from which it can be seen that *Polystichum vestitum* and the shrubs *Coprosma ciliata* and *C. cuneata* were fairly abundant. The *Coprosma* grew both between the tussocks and within the grass canopy, but always lower than the top of the latter. This condition was not unlike the high '*Danthonia* meadow' from Auckland Island, described by Cockayne (1909, p.109).

The Beeman Hill site was located on the steep, north facing wall of a large, columnar-jointed mass of basalt. Bare rock was exposed on both sides of and below the small ravine. Site details are summarized in Table 2.2 and site locations are shown in Figure 2.10. The soil was variable in



taken from a bird distribution map based on a map by L. Clifton for the Dominion Museum Wellington, New Zealand.

FIGURE 2.10

FIGURE 2.11 CBH tussock grassland, 105 m, Campbell Island. Study area is not shown in the Figure but occurs on steeper ground immediately to the left. The scene is typical of areas where *Chionochloa antarctica* now grows. It can be seen in the lower third of the valley which divides the hill.

Table 2.5: Floristic composition of Beeman Hill site, Campbell Island

Species	% cover
Chionochloa antarctica	71.4
Coprosma ciliata and *C. cuneata*	12.8
Polystichum vestitum [a]	4.6
Dracophyllum longifolium and *D. scoparium*	0.9
litter	10.3

a. mostly occurs as understorey to one layered grass-shrub canopy

depth depending upon the occurrence of pockets in the bed rock beneath. A pit dug into one such depression yielded 0.75 m of black, highly organic soil and some black and grey sand, overlying broken bed rock. No horizons were clearly distinguishable in the profile. Roots occurred down to bed rock but were primarily concentrated in the upper 0.1 m, with the upper 0.25 m containing at least 85 to 90% of the roots. Fern roots tended to form a dense mat 3-5 cm thick beneath an angiosperm root mat.

Chionochloa antarctica dominated the vegetation in the small ravine. However, on the slopes directly adjacent and above, the tussock forming *Poa littorosa* was the dominant plant. *Coprosma cuneata*, *C. ciliata*, *Anisotome latifolia*, *Bulbinella rossii*, *Pleurophyllum speciosum* and *Polystichum vestitum* all occurred in the immediate vicinity. The site belonged to the 'tussock grassland formation' of Oliver and Sorensen (1951).

Two major sites for monitoring temperature were selected: one at the WFS site (3510 m) and the other at the WUV1 site (4350 m). Both sites were subject to cold air ponding at night, but were representative of areas where *Deschampsia* was dominant. Two Sumner thermographs were positioned, each with a sensor at the top of the tussock canopy (63 cm at WFS, and 50 cm at WUV1) and another sensor below the tussock canopy (20 cm WFS, and 17 cm WUV1). A single sensor Ota soil thermograph measured soil temperature at 2.5 cm at WUV1 (soil was only 5-10 cm deep over bed rock) and a similar, but two sensor, instrument recorded soil temperatures at 15 cm and 50 cm depth below surface at WFS. These latter two instruments were not completely satisfactory because they proved sensitive to air temperature both on the cable leads and at the recorder. The Sumner instruments were accurate for temperature recording, but chart advance mechanisms ran at varying speeds making accurate determination of hourly temperatures impossible for periods when time was marked at greater than weekly intervals. The WFS and WUV1 sites were operational for about 12 months but malfunctions reduced the net useable period to three to six months (see Figure 2.12).

Subsidiary and shorter term installations for monitoring air temperature were set up at four other sites on the mountain where growth measurements were collected. These sites had Casella hygrothermographs in white, ventilated, foam plastic shelters, set amongst the *Deschampsia* tussocks. Weekly maximum and minimum temperatures were obtained at two other sites in the Upper Valley to further evaluate cold air ponding and aspect effects on temperature.

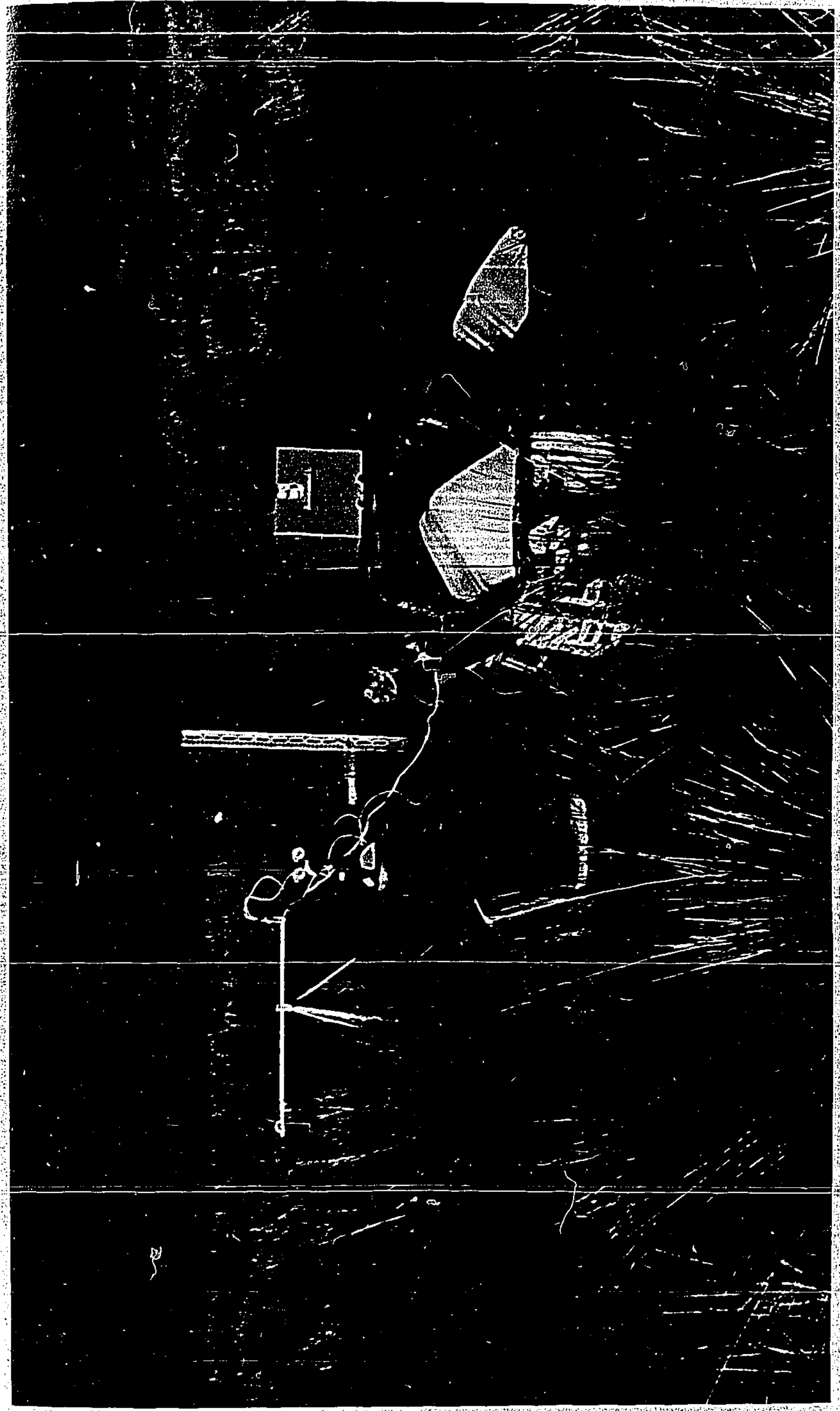
b. Macquarie Island

No instruments were set up at Macquarie Island. Data were taken from Commonwealth Bureau of Meteorology records, as well as from published summaries of records collected by various expeditions to the island before the establishment of the meteorological station.

c. Campbell Island

Positive global radiation was measured for a five-week period, 31 January 1970 to 8 March 1970, using an Ogawa Seiki pyranograph. The instrument was set up on the edge of a hard cushion bog between Mt Lyal and Beeman Hill. Air temperature at about 30 cm was measured on a Casella, continuously recording hygrothermograph, and soil temperatures at 10 and 20 cm depth were measured at irregular intervals using mercury in glass thermometers. Long term meteorological records were taken from

FIGURE 2.12 WFS meteorological station. Net radiation sensor is held by tripod on left; centre pole holds air temperature sensors; (soil temperature sensors are below the air sensors); recording instruments are in boxes at the right.



published summaries of New Zealand Meteorological Service records or from summaries of earlier expeditions.

d. Analysis

In addition to the usual methods of comparing maximum, minimum, and mean temperatures, the method of 'thermoisopleth diagrams' for comparing the monthly and daily course of temperatures was employed (*e.g.* Erk, 1885; Troll, 1943, 1958). The monthly mean temperature for each hour of the day (or for as many hours as there were data) was entered in a two dimensional matrix. Isotherms were then plotted on this matrix, linearly interpolating positions between matrix points where necessary. Troll (1943) recommends using a plotting field of 18 cm for the hour dimension and 24 cm for the month dimension to standardize the diagrams for ease of comparison.

The completed thermoisopleth diagram resembles a contour map with hills of high temperature and valleys of low temperature. The diagrams readily permit the determination of the time of day and year when high and low temperatures are likely to occur and also their mean durations. On a world scale, the form of the diagrams is characteristic for particular regions (see Troll, 1958). Two extreme forms of diagram occur: i) tropical, in which the isotherms are straight lines parallel to the month axis, indicating little seasonal temperature range but strong daily fluctuations; and ii) polar, the isotherms again being straight lines but parallel to the hour axis, indicating little or no daily fluctuations but strong seasonal changes. A third form can be recognized from extremely oceanic places, such as the sub-Antarctic islands and high tropical mountains, where temperature change throughout the day or the year is small.

The diagrams presented in Chapter 4 were produced by a PDP-11 digital computer and Calcomp plotter at the Australian National University Computer Center using a program developed by Mr Robert Crago.

C. CARBOHYDRATES

Field specimens were collected between 0730 hr and 0900 hr, except for those destined to provide data on diurnal fluctuations and a few others. Leaves, leaf sheaths, and roots were collected at all sites. In addition, culms and inflorescences, and dead leaves were collected at Mt Wilhelm; and stems at Campbell Island, and Macquarie Island.

Sample times at Mt Wilhelm were selected for i) early morning, and ii) later in the day if it either remained completely cloudy or sunny which ever it was at the time of the first sample. This procedure avoided variation due to fluctuating light intensity caused by intermittent cloudiness, but also resulted in erratic sample times. Loss of specimens in transit to Canberra further depleted sample sequences.

In the field, specimens were cut into 5-10 cm lengths, placed in glass vials, covered with boiling 80% ethanol, boiled for 15 minutes, capped, and sealed with paraffin wax. In the laboratory, the water- and alcohol-soluble sugars were extracted by comminuting the specimens in 60% ethanol with a high speed homogenizer. Each sample was then heated for half an hour in a water bath, centrifuged, and washed twice with 60% ethanol. The fluid portion was then clarified using the method of Hassid (1936), non-reducing sugars were hydrolized after the method of Lehman (1931), and analyzed for total reducing sugars using Nelson's colorimetric modification of Somogyi's copper method, as described by Hodge and Hofreiter (1962). A Bausch and Lomb Spectronic 20 spectrometer set at 560μ was used in the analysis.

The alcohol insoluble portion of the sample was oven dried at 100°C, weighed, and then analyzed for starch content by the method of Hassid and Newfeld (1964), using Loewus' (1953) modification of the anthrone technique.

All sugar and starch values are presented as a percentage of the alcohol insoluble dry weight.

D. BIOMASS

a. Mt Wilhelm

Five 1.0 m x 0.75 m quadrats were clipped to about two cm above ground level and all nonvascular green plants on the soil surface were collected at each site. A check of the first site (WFS) showed that five quadrats were sufficient to obtain a mean dry weight with a standard error within 10% of the mean. Some sites proved to be slightly more heterogeneous than the WFS site, but not by a large amount. The collected material was sorted into: grass (living, dead), herbs (living), cryptogams (living), shrubs (living, including woody parts). All samples were oven dried at 88°C (near the boiling point of water at 3500 m), and then weighed to the nearest gram for large samples or the nearest 0.001 g for small samples.

Root biomass in the upper 24 cm of soil (estimated to contain about 80% of all roots) was randomly sampled using a cylindrical copper pipe (30 cm x 7 cm). These samples excluded roots within the pedestal which were estimated from separate samples taken from pedestals. The cores were washed free of soil on a 1.5 mm mesh screen. An attempt was made to separate living and dead roots on the basis of colour and firmness.

b. Macquarie Island

The data of Jenkin (1972) were used.

c. Campbell Island

In order to avoid too much destruction amongst the small amount of material available, only one *Chionochloa* tussock of known crown area was clipped. Other small areas of known size were clipped to determine shrub and fern biomass; there were no other plants in any abundance at the site. All samples were oven dried at 105°C for 24 hours and then weighed to the nearest 1.0 g or 0.1 g depending upon sample size. Root biomass was sampled in a similar way to that used in New Guinea, except that no estimates were made of pedestal mass.

E. POPULATION STRUCTURE

a. Size and distribution

The following measurements were made in a similar manner at all sites:

i) tussock crown size (primary diameter and secondary diameter of elliptic crowns) and height (to top of leaves in growth position), pedestal diameter and height in 2 m by 2 m quadrats;

ii) tussock density in 2 m by 2 m quadrats (a tussock was counted if half or more of its crown area was within the quadrat);

iii) frequency distribution of leaf lengths from clipped tussocks and, from this, leaf density; alternatively, actual counts of tiller density and numbers per tiller provided a basis for estimates of leaf density.

b. Viability

For *Deschampsia klossii* only, seed viability and production were tested on ripe inflorescences, collected by Mr J.M.B. Smith in 1972 and grown in a glasshouse in Canberra.

c. Leaf area

For each site, leaf area was estimated from certain measurements and counts of leaves. The leaves of each species studied could be represented by simple, geometric shapes for which surface areas could be calculated from basic dimensions. By knowing the frequency with which each shape occurred per unit area of ground, the leaf area index (LAI) (*i.e.* the area of the adaxial leaf surface/unit of ground) could be calculated. The shapes used for each species are given in Table 2.6.

Table 2.6: Geometric analogues of leaf shapes

Species	Shape
Deschampsia klossii	cylinder, cone (rt. x-section a circle)
Poa foliosa	trapezoid, cone (rt. x-section an ellipse)
Chionochloa antarctica	" " "

Deschampsia klossii leaves formed very regular, narrow cylinders each of which had a conical apex approximately 2-10 cm long. In calculating LAI, leaves less than 10 cm long were treated as cones while leaves greater than 10 cm long were treated as combined cones and cylinders.

i. *Deschampsia klossii*

Deschampsia klossii leaf area per tussock =

$$LA = (A_s + A_c + A_a) \qquad [1]$$

where A_s = area of leaves < 10 cm long

$$= \sum_{i=1}^{n} \pi r L N_i$$

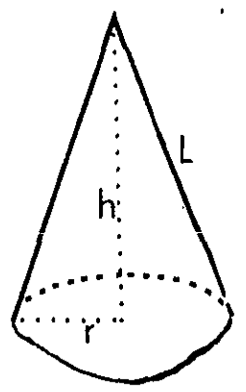
and r = radius of cone base;

n = no. of leaf classes

L = length of sloping side of cone

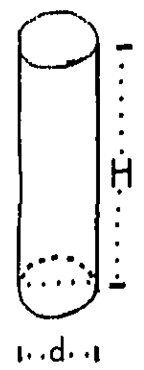
$$= \sqrt{(r^2 + h^2)}$$

where h = average cone height = length-class mid-point*;



N = number of leaves in class.

(* A study of leaf area for two tussocks, using leaf length equal to the class mid-point and then equal to the actual leaf lengths, showed a difference of less than 1.5%; therefore the class mid-point was used because it simplified calculations.)

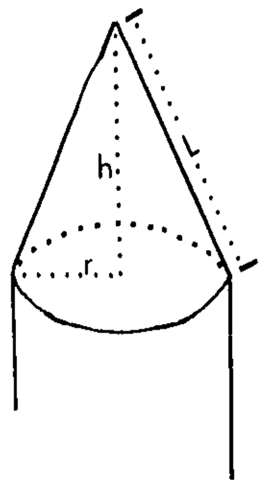


A_c = area of cylindrical leaves

$= \pi dH$

and d = cylinder diameter;

H = (total leaf length for all leaves >10 cm) - 0.1 (total leaf length for all leaves).



A_a = area of conical apex to cylindrical leaves,

$= \sum_{i=1}^{n} \pi r L N_i$

and r = radius of cone base

n = no. of leaf classes

L = length of sloping side of cone

$= \sqrt{(r^2 + h^2)}$

and h = cone height = [0.1 (total length of leaves greater than 10 cm long) / number of such leaves].

N = no. of leaves in class

Because the A's were calculated on a per tussock basis and the ground area occupied by each tussock was known, the LA per tussock was converted to a per unit land area basis = leaf area index (LAI).

$$(LA)\ (C/m^2) = LAI \qquad [2]$$

where LA = equation [1], which was calculated for tussocks of known vertically projected crown area;

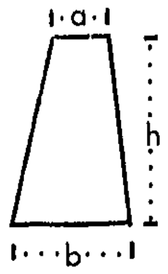
C/m^2 = mean crown area per m^2 from measurements made in 2 m by 2 m quadrats at each site.

ii. *Poa foliosa*

Poa foliosa leaf area index = LAI [3]

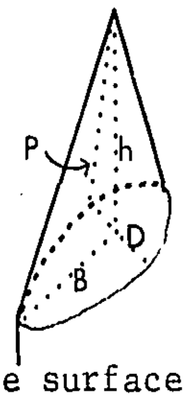
$$= (A_t + A_s)\ (f_t/m^2)$$

where A_t = area of mature leaves which have opened out and assumed a trapezoidal shape:



$= \frac{(a + b)\,h}{2}$ where a and b are the lengths of the parallel sides of the trapezoid, *i.e.* the width of the leaf at its distal and proximal ends;

h = height of trapezoid, *i.e.* leaf length;



A_s = area of young, folded leaves which had the shape of a regular cone with an elliptic base. (A_t and A_s were calculated on a per tiller basis for a sample of 50 tillers per site. Where a leaf had a complete apex, its shape was taken as triangular; where a leaf was partly folded and partly open, its area was proportionately assigned to the two shapes and added respectively to each total.)

The surface area of a regular cone with elliptic base can be found from:

Area = BPE

where B = 1/2 the length of the major axis of the base;

P = the length of the shortest, lateral side of the cone

$= \sqrt{D^2 + h^2}$;

and D = 1/2 the length of the secondary axis of the base;

h = the height of the cone;

$$E = \pi\left(1 - \frac{1}{2^2}(k^2) - \frac{1^2 3}{2^2 4^2}(k^4) - \frac{1^2 3^2 5}{2^2 4^2 6^2}(k^6) - \ldots\right)$$

$$\text{and } k = \frac{(B^2 - D^2)\,h^2}{(D^2 + h^2)\,B^2}$$

(Dr H. Edwards, Courant Institute, New York, derived the formula for calculating the area of a regular cone with an elliptic base.)

f_t/m^2 = number of tillers per metre^2 of ground area calculated from counts of four 1 m by 1 m quadrats at each site.

iii. *Chionochloa antarctica*

LAI for Campbell Island sites was calculated in a manner similar to that for Macquarie Island in that areas per tiller were determined for trapezoidal and elliptical-conic leaves, but their average was expressed in a way similar to that of Mt Wilhelm sites, *i.e.* LA and then converted to LA/m^2 of ground.

d. Leaf longevity

i. Mt Wilhelm

Leaf longevity for *Deschampsia klossii* was calculated from the records of leaf initiation and death collected as part of the growth rate study. The number of days between successive initiations was calculated for each tiller at a site and averaged for each site. The two sample periods were April-October 1970 and October 1970-July 1971.

ii. Macquarie Island

Longevity data are available from the work of Jenkin (1972).

No longevity data are available for the other sites.

e. Leaf length: weight relationship

These data were obtained from measurements of leaf length and weight made in the course of the growth rate study (see section F below).

F. GROWTH RATE

A simple method of measurement and sampling was devised to determine the rate of increase in above ground, vegetative biomass of the large, perennial, tussock grasses. Both the ruggedness and remoteness of the study areas, as well as the rigorous climates, prohibited the use of more sophisticated techniques requiring heavy, bulky equipment and an electric power source.

The method devised is a 'nondestructive index technique' (Milner and Hughes, 1968), which combines the average rate of leaf extension with average weight of unit length of leaf and leaf abundance per unit of ground, *i.e.* daily dry matter increment ($g/m^2/day$) = EWD

where E = leaf extension rate in cm/day/leaf (or tiller);
W = average weight per cm of leaf in g ;
D = leaf (or tillers) density in leaves (or tillers) $/m^2$.

The actual application of the method varied slightly both according to the special requirements of each site and with improvements incorporated with experience. Despite the slight variation of method, data derived for each site were thought to be comparable. The data are summarized in Appendix 4.4.

a. Mt Wilhelm

i. E: leaf extension rate

The leaf was taken as the basic unit for determining productivity. Measurements were begun on young leaves as they emerged from the short, outer sheaths and continued throughout the sampling period, until the leaf died, or until the apex was lost through accident, or very rarely, by insect grazing. When a newer leaf appeared, both it and the former leaf (leaves) were measured. The collar of the outer-most, and therefore oldest, living leaf was used as a reference point for measurements. Control measurements showed that the outermost leaf had stopped vertical elongation and was a reliable reference.

The curve of leaf length increase through time for individual leaves tended to be sigmoid, with the lower portion often truncated probably because measurements could be started only when leaves were at least five centimetres long. Ideally it would have been desirable to calculate the extension rate for only the exponential portions of the curves. Because many leaves only gradually slowed their rate of length increase, it was decided to avoid the subjectivity involved in estimating when exponential growth was completed. This was done by taking the end point of growth as the time when a leaf began to die back from the apex (3 mm or more of die back was the criterion used).

Some leaves did not begin to die back for several weeks after all measurable length increase had ceased, but virtually no leaves grew more than about 5% of their length after die back commenced. Because die back did not always begin when extension ceased, the rate of extension (cm/day) for such leaves would be underestimated according to the increase in the number of days, thus leading to an underestimate of productivity. However, a counter tendency is also operative in that older leaves commonly weighed more per centimetre of length than did younger leaves of the same length class; presumably structural thickening of cells continued after growth in length ceased. It is not known how these two potential errors in the estimates are balanced.

Inspection of the extension rate (and weight/cm) data revealed that these leaf characteristics were different for leaves of different lengths. These data were therefore grouped by leaf length classes for all calculations (see Appendix 4.4). Because the average linear rate of growth of leaves showed no consistent relationship to tussock crown size measured as vertically projected crown areas, leaves from all tussocks were pooled into one set of length classes for a site and the average rate of extension per leaf class calculated.

Measurements were begun on 10 new leaves on each of 10 tillers in each of five tussocks at each site. These were increased during the measurement period to include eight tussocks. Measurements were made over a seven to eight month period from April to October-November 1970.

ii. W: average weight per cm of leaf

Five tussocks, representing the range of vertically projected crown areas for WUV2 site, and two tussocks of median size from each of WGAP, WFS, and WKOM sites were clipped and the green leaves (from collar to apex) sorted into growing (*i.e.* with green apex) and non-growing (*i.e.* with greater than 3 mm of die back from apex). Each class was subdivided according to length. Average dry weight per centimetre of leaf in each class of each group was determined.

iii. D: leaf and tiller density

Leaf density was determined by counting the leaves clipped for determination of W. Only leaves from some tussocks (those clipped by Mr J.M.B. Smith (Australian National University) in 1971 from four sites mentioned in ii above) were sorted into growing and non-growing leaves. Growing leaves constituted about 52% of total leaves (range 49-54%) for the high altitude sites (WUV2 and WGAP), and about 46% (range 46.1-46.6%) for the low altitude sites (WFS and WKOM). These proportions were used to estimate the number of growing leaves in the 1970 samples. The average density for the combined years was then calculated and expressed as numbers of leaves/m^2 of crown area. The relationship of crown area to ground area was determined from the measurement of large numbers (range 35-222/site) of tussocks in 2 m x 2 m quadrats at each site. Thus, D = (number of leaves/m^2 crown area) (m^2 crown area/m^2 ground area).

b. Campbell Island

i. E: leaf extension rate

The same measurement methods as at Mt Wilhelm were used except that all leaves of the tiller were measured instead of only one. Ten tillers in each of six tussocks were measured. The measurements included the youngest leaf which could be found by opening, without damage, the folded, outer, enclosing leaves and leaf sheaths; all leaves were returned to their original positions after measuring. Leaf measurements were allocated to 10 cm length classes according to the dimensions between which the leaf had spent most of its time during the brief sampling period of 29 days (2/2/71-3/3/71). The average length increase for entire leaves was calculated for each class. Therefore E = g/cm for each of the two groups.

ii. W: average weight per cm of leaf

Leaves were clipped from a single tussock of known vertically projected crown area, measured for length, and separated into 10 cm length classes. They were initially field dried over a kerosene heater, then oven dried at 105°C, and weighed in a laboratory of the Department of Geography, University of Christchurch. The average weights per cm of leaf in each class were calculated from total class weight/total class length.

iii. D: leaf and tiller density

The number of tillers per tussock of known vertically projected crown area was determined from the clipped tussock. The crown area per unit ground area was determined for an area of approximately 40 m^2. Thus, D = (tillers/m^2 crown area) (m^2 crown area/m^2 ground area), and for Campbell Island, the production equation for above ground vegetative matter (exclusive of pedestal) =

$$D\left(\sum_{i=1}^{n}(E.D)_i\right) = g/m^2/day$$

where i = leaf length class

n = number of length classes

c. Macquarie Island

In order to simplify the calculations of growth rate, it was decided to use the tiller rather than the leaf as the basic unit.

i. E: leaf extension rate

The measuring of 10 tillers in each of five tussocks at each site followed the method used at Campbell Island. Two measurements were made, one in December and another in early February. The average rate of extension was calculated for the period for each complete leaf (leaves with tattered ends were excluded from the calculations). The leaves were grouped according to leaf positions on the tiller at the start of the period. For new leaves produced during the period an average rate was calculated as if the leaf was present and 0.0 cm long at the start of the period. This method underestimates the extension rate of the new leaves but no better estimate is available.

ii. W: average weight per cm of leaf

Twenty-five tillers from each of four tussocks were clipped, cut at collar level, measured for length, sorted in leaf position classes, oven dried at 105°C, and weighed. The average weight per cm of leaf by classes was then calculated.

iii. D: tiller density

The number of tillers per square metre of ground was determined from actual counts of three, metre square quadrats at each site. The mean of each site is the D-factor: tillers/m^2 ground.

For leaves produced during the period of observation an arbitrary decision was made to use the "W" of the 4th oldest leaf of leaves present at the start of the period. This decision tends to overestimate D for the new leaves but will tend to counteract the underestimate of E.

The productivity equation for above ground, vegetative matter (exclusive of pedestal) for Macquarie Island *Poa foliosa* becomes:

$$D((\Sigma_{i=1}^{n} (E_a . W_a)_i) + (E_b . W_b)) = g/m^2/day$$

where: a refers to leaves present at start of period of measurement

b refers to leaves produced during the period

n = number of leaves .

CHAPTER 3

CLIMATE

A. THE SUB-ANTARCTIC

Ever since 1520 when Magellan first sailed into the high southern latitudes around Cape Horn, the southern ocean and its widely scattered small islands have been ascribed one of the most unfavourable climates on earth. This is surprising because, although it is never hot (maximum temperatures always less than 10°C), neither is it ever very cold (minimum temperatures always greater than -3°C). Furthermore, the annual range of temperatures is usually between 3.5 and 5.4°C. However, the incessant procession of cold, strong, blusterous storms, which often occur with sudden violence, and the almost continuous cloud cover do make the climate unpleasant for people (data from Fabricius, 1957).

But from the point of view of some plant species, the climate of the sub-Antarctic affords excellent living conditions. Although the absence of warm temperatures and the presence of strong winds seems to restrict or preclude much woody growth on most sub-Antarctic islands, the growth of tussock-forming grasses plus certain cushion and rosette plants can only be described as luxuriant.

What then are the conditions under which tussock-forming grasses live? There is a growing body of analyzed, standard meteorological data for several of the sub-Antarctic islands (*e.g.* Fabricius, 1957; DeLisle, 1965). Micrometeorological studies are beginning to appear in the literature, but as yet most are either unpublished or for short periods only. Microclimatological research done under the auspices of the British Antarctic Survey on the islands of the Scotia Sea is building a strong base of information for islands in this area. What follows in this section is a summary of what is known of standard, screen-level climate (1.5 m), supplemented with what information is available regarding that at plant level.

a. Air temperature

Fabricius (1957) has summarized data for seven circumpolar stations while DeLisle (1965) has compared data for Auckland Islands, Campbell Island, and Macquarie Island. The mean monthly temperatures presented by these two authors vary by only 0.4°C or less, with greater discrepancy in summer than winter months, and so the data of both have been used where applicable.

The course of mean monthly temperatures at seven sub-Antarctic stations can be seen in Figure 3.1 (taken from Figure 5, Fabricius,1957). Definite seasonal fluctuations are immediately apparent in the Figure, but the narrow range of these changes is probably most important in relation to plant growth. With regard to Campbell Island and Macquarie Island, the important features are that i) mean monthly temperatures of neither station fall below 0°C, and ii) Campbell Island is warmer on average than Macquarie Island at all times of the year. There is considerable overlap in the frequency distribution of temperatures for these two stations (cf. Figure 6, Fabricius, 1957) but both the modal and maximum temperatures at Campbell Island (ca 8°C and 16.1°C respectively, ibid.) are greater than at Macquarie Island (ca 6°C and 10.6°C respectively, ibid.). The latter place has lower minimum temperatures.

Of greater importance than absolute range of temperatures to the growth of plants is the duration of any temperature. The 'thermoisopleth diagrams' of Troll (e.g.1943, 1958) provide the most convenient method for comparing both value and duration of particular mean hourly temperatures per month. Figures 3.2a, 3.2b, and 3.2c present such diagrams for Campbell, Macquarie, and Kerguelen Islands. All show clear but unpronounced characteristics of temperate climates, i.e. the isopleths tend to the vertical. In addition, the small number and wide spacing of the lines clearly demonstrate the strongly isothermal nature of the climate. Although Kerguelen is the furthest north, its cooler climate than Campbell Island is probably attributable to the nearer position of the mean location of the Antarctic convergence to the Kerguelen Islands than to Campbell Island. By contrast, the thermoisopleths for three other areas are given in Figure 3.3a,b,c. The Framdrift (82°40'N.Lat.,89°11'E.Long.) diagram, taken from Troll (1964), illustrates an extreme polar form with nearly vertical isolines, while that for Para (1°27'S.Lat.,48°29'W.Long.)(Troll,1964) represents the tropical form with isolines more or less horizontal. The polar form reflects the domination of strong, seasonal changes in temperature over the weak, diurnal changes, while the tropical form of diagram shows the reverse situation. The diagram for Adelaide (35° S.Lat.,139°E.Long.;Wace, Australian National University,pers.comm.)

illustrates the form of a temperate climate which is a hybrid between the former two types.

b. Soil temperature

The 25 days for which I collected data on soil temperatures on Campbell Island (February, March, 1971) indicated an average temperature of 8.4°C at 20 cm and 8.5°C at 10 cm. Diurnal fluctuations were small with a maximum range of 0.9°C between 0800 hours and 1700 hours. These temperatures were recorded in soil beneath a dense canopy of tussock leaves. Soil surface temperatures (recorded between tussock crowns) were always higher than soil temperatures. The average surface temperature for the same period was 10.5°C (range 8.3° to 12.8°C). Air temperatures at 0.2 m were always lower than soil or surface temperatures (mean of 6.6°C, range 4.4° to 9.7°C).

An annual, mean, 30cm earth temperature at Campbell Island was estimated from monthly means (DeLisle,1965) to be 7.2°C (range:4.2°C in July to 10.6°C in January). Soil temperature at Macquarie Island during 1967 are summarized in Table 3.1.

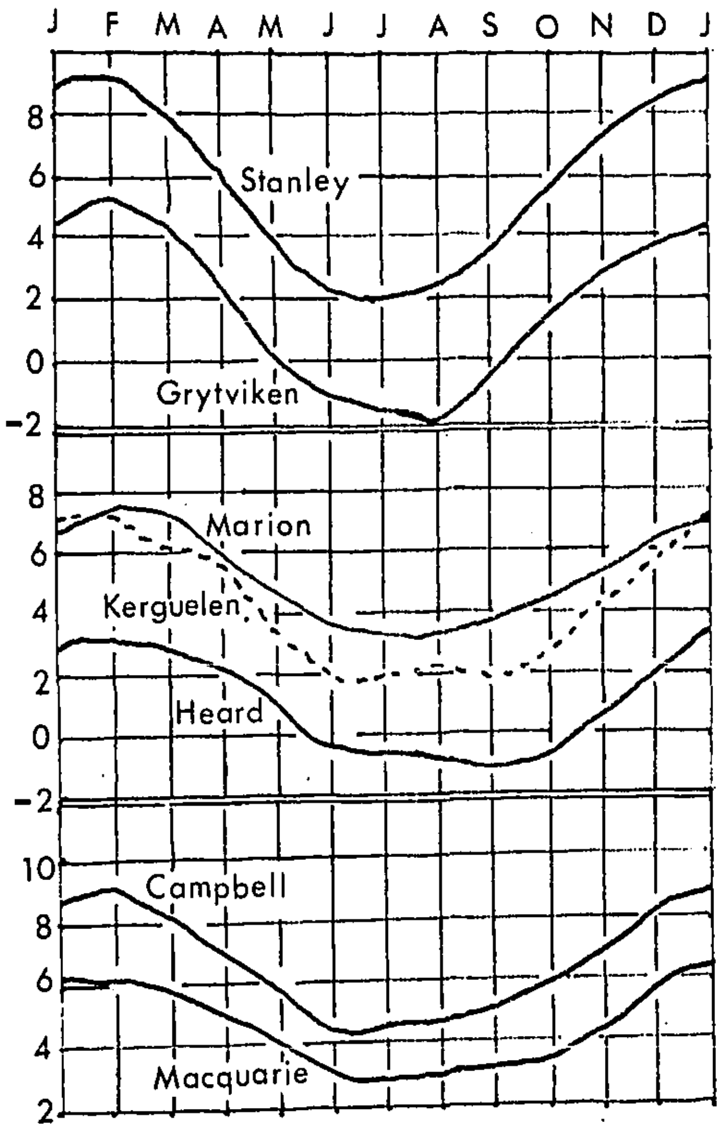


Figure 3.1. Mean monthly temperatures for seven sub-Antarctic stations (From Fabricius, 1957, Fig.5).

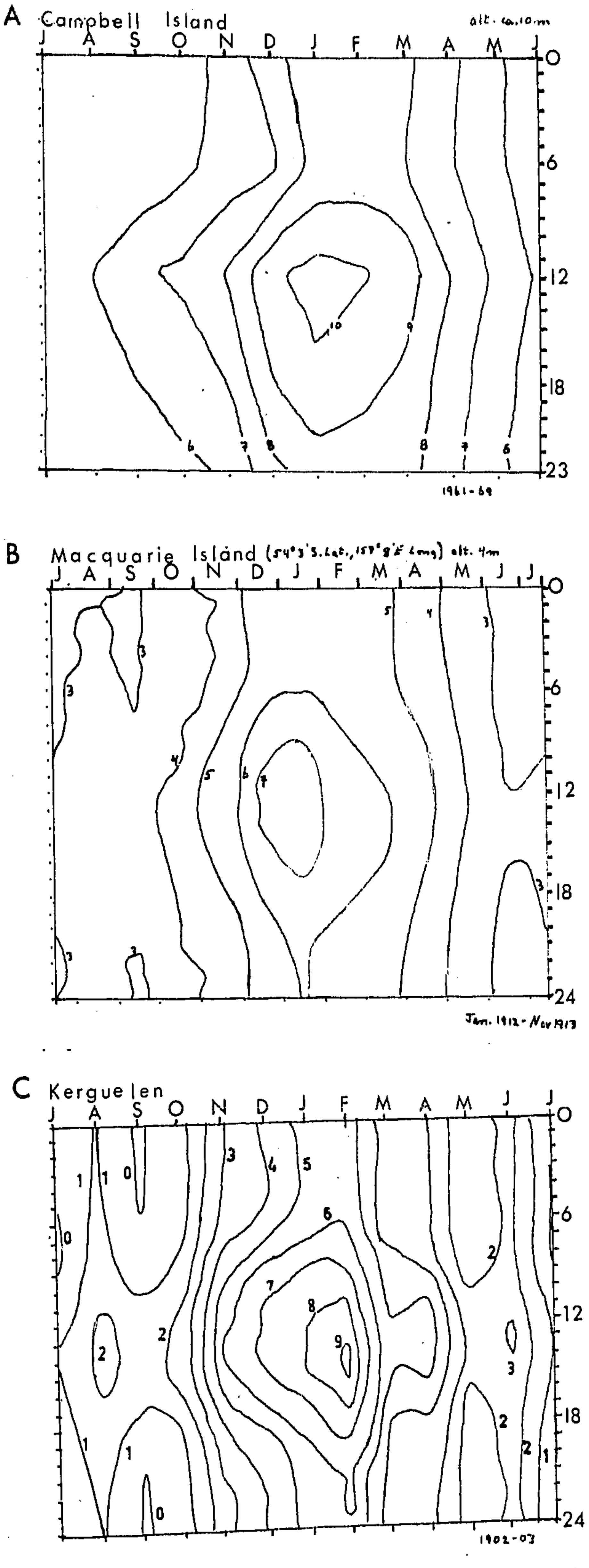


Figure 3.2. Thermoisopleth diagrams for: A) Campbell Island (data from the New Zealand Meteorological Service, Ministry of Transport), B) Macquarie Island (from Troll, 1964), and C) Kerguelen Island (data from Meinardus, 1923, copy of drawing by N.M.Wace, The Australian National University, personal communication).

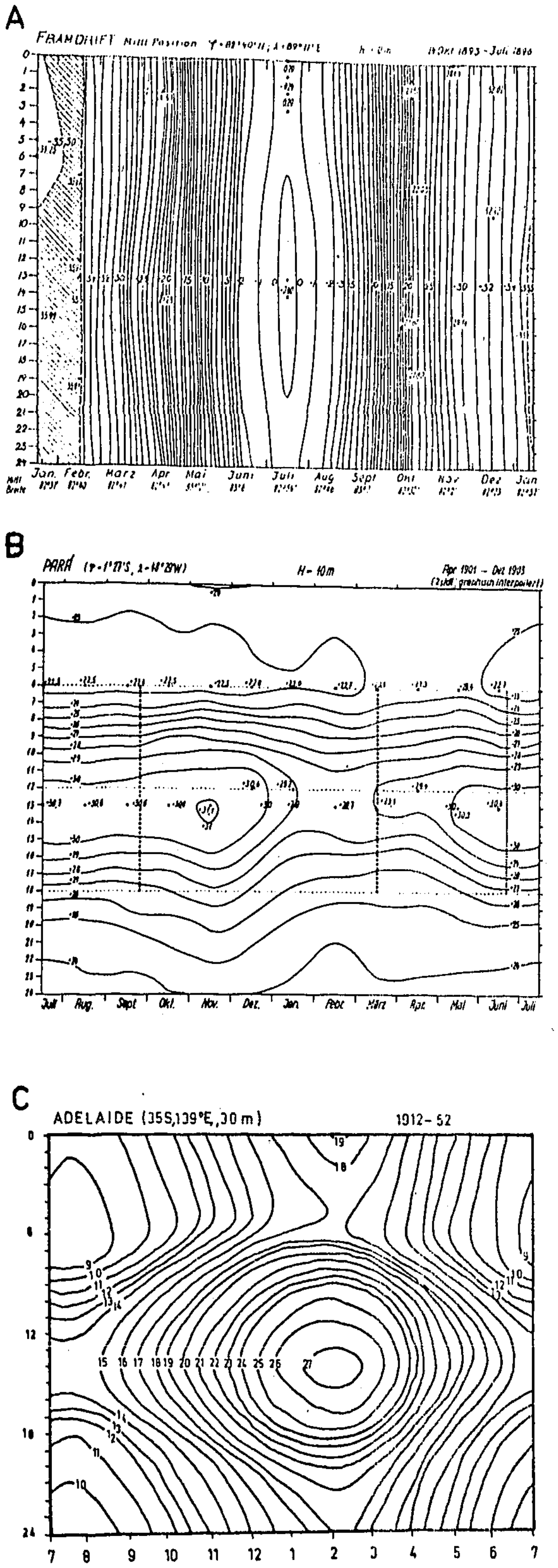


FIGURE 3.3 Thermoisopleth diagrams for: a) polar form, Framdrift,North Polar Sea Expedition (Troll, 1964); b) tropical form, Para, Brazil, (from Troll, 1964); c) temperate form, Adelaide, Australia, (Wace, pers comm.)

Table 3.1: Soil and air temperature summary for Macquarie Island during 1967, A.N.A.R.E. Data Reports no. 113 (1970)

Depth (cm)	Annual mean °C	Max. °C	Min. °C	Month of max.	Month of min.
10	5.8	14.4	0.0	1, 12	6
20	4.5	12.8	1.1	1, 12	4, 5, 7, 9
50	5.6	10.0	2.2	1	9
101	3.6	8.9	3.3	1	7, 9
air (150)	3.6	6.1	3.9	1	10

The temperature of the upper soil layers varies little more on an annual basis (14.4°C) than the air temperature at 1.5 m (*ca.* 13.9°C). The mean annual temperature ~~range~~ at 1.01 m in the soil (3.6°C) is nearly the same as the mean annual air temperature at 1.5 m (Table 3.1).

Kerguelen Island soil temperature data for 1902-3 (Meinardus, 1923), indicate similar patterns of yearly temperature change as are found at Macquarie and Campbell Islands but Kerguelen is cooler as was shown for air temperature (Fig3 .1). The mean monthly range of diurnal temperature -change at 0.05 m is small (less than 2.5°C). Soil surface temperatures are also lower on Kerguelen than on Macquarie. For example, the mean monthly minimum is less than 0°C for 8 months in Kerguelen and for only 1 month on Macquarie.

The information detailed in sections A.a. and A.b. suggests that the temperature climate of the sub-Antarctic is one of extreme invariability. The small land masses of the islands have only minor influences on the dominant, ameliorating presence of the vast, surrounding ocean. Both diurnal and annual temperature cycles are dampened by the enormous heat capacity of the ocean and the reduced insolation under nearly perpetual cloud. Indeed, as Troll (1958) has written, the sub-Antarctic islands may have 'the most uniform temperature climate on the earth' (p 147).

c. Humidity and precipitation

There are few summaries of average relative humidity (RH) for the region. In Tables published by the Meteorological Office, Air Ministry, London (1958), the yearly average RH at Macquarie Island at 0600 hr is reported as 92% (range for year 90-94%) and at 1400 hr the average RH was 91% (range 88-93%), based on four years' observations. Similarly, moist conditions can be expected at Campbell Island in view of DeLisle's (1965) discussion of the very moist air currents which are a dominant feature of that island's weather. A short run of RH measures on Campbell Island (2 February-8 March 1971) are presented in Table 3.2. From these data, the RH can be seen to have decreased slightly during the morning and mid-day from the otherwise uniformly high RH at other times. The 0900 hr and 1200 hr RH's were statistically lower than the other RH measures but were not significantly different (5% level) from each other (Table 3.3).

Table 3.2: Tussock canopy level relative humidity means for a run of measurements during February and early March, 1971, at Campbell Island.

Hour	Mean	St.Dev.	N
0600	95.8	5.3	32
0900	89.5	11.4	34
1200	88.0	11.8	33
1800	96.0	5.9	33
2400	97.6	3.4	33

Table 3.3: Comparison of mean relative humidity values of Table 3.2. * = significantly different at 5% level; ** = significantly different at 1% level (t-test).

	0600	0900	1200	1800	2400
0600					
0900	**				
1200	**	.			
1800	.	**	**		
2400	.	**	**	.	

The drop in RH was due to the morning rise in temperature. These data were collected below plant canopy level (*ca.* 0.2 m) on a north facing slope and therefore were not strictly comparable with the Macquarie Island data. The greater range seen in RH's at Campbell was probably more indicative of the range existing at plant level at both islands than of differences between the islands. Meinardus'(1923) data for Kerguelen indicate a drier atmosphere there (mean max.88%, mean min.60%) than that found on Macquarie or Campbell Island.

According to DeLisle (1965), rainfall at Auckland, Campbell, and Macquarie Islands is evenly distributed throughout the year with a slight peak in autumn. The range of annual rainfall is from about 1500 mm at Auckland Island to 1050 mm at Macquarie Island. Rainfalls of at least 0.25 mm occur on 322 or 88% of days in a year, while 70% of days register between 0.25 mm and 4.8 mm. Falls of greater than 40 mm in 24 hours are rare and are expected on less than 0.2 days per year. Heavy falls are more common at Campbell Island, for example, about 28 mm in 24 hours can be expected on 0.5 days per year (DeLisle,1965).

The conclusions to be drawn, therefore, are that i) the air is generally moist at all times of the year because of close proximity to the sea, but ii) a wider range of RH's occur at plant level than at standard screen level in response to diurnal temperature changes,and iii) rainfall is evenly distributed throughout the year and heavy falls are uncommon.

d. Radiation

i. Sunshine

The southern oceans between latitudes 40° and 60°S are amongst the most cloudy areas on earth (Fabricius,1957; National Geographic Antarctic Folio Series,1968). Cold air from higher latitudes meeting moist air from lower latitudes produces conditions of extreme cloudiness in these regions (cf. Rumney, 1968, p 633). In addition, orographic cloud forms from moisture-laden air forced upward while passing over the islands (Fabricius,1957). Consequently, the mean monthly hours of bright sunshine at Macquarie and Campbell Islands are low. Table 3.4 shows a yearly mean of 17.9% of the total possible sunshine for Macquarie Island and 12.9% for Campbell Island (Jenkin,1972, reports 18% for Macquarie Island). The difference is attributed to the greater frequency of blocking, high pressure systems near Macquarie Island which produce more stable, and therefore clearer air than near Campbell Island. Furthermore, the more frequent occurrence of stratiform cloud near Campbell Island, formed by advection of moist, warm, northwest winds, increases the cloudiness there (Fabricius,1957).

Table 3.4: Mean daily sunshine duration (S) in hours and as percentage (%) of possible sunshine at seven sub-Antarctic stations (from Fabricius, 1957, p 112).

Station	Period		Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Year
Stanley	1944-53	S	5.48	4.86	4.02	2.64	1.90	1.79	1.92	2.55	3.29	5.00	5.77	5.01	
		%	34	34	32	25	22	20	23	26	28	37	37	30	29.0
Grytviken	1953	S	5.7	6.6	4.1	2.8	1.0	0.0	0.5	1.9	3.4	6.1	6.2	5.9	
		S*	5.8	6.7	4.5	3.9	2.6	2.4	2.9	3.4	4.3	6.8	6.7	6.4	*ca.*
		%*	35	46	36	38	31	33	37	36	37	49	42	37	38.0
Marion I	1949-55	S	5.21	4.99	3.86	2.59	2.09	1.57	1.90	2.12	3.18	4.07	4.38	5.04	
		%	35	36	31	26	23	20	22	21	28	31	31	34	28.2
Kerguelen I	1902-03	S	5.60	5.47	3.52	3.57	2.54	1.16	2.19	2.89	3.66	4.01	4.33	5.65	*ca.*
		%	36	39	28	34	28	14	26	29	31	29	28	35	24.8
Heard I	Apr.1948-Jan.1953	S	1.68	1.70	1.23	1.42	1.04	0.84	0.86	1.14	1.66	1.98	2.16	1.58	
		%	10	12	10	14	12	11	11	12	14	15	14	9	11.9
Macquarie I	Mar.1948-Dec.1953	S	3.52	4.28	2.88	1.86	1.14	0.42	0.75	1.37	2.25	2.73	3.47	3.34	
		%	21	29	23	18	13	6	10	14	19	20	22	20	17.9
Campbell I	Aug.1941-Dec.1947	S	3.10	2.81	1.94	1.07	0.59	0.39	0.40	0.78	1.74	2.02	2.72	3.13	
	Jan.1949-Nov.1955	%	19	19	15	10	7	5	5	8	15	15	18	19	12.9

S* Estimated. %* Derived from S*.

ii. Energy

Measurements of solar radiation fluxes in sub-Antarctic regions are very rare. Records for a 36-day period at Campbell Island in February-March 1971, using an Ogawa Seiki actinograph yielded a mean of 235.2 ± 126.9 cal/cm^2/day (ca. 0.28 ± 0.15 cal/cm^2/min). This very short term sample, although highly variable, yielded values that were roughly half those which Fabricius (1957) reports for Marion Island (46°51'S.Lat., 37°52'E.Long). According to Fabricius, however, Campbell Island receives just under half as much bright sunshine as Marion Island. The 0.28 cal/cm^2/min at Campbell Island may be somewhat below the long term average because less than half the average bright sunshine hours per day were recorded at the Campbell Island Meteorological Station during February 1971, and about 20% above average for the first eight days of March.

The average daily, global radiation for January and February at Macquarie Island, based on three years of records (Table 3.5), is 0.32 cal/cm^2/min. This figure cannot be directly compared with that from Campbell Island, however, because of the different instruments used (a bimetallic-strip actinograph at Campbell Island, sensitive to 0.28-3.0m μ radiation and an Eppley pyranometer, sensitive to all wavelengths of global radiation, at Macquarie Island). Given the wider range of sensitivity of the Macquarie instrument and the greater amount of bright sunshine there, the difference between the two sites does not appear to be very large and probably indicates the dominant contribution of diffuse radiation at both places. Diffuse radiation at Macquarie Island comprises more than 50% of the total, being highest in mid-winter and lowest in January and February (Table 3.5). Undoubtedly the amount of cloud cover is an important variable here, but long term records might present a different view. The high proportion of diffuse radiation is, however, probably characteristic of the region (Jenkin, 1972).

Detailed comparison between the Macquarie Island and Marion Island radiation data is not possible because of the short run of records and the different instruments used. A few points merit brief mention. The average daily, global radiation at Macquarie Island is less than half that at Marion Island in mid-winter and only three quarters of it in mid-summer. The lower values probably derive from the higher latitude of Macquarie Island, which results in lower sun angles and greater attenuation of the solar beam. The amount of direct sunshine received also affects the radiation levels. Macquarie receives only 27% as much sunshine at mid-winter and 66% as much at mid-summer as does Marion Island (from Table 1, Fabricius, 1957).

Table 3 5: Global (G) and diffuse radiation at Macquarie Island, Campbell Island, and Marion Island (cal/cm^2).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
cal/cm^2/day Macquarie I*	385	271	200	106	51	38	67	93	166	246	321	410	(G)
diffuse as % of global Macquarie I*	47	47			56	88	81	72	58	59	64	54	
cal/cm^2/day Marion I+	554	476	337	219	139	96	110	175	277	412	473	544	(G)
cal/cm^2/day Campbell I#		235											(G)
cal/cm^2/day Mt Wilhelm#				376	367	373	335	433	440	348	415		(G)

*Commonwealth Bureau of Meteorology, Melbourne; +Fabricius, 1957; #Hnatiuk, this study.

The solar energy input on Campbell Island, as measured in February 1971, was nearly equal to the 0.30 cal/cm^2/min for mid-summer (July) at Barrow, Alaska (71°N.Lat.,156°W.Long.)(Billings and Mooney,1968).

The energy climate of sub-Antarctic islands is thus one of low level input, primarily due to the small solar radiation levels under persistently heavy cloud. Despite these low levels of radiation, the seasonal amplitude of energy received is one of the few strongly seasonal climatic variables of these parts. Its importance to plant growth may be effected through both soil temperatures and energy available for photosynthesis and growth.

e. Wind

Any discussion of the plant environment in the sub-Antarctic must take account of wind. An experiment to compare the exposure of six sites to wind was conducted on Macquarie Island. Using the flag-tatter technique of Lines and Howell (1963), an estimate of the variation in exposure at different sites was made. Because of the small sample at each site and the short period of observations, a detailed discussion of these results is superfluous. However, certain features in Figure 3.4 are of particular interest in illustrating the local variation in wind exposure. i) Site altitude was not related to wind exposure (MRB = 12 m, MWE = 60 m, MPB = 222 m, MGC = 30 m, MWS = 60 m, MMS = 12 m); ii) wind exposure, measured as miles of wind run, ranged from about 4×10^3 to 16×10^3 for the same 62-63 day period. Thus it was evident that, even in a region of nearly continuous, strong wind, a large range of local wind climates existed. In the case of the six sites at Macquarie, the major controlling factors were thought to be site aspect (winds are dominantly from the west and northwest, Fabricius, 1957), and proximity of wind breaks such as hill crests. Jenkin (1972) reports data from 90 days of observations that showed wind run on the plateau at over 200m altitude was 32% greater than that measured at the main meteorological site at 12 m.

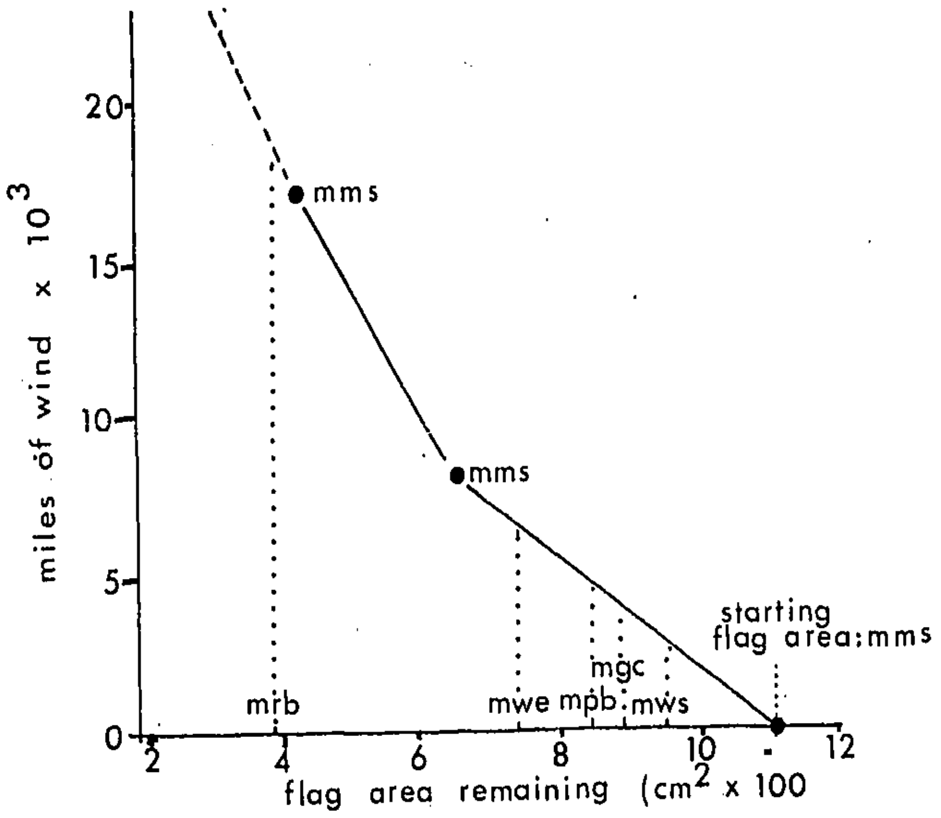


Figure 3.4. Relative wind exposure of six Macquarie Island sites.

B. THE EQUATORIAL HIGH MONTANE

a. Wind

In marked contrast to the gale-swept, sub-Antarctic islands is the extreme calmness of the air on equatorial mountains. Coe (1967) comments on the existence of valley winds on Mt Kenya but finds wind to be an unimportant factor there.

Valley and slope winds of the type discussed by Geiger (1965), who uses the mountain wind theory of Defant (1951), were frequently observed in the Pindaunde Valley on Mt Wilhelm from April to October 1970. Light to gusty, down-valley winds were common in the early morning hours, dying out between 0600 and 0700 hours (*i.e.* within 1 to 1-1/4 hr after sunrise). A brief calm often occurred before up-slope and up-valley winds developed. These persisted until late afternoon when a second calm period was characteristic. The latter was often associated with descending air made visible by rapidly descending tongues of cloud, which either dissipated a short height above the valley floor or else completely filled the valley.

Only above 4200 m was there any evidence that wind was detrimental to plant growth in the way that it is in temperate, high mountain areas, for example, the shaping of krumholtz trees and shrubs. The effects of wind on plant growth were therefore restricted to the less dramatic roles of mixing the air at the air-plant interface, thus facilitating the exchange of gases and heat.

b. Radiation

Radiation measurements, either of hours of bright sunshine or of energy levels of incoming and outgoing radiation, have not been made for any length of time in equatorial, montane locations. Hedberg (1964) and Coe (1967) have discussed in detail the great importance of the intense radiation exchange for individual plant species, for communities, and for the physical habitat in the Afroalpine region, but were unable to quantify it.

Caldwell (1968) studied the increase in UV-B (0.28-0.315m$_{\mu}$) in the mountains of Colorado and found an increase of only 26% from low (1670 m) to high (4350 m) altitude on a clear, mid-summer day, 'in contrast to some indications in the present literature' (p 266). Caldwell's data show an absolute decrease in sky UV-B with increasing altitude, which largely compensates for the increased intensity of direct solar UV-B with altitude. Billings and Mooney (1968) report an average summer rate of energy input at an alpine site (3740 m) in Colorado as 0.56 cal/cm^2/min, compared with 0.58 cal/cm^2/min in a nearby temperate forest region (2195 m).

Based on seven months of records in 1970, using a bimetallic-strip actinograph sensitive to 0.28-3.0m$_{\mu}$ at 3510m on Mt Wilhelm, an average rate of radiant energy input of 0.56 ± 0.05 cal/cm^2/min was determined. Since long and short wave radiation was not measured, the total input was, in fact, greater than this figure, but still comparable with the Colorado, alpine, July level reported by Billings and Mooney (1968).

The harshness of the radiation exchange in the equatorial alpine is due in part to the increased intensity of direct solar energy in the rarefied atmosphere (Caldwell, 1968) but also, and perhaps more importantly, to the very great loss of energy to the clear night sky. Thus, while daytime temperatures at plant level can rise above 37^{o}C, night temperatures often fall below 0^{o}C producing what is often referred to as 'summer every day and winter every night'.

In the Pindaunde Valley (3510 m) in 1966-67, McVean (1968) recorded ground frosts on 55% of nights (excluding December, January, and February). In 1970 at 3510 m at Pindaunde, I recorded frost on 72% of nights at tussock level, a similar frequency beneath tussock crowns, but a 35% frequency at ground level above a short grass turf. The latter observation was made at McVean's (1966-67) site. On 20% of nights in 1970, visible ground frost occurred in low areas near the meteorological station when ground temperatures there remained above freezing. (The station was located on a small knoll about 10 m in diameter and about 2 m high.) It is clear, then, that at Pindaunde there was much variability from year to year and from place to place with topography playing an important role, and that ground frost could occur at any time during the year when the night sky was clear.

The extent and intensity of freezing depended primarily upon the extent and duration of a clear night sky which permitted rapid radiation cooling.

At higher altitudes on Mt Wilhelm (4350 m), night freezing was more common. An 88% frequency of night frost was recorded from June to September 1970, just above tussock canopy level (50 cm), while only 49% of those nights experienced frosts below the tussock crowns (20 cm). This frequency difference was in contrast to that at WFS and was probably caused by the difference in leaf density at the two sites. The higher site had more crowns and leaves per square metre than the lower site. The greater density of plant material at the higher site facilitated the development of a narrower, effective boundary surface for heat exchange than was possible with a more diffuse canopy structure. Thus, steeper temperature gradients developed in the more dense, than in the less dense, canopy.

The higher frequency of night frosts at canopy level at the higher altitude could not be confidently accounted for, but some of the following factors could have contributed. i) A more intense radiation loss to clear skies occurred so that frost developed sooner than was possible in equal time periods at lower altitudes. Two factors of importance here, in contrast to lower altitude sites, were the lower air density, resulting in less effective insulation against heat loss, whilst lower maximum day temperatures indicated that less heat needed to be lost before freezing occurred. ii) Precipitation was often in the form of snow, sleet, or hail at the higher altitude and only rarely was it frozen at WFS. Frozen precipitation was observed lying on and amongst the tussocks at 4350 m for several days on different occasions and also appeared to fall mostly at night. Thus, it was possible for freezing temperatures to occur at canopy level on cloudy nights at higher, but not at lower, altitudes.

The radiation climate of the high equatorial mountains is extreme in its diurnal fluctuations. One major result of the intense radiation exchange is seen in air temperature changes which are discussed later in this chapter. The pronounced development of anthocyanins, which is often associated with plants exposed to high levels of ultra-violet radiation, was not a prominent feature of Mt Wilhelm tussock grasses.

c. Humidity and precipitation

Hedberg (1964) reports very short and fragmentary relative humidity data from the Afroalpine. At 4160 m the R.H varies between 60% and 90%, with sudden changes being usually less than 30% and related to changes in cloudiness. RH values as low as 50% occur occasionally. R.H minima occur predominantly at noon (related to temperature maxima) with a secondary low at night related to a 'dry Fohn'.

My observations for Pindaunde (3510 m) in 1970 (Hnatiuk et al. 1975) were similar to McVean's (1968) records. The most striking feature of the RH changes was the small influence that temperature appeared to have. An RH minimum generally occurred between 0800 and 1200 hr in association with the temperature maximum; but of equal frequency was the occurrence of a night-time minimum, which usually commenced between 2200 and 0100 hour and corresponded to the period of stable night temperatures (see next section). On a few occasions, the night low dropped below 50% before sunrise and then gradually increased throughout the day, despite the daytime warming.

The night-time lows may well have been related to down-valley winds which, although they were cold, would have increased in temperature as they descended and thus progressively lowered RH. The hygrothermograph traces indicated periodic changes in RH at night which varied in frequency from five minutes to two hours, the five and 30 minute frequencies being most common. Both 'air avalanches' and shorter period, rhythmic pulsations in the flow of down-valley night-winds have been described by Scaëtta (1935) and Küttner (1949). The subsidence of dry air aloft has been implicated by Green (1965) and Hnatiuk et al.(1975).

With regard to plant level RH, fluctuations were much more extreme than those recorded in a Stevenson screen at 1.5 m. The RH tended to follow air temperature more closely at plant level than further above the canopy, but the occasional influx of dry air unrelated to temperature was still evident, as were conditions of water-saturated air during periods of low cloud and mist.

Precipitation on the high, equatorial mountains is extremely varied both between and within regions, because of the seasonal changes in wind patterns as well as the orientation of the mountain ranges in relation to the prevailing winds. Orographic precipitation, as well as 'rain-shadows , also help to make the mountain precipitation highly varied. However, a few general points can be made about the three main areas of equatorial, high mountains.

Coe (1967) reports a comprehensive study of precipitation in nearly all valleys and at all altitudes on Mt Kenya and for selected aspects and altitudes on Mt Kilimanjaro. Major features of both mountains are the precipitation maxima at *ca.* 2400 m and the occurrence of two wet and two dry seasons. The average precipitation at 3048 m on Mt Kenya ranges from *ca.* 890 mm to 2030 mm, while at 4191 m the range is 760 mm to 1520 mm (*cf.* Table 3.6).

Table 3.6: Climatic data for three equatorial high mountain regions

Site	Alt. m.	Mean daily amplitude °C	Mean max. °C	Mean min. °C	Absol. max. °C	Absol. min. °C	Annual precip. mm
New Guinea							
Mt Wilhelm	3510	3-4	11.6	3.7	16.7	-0.8	ca 3450
Java							
Pangerango	3022	2-5	?	?	12.8	6.5	*ca.* 3500
Ecuador							
Cotopaxi	3600	8.6	7.5	5.4	17.3	-1.5	500-1000?
Cruz Loma	3950	6.4	6.8	5.9	14.0	1.5	?
Gomessiat	4750	2.5	0.9	0.7	3.5	-2.0	?
Mt Kenya							
Naro Moro Trk	3048	14.4	16.2	1.7	19.4	-1.6	1397
Teleki Valley	4191	8.9	5.3	-3.6	11.0	-6.7	889

(Mt Wilhelm data are from Hnatiuk, McVean, and Smith, 1975.

Ecuadorian data from Troll, 1959. Mt Kenya data from Coe, 1967.
Precipitation estimate for Cotopaxi from Oxford Atlas, 1966.)

Whereas the east African mountains rise abruptly from a semi-arid, continental plateau, well removed from major sources of atmospheric moisture, the northwest Andes are situated so as to receive moisture from the Pacific Ocean to the west and from the Amazon Basin to the southeast. It has been estimated that the Ecuadorian Andes receive 500-1000 mm of precipitation annually (Oxford Atlas, 1966). Schmidt (1952) gives precipitation data for Columbian sites, from which it is evident that precipitation generally decreases with increasing altitude. His highest altitude site, Chita (3005 m, 6°11'S.Lat.), has an annual precipitation of 896 mm. Ipiales (2890m, $0^{o}49'$S.Lat.) has 994 mm per annum. Troll (1959) describes the precipitation gradient across the Andes as running from a high in the northwest to a low in the southeast. Thus, Ecuador would be expected to be more arid than Columbia and, therefore, the Columbian data given above could be maximal estimates of what to expect in Ecuador.

Precipitation data for Mt Wilhelm are fragmentary. Hnatiuk et al (1975) summarized the available records and only conclude that while the Pindaunde Valley appears drier than the Bundi flank to the NE and wetter than the lower Chimbu Valley to the south and southeast, the relation of precipitation to altitude for the Pindaunde Valley to the summit is not obvious and may vary from year to year. However, because the higher altitude data are incomplete, especially for the wettest period of the year, no further analysis of the altitude-rainfall relationship can be made here. It is interesting to note that Osmaston (1965) reports that the Ruwenzori (central Africa) show a rainfall pattern that varies with aspect and altitude of the massif, except that above about 3200 m, the altitude rainfall relationship disappears.

Precipitation is seasonal at Pindaunde as it is in most of the main valleys of the Eastern Highlands (McAlpine, 1970). Monthly means for the entire year are available for Keglsugl (1830 m alt.)(Brookfield and Hart, 1966) and show a peak of 1222 mm during the wet season in February, falling to nearly one quarter of this value (382 mm) in June. At WFS in 1970, the May precipitation of 250 mm was about 3.5 times the August low of 70.3 mm. The period of maximum rain at WFS appears from the incomplete records available to occur between December and March, thus the seasonal range there is probably greater than at Keglsugl, being both wetter during the rainy season and drier during the dry season. Certainly the low figure for August 1970 does not represent a constant feature of the climate, though neither is it unusual. The months of May to October in 1966, 1969, 1971, are known to have been 'wet' while 1970 and 1972 were 'dry' for the June to September period, at least in the high montane zones.

d. Temperature

The main features of the equatorial, high mountain, temperature climates are well known (*cf.* Troll, 1959; Hedberg, 1964; Coe, 1967; McVean, 1968) and are best characterized by 'thermoisopleth diagrams' (*e.g.* Troll, 1958). The primary features of little, seasonal and strong, diurnal change, *i.e.* 'Tageszeitenklima' of Troll (1943) or daily climate, are readily seen in the diagrams (Figure 3.5a, b). The Pangerango ($6^{o}47$'S.Lat., $106^{o}58$'E.Long.) and Quito ($0^{o}14$'S.Lat., $78^{o}32$' W.Long.) diagrams are clearly tropical in form ('Das Diagramm für Quito ...stellt das reinste aquatoriale Tageszeitenklima dar.' Troll, 1959, p 20) (*cf.* Figure 3.3b). The Quito isopleths run parallel to the abscissa, but the greater oceanicity of Pangerango is evident in the smaller number of isopleths in its diagram compared with the number in that for Quito.

The more arid the high mountain climate, the greater is the amplitude of temperature fluctuations. For example, Mt Wilhelm and Pangerango (Table 3.6) received respectively 3450 mm and 3500 mm precipitation annually and have a mean daily amplitude of temperatures of between 2 and 5^{o}C, whereas the drier Andes and Afroalpine (500-1400 mm annually) have daily temperature amplitudes of 8.6 to 14.4^{o}C. The humid, tropical, high-Andean mountain climate appears to be more like the high, New Guinean mountain climate than is the climate of the Afroalpine region. For example, at comparable altitudes, the daily temperature range is greatest in the Afroalpine (14.4^{o}C at 3045 m, Mt Kenya), least in the New Guinea-Java mountains, and intermediate at Cotopaxi (8.6^{o}, 3600 m, Ecuador).

Nine months of temperature data were collected on Mt Wilhelm (WFS, 3510 m) in a Stevenson screen at 1.5 m above ground. A thermoisopleth diagram for these data is presented in Figure 3.6a. The oceanic nature of the climate is clearly seen from the small number of isopleths. In this respect it is similar to the Javanese mountains of Pangerango ($2^{o}47$' S.Lat., 3022 m altitude) (Figure 3.5a) which has a daily temperature range of 2^{o} to 5^{o}C compared with a 4^{o}C daily range at 3510 m on Mt Wilhelm.

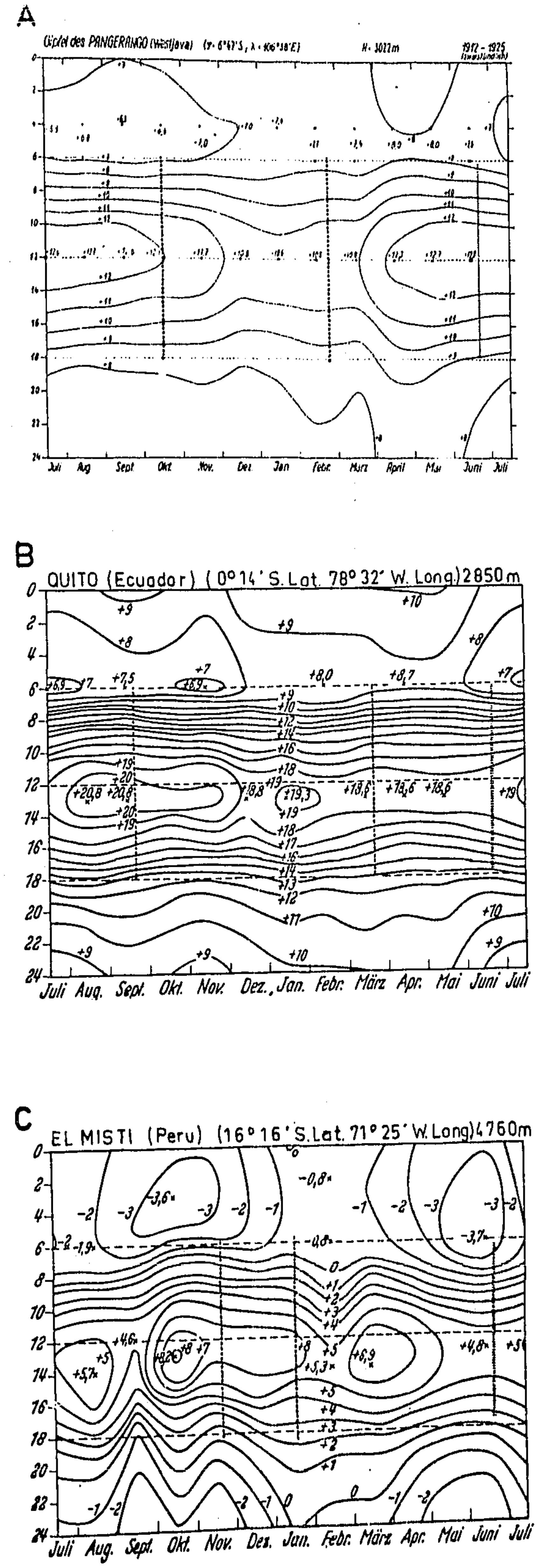


FIGURE 3.5 Thermoisopleth diagrams for:
a) Pangerango, Java (from Troll, 1964);
b) Quito, Ecuador (from Troll, 1964);
c) El Misti, Peru (from Troll, 1961).

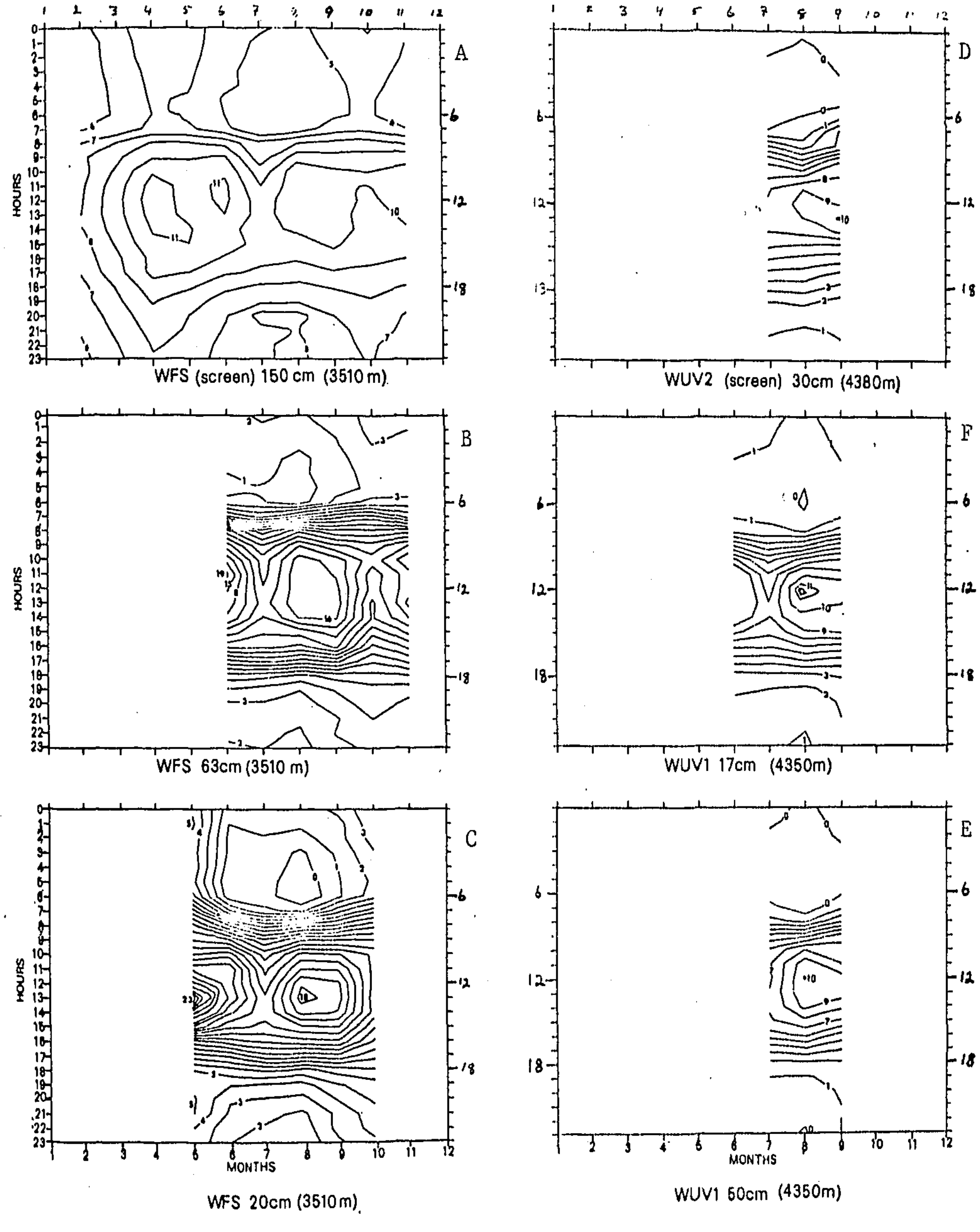


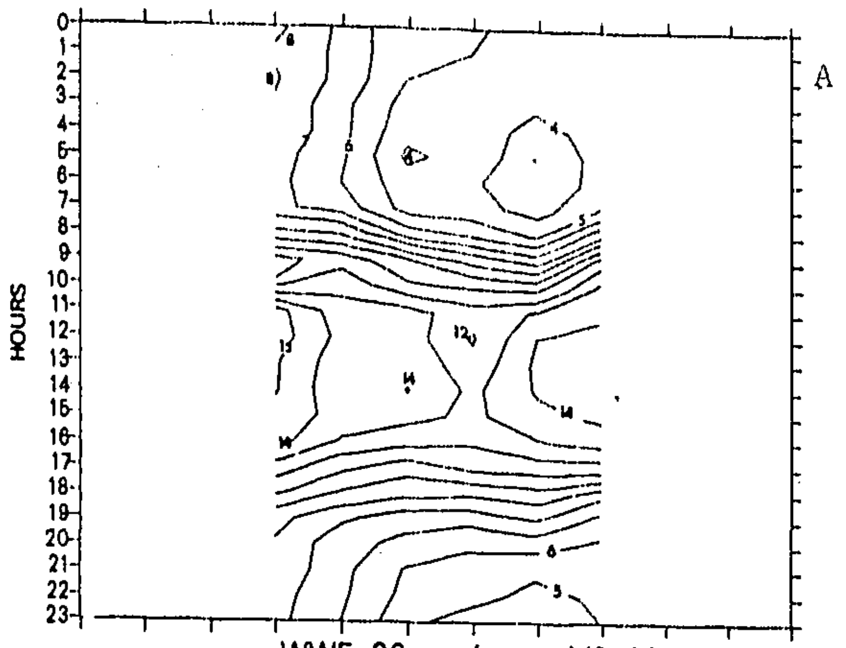
FIGURE 3.6 Thermoisopleth diagrams for Mt Wilhelm sites.

Although the Mt Wilhelm climate can be seen to be a daily climate, the features of the thermoisopleth diagram, which distinguish the daily climate as exemplified by that for Quito, were less well developed at Mt Wilhelm. That the night-time isolines in Figure 3.6a tend to parallel the ordinate axis and thus are 'polar' in form, while the daytime isolines parallel the abscissa and so are 'equatorial' in form, illustrates remarkably well the 'summer every day, winter every night' description of the equatorial, high mountain climate. Troll (1961) presents, but does not discuss, this aspect of a similar type of diagram from Montblanc Station (4760 m) on El Misti in southern Peru ($16^{o}16$'S.Lat.).

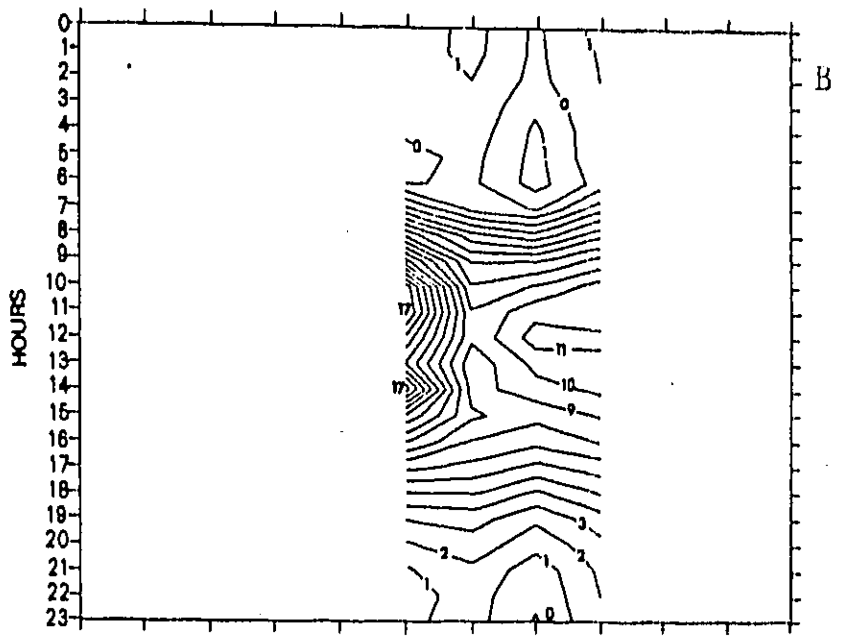
Other features of Figure 3.6a are the relatively rapid temperature rise from sunrise to late morning (0700-1000hrs), the fairly stable temperatures until late afternoon or sunset (1600-1730 hrs, early sunset behind mountain), then the more gradual cooling which is nearly finished by 2200-2400 hrs and is followed by stable temperatures until sunrise. There is a weakly developed tendency for minimum temperatures to occur just before sunrise.

That air temperatures are more extreme closer to the effective energy exchange surface (*i.e.* ground surface or plant canopy) than further from it, is a well known phenomenon that has been thoroughly discussed (*e.g.* Geiger, 1965). It is therefore imperative, where possible, that climatic data derived from measurements at 1.5 m above the primary energy exchange surface be related to the climate in which the plants are actually growing. It was partly to this end that measurements at tussock canopy level were made at six sites on Mt Wilhelm. At two of the sites, records of temperature were kept just above and below the canopy layer. The sites represented a range of altitudes, aspects, and topography on the mountain. The data are summarized in thermoisopleth diagrams in Figures 3.6 and 3.7 for as much of the year 1970, as there were records.

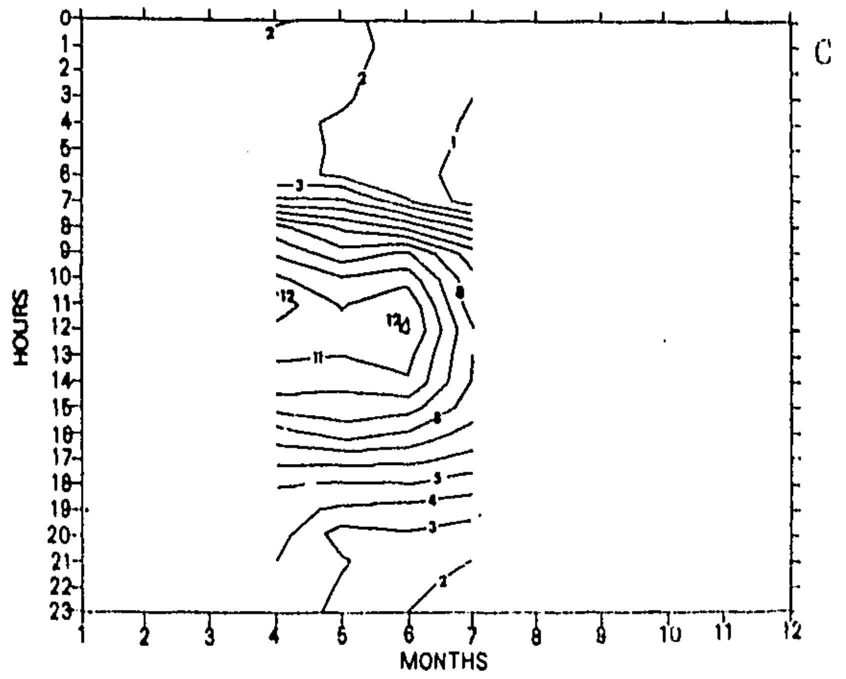
The most pronounced difference in form between the diagrams relates to the height above ground at which temperatures were measured, and can be seen by comparing Figures 3.6a and b, *i.e.* the 1.5 m screen temperature and the 0.63 m canopy-top temperature. Clearly the tussocks lived in a more extreme temperature-climate than is indicated by the 'standard' meteorological observations. However, the change in thermal climate as one approaches the active energy exchange surface, is to intensify the



WWF 20cm (screen)(3400m)



WGAP 30cm (screen)(4190m)



WWT 20cm (screen)(4300m)

FIGURE 3.7 Thermoisopleth diagrams for Mt Wilhelm.

pattern characteristic of a daily-climate region: nonseasonal, rapid rise and fall of diurnal temperatures in response to the diurnal radiation flux, and near isothermal midday and night conditions.

The 0.2 m WFS thermoisopleth is of the same form as that at 0.63 m (WFS) (Figures 3.6b and c), but shows even greater intensification of the thermal-time gradient. At 0.2 m at midday, there is a period of reduced rate of temperature change between the steep morning rise and the evening fall, whereas at 0.63 m the midday period is nearly isothermal. However at night, there is a continuous but slow decrease in temperature throughout at 0.63 m, but an isothermal night period occurs at 0.20 m.

The thermoisopleths for WUV2 (Figure 3.6d), WUV1 (Figure 3.6e), WWF (Figure 3.7a), and WWT (Figure 3.7c), all differ similarly from those at WFS canopy-top (Figure 3.6b). In contrast to WFS canopy-top, the other sites showed a less steep morning and evening temperature gradient and had a narrower range of temperatures. The tendency for lowest temperatures to occur just before sunrise was better developed at the sites below 4200 m than above. At the lower altitude WWF site, both maximum and minimum temperatures were less extreme while at the higher altitude WUV2 and WWT sites, only the maximum temperatures were reduced. Thus there is a trend for decreased temperatures at higher altitudes, but this trend may be locally overridden by particular features of the topography. An example of this was seen at WGAP which was on a very steep easterly facing slope and thus received much more intense insolation, especially during the predominantly cloudless mornings. At this site, very high temperatures have been recorded (Figure 3.7b).

The thermoisopleth diagrams for points above and below tussock canopies illustrate differences induced by the plants. Effective energy exchange was more intense within the shallower canopy than below it; at the WUV1 site both leaves and crowns were more densely spaced than at the WFS site, where the more diffuse arrangement of leaves and crown extended the effective energy exchange boundary below the region of crown development (cf. Coe, 1969; Scott, 1962).

In the thermoisopleth diagrams for which four or more months data are available, seasonal fluctuations are evident, *e.g.* the midday maxima occurring in April to June, and August to September, are separated by a cooler period in July, and the coldest nights occurred in August. These changes were caused by the presence or absence of clouds which, when present, moderated temperatures by reducing both daytime irradiation and night-time radiation loss and, when absent, permitted higher day and lower night temperatures to occur. The extent to which these changes are truly seasonal, and not simply periodic weather changes peculiar to the year 1970 and unrelated to season, could only be determined from longer term records.

At 3510 m at Pindaunde, over the May-October period 1970, soil temperatures at 15 and 50 cm varied diurnally by less than 1°C, and for a given hour of the day by less than 0.5°C. The mean temperatures for all hours at both depths were 7.5°C which clearly indicates the weak penetration of the diurnal heat wave into the soil, if indeed there is such beneath the tussock canopy. At 4350 m, beneath only 2.5 cm of soil (which makes direct comparisons with the observations at the 3510 m site difficult), the mean temperature was 0.58°C but the range was 23° (-6°C to +17°C).

A series of weekly observations was made between May and October, 1970, at canopy level at four sites between 4250 m and 4300 m and with different aspect and topography, in order to determine the effect of these factors upon local, mean temperatures. The results are presented in Table 3.7 and the comparison of the mean weekly maxima and minima are shown in Table 3.8.

Table 3.7: Temperatures (°C average of weekly readings) at four sites with differing aspect and topography between 4350 m and 4300 m on Mt Wilhelm

Site	mean Max.	St.dev. of mean	N	mean Min.	St.dev. of mean	N	Absolute max.	Absolute min.
No.4	17.1	3.3	22	-1.1	1.2	22	22.0	-3
WUV2	15.6	3.0	7	-4.1	1.7	7	20.5	-6.0
Above-WUV1	15.3	3.1	19	-4.2	1.4	19	17.0	-7.0
WWT	16.9	1.7	11	-4.5	1.7	11	18.5	-7.0

All sites except WWT were in the Upper Valley. No. 4, which was not described in Chapter 2, was situated in tussock grassland about 60 m above the valley bottom. The site sloped very steeply to the west and was about 30 m below the crest of the valley wall. It was expected

Table 3.8. Comparison of mean maxima and minima at the four sites listed in Table 3.7.

	Minimum temperatures					Maximum temperatures			
	No.4	WUV2	WUV1	WWT		No.4	WUV2	WUV1	WWT
No.4					No.4				
WUV2	**				WUV2				
Above-WUV1	**				WUV1				
WWT	**				WWT				

(** = significant difference at 1% level ,t-test for small sample size)

that in this location, at night, rapid, cold air drainage away from the site would take place, as it would at the site Above-WUV1, but not at WUV2, on a bench on the side of the valley, or at WWT on an extensive slope. However, the results of my measurements are ambiguous. Only No4 showed the expected higher minima. Cold air ponding could account for the lower minima at WWT and WUV2 but not at the site Above-WUV1. A possible explanation for the unexpectedly low temperatures of the Above-WUV1 site is that cold air draining from higher passes across the site and into the valley; whereas, No4, being on the other side of the valley.does not receive this washing of cold night air.

The mean, weekly maxima showed no statistical difference between any site (Table 3.7). However, the absolute maxima (Table 3.7) occurred at different times at each site and ranged from the highest at No.4 (22°C) to the lowest at Above-WUV1 (17°C).

It appeared, then, that within the narrow range of 50 m altitude studied, aspect and slope only affected mean, minimum temperatures and not mean, maximum temperatures. During the observation period from May 1970 to October 1970, absolute maxima and minima occurred in August and coincided with the height of the 'dry' period, when the greatest number of clear days and nights occurred.

C. SUMMARY

The sub-Antarctic and equatorial montane climates are seen to have a number of similarities and differences. They share the dominant features of nearly isothermal conditions at 1.5 m above ground, with only weak diurnal changes at the high latitude stations and similarly weak seasonal changes at the low latitude station. They are also similar in that soil-water stress is probably only rarely limiting. Precipitation is evenly distributed over the year at the sub-Antarctic Islands and the nearly continuous cloud cover and low temperatures reduce evaporation. In the Pindaunde Valley, there is a seasonal 'dry' and 'wet' cycle, but the dry is variable in occurrence from year to year and usually lasts less than six weeks. Even after 'long' dry spells, which cause the soil water table to drop from the surface to below 1 m, the very peaty soils remain wet and free water can generally be found beneath the dense girdle of marcescent tussock leaves. Furthermore, in both regions, an unknown, but very obvious, amount of water is deposited on leaves either from mist or from night-time condensation and this undoubtedly brings some water to the numerous roots growing amongst the decaying leaf-bases and stems of the pedestal.

Major differences in climate between these two regions are also important. The incessant, often gale force, winds of the sub-Antarctic contrast markedly with the gentle ebb and flow of predominantly slope and valley winds in the equatorial montane (although very brief wind gusts occur occasionally in the latter areas). Total radiation flux at plant level is much less in the sub-Antarctic than in the equatorial montane. Even during the summer with long daylight hours, islands like Macquarie and Campbell, because of the nearly continuous cloud cover, receive only a little more than half as much energy as Pindaunde. As a direct consequence of this, diurnal temperatures have a far greater range in the equatorial montane than in the sub-Antarctic.

The soil climate on the equatorial high mountains appears to be substantially different from that found on the sub-Antarctic islands. In both cases the tussock grasses are growing in constantly moist to wet highly organic soils. However, at the low latitude site at 3510 m there was only a very small change in temperature at 15 cm (0.5°C, _i.e._within the limits of error of the measurement) over a six month period while on Macquarie Island (12 m)(Jenkin, 1972) the mean temperature at 15 cm ranged from 3.4°C to 5.2°C over the May-October period and from 2.8°C (July)to 9.8°C(January) annually. With radiation in the tropics at 5°S Lat. varying by only a small amount from annual maximun to minimum, soil temperatures are not expected to vary much in excess of that reported above. The constantly cool soil of the high equatorial region may inhibit root development in comparison with that in the seasonally warm soil of the sub-Antarctic islands.

Although exactly comparable data for the soil surface are not available for the two regions, it appears that the high tropical sites may experience a more rigorous temperature regime than that found in the sub-Antarctic. For example, surface temperatures at Macquarie Island have an annual range of about -6.6°C to +7.2°C while at 2.5 cm below soil surface at 4350 m on Mt Wilhelm temperatures over 6 months ranged from -6.0°C to +17.2°C. Surface temperatures at the latter site could be expected to have an even wider range because the closer to the active energy exchange surface, the greater is the absolute range of temperature found (Geiger,1965).

CHAPTER 4

GROWTH OF TUSSOCKS

A. Introduction

In the preceding chapter, the climate of the sub-Antarctic islands and the equatorial high mountains was discussed in detail. I shall now direct attention to the tussock grasses themselves and compare their growth in these two geographically remote, yet somewhat similar, environments.

The two regions under study are characterized by a prodigious and conspicuous growth of grasses which are made up of several genetically distinct taxa and yet show the common tussock form. The supposition thus arises that, despite genetic differences, the environments of the regions have strongly influenced selection for this particular growth form. In this chapter, details of some of the growth processes and characteristics shall be examined to see if the similarities found in the outward appearance of the vegetation are also found in the less obvious aspects of growth. Finally, I will attempt to answer the question: can the characteristics of growth which are similar between regions be related to the aspects of environment which are similar, and those which are different to environmental or genetic differences?

It is first necessary to establish definitions of certain terms used. (See also Chapter 2: Methods).

1. BIOMASS:	the dry weight of plant material, usually expressed on the basis of unit area of ground. It is often accompanied by an adjective(s) specifying a particular component *e.g.* living, above-ground biomass.
2. DORMANCY:	the virtual cessation of a plant's autotrophic activity as found in organs no longer in active contact with photosynthesizing tissue; for example, seeds, corms, or rhizomes.
3. GROWTH:	the net increase in biomass.
4. GROSS PRODUCTIVITY:	the rate at which carbon and minerals are fixed in photosynthesis and related reactions.
5. NET PRODUCTIVITY:	the rate of dry matter accumulation, i.e. gross productivity minus respiratory losses.

The literature on how plants grow is prodigious (for example, at least 146 different journals were used in making up a single recent issue of 'Current Advances in Plant Science', Maxwell, Oxford). Much of this information relates to agricultural crops, although some interesting comparisons have been made between natural areas of similar and contrasting vegetation *e.g.* arctic and alpine regions by Billings and Mooney (1968) and arctic regions by Wielgolaski (1972). Studies of natural plant growth in largely aseasonal climates are very few. That of Kira *et al.* (1967) on Thailand rainforests, and Jenkin and Ashton (1970) on Macquarie Island grassland and herbfield are among the most detailed of productivity studies in aseasonal places. Huxley and van Eck (1974) and Tomlinson and Gill (1973) discuss the growth habits of tropical trees in aseasonal environments. Although there is little in the literature which is directly relevant to the topic of this thesis, there is much about the ability of plants to perform particular functions and their modification by changed environmental conditions. Also, values determined for the places studied in the current work (*e.g.* leaf area, or productivity) can be related to the broader context of plant performance elsewhere in the world.

In 1969, when work on this thesis began, little was known about the growth or structure of tussock grasses in the equatorial high mountains and sub-Antarctic islands. Biomass was reputed to be uncommonly high (Walker, 1968) and growth ~~was thought~~ to be possibly continuous throughout the year (Cuatrecasas, 1968 ; Walker, 1968). Apart from floristic and physiognomic data (see for example Coe, 1967; Hedberg, 1964; Taylor, 1955; Troll, 1959, 1960; Wace, 1965; Wade and McVean, 1969) this was the virtual limit of information on these regions.

B. Biomass

As recently as 1960, Bliss (1962) could comment on the paucity of information about primary production in widespread communities like those of the arctic and alpine regions. This is no longer the case and, indeed, maps of the distribution of world primary production (*e.g.* Lieth, 1972) provide a source of data on regional primary production against which the results of further work can be measured. Still, only the broad outlines are known of what is the primary production of the world's 144,000 or more species of flowering plants (number of species from Hutchinson, 1964).

Biomass data collected in this study for Mt Wilhelm and Campbell Island, and that of Jenkin (1972) for Macquarie Island are presented in Table 4.1. The data of Jenkin (1972) will be used in preference to that of Jenkin and Ashton (1970) because the former contains more detail.

Table 4.1: Plant biomass (Kg/m^2) for three Mt Wilhelm sites and two sub-Antarctic islands

	dead grass	living grass	herbs	cryptogams	woody plants	roots		total	shoot/ root
						live	dead		
WMF									
aerial	2.053	.401	.021	.086	.007	.	.	.	.
pedestal	.223	.106	.	.	.	.017	.	.	.
subterranean	.	.	.	.	.	.033	.195	.	.
Totals	2.276	.607	.021	.086	.007	.050	.195	3.242	12.2
WFS									
aerial	1.942	.346	.032	.140	.000	.	.	.	.
pedestal	.250	.119	.	.	.	.017	.	.	.
subterranean	.	.	.	.	.	.037	.304	.	.
Totals	2.192	.465	.032	.140	.000	.054	.304	3.187	7.9
WUV1									
aerial	2.978	.378	.019	.056	.000	.	.	.	.
pedestal	.083	.039	.	.	.	.005	.	.	.
subterranean	.	.	.	.	.	.041	.253	.	.
Totals	3.061	.417	.019	.056	.000	.045	.253	3.851	11.9
CBH									
aerial live	.	.634	.034	0	.215	.	.		
" dead	1.742	.	.025	0	.067	.	.		
subterranean	.	.	.	.	.	1.116	.		
" dead	.	.	.	.	.	.	1.206		
Totals	1.742	.634	.059	0	.282	1.116	1.206	5.039	1.2
Macquarie 45m*									
aerial live	.	.637	.262	.006	.012	.	.		
" dead	2.573	.	.110	?	.010	.	.		
subterranean	.	.	.	.	.	1.686	.		
" dead	.	.	.	.	.	.	3.110		
Totals	2.573	.637	.372	.006	.022	1.686	3.110	8.406	0.8

* from Jenkin, 1972

As the relative distribution of plant mass is an important element in the structure of a plant community, the biomass data have also been expressed in terms of the proportions of plant mass in the categories dead attached grass, living grass, herbs, cryptogams, woody plants, and roots (Table 4.2).

The proportions are calculated in two ways: a) on the basis of total above and below ground plant mass, and b) on the basis of above ground plant mass.

Table 4.2: Distribution of plant mass for sites of Table 4.1. (Expressed as a: percent of total plant mass, and b: percent of above ground mass (including pedestal root mass)).

	dead grass	living grass	herbs	cryptogams	woody plants	roots		total wt Kg/m^2
						live	dead	
<u>WWF</u>								
a	70.2	18.7	0.6	2.7	0.2	1.5	6.0	3.242
b	75.9	20.3	0.7	2.9	0.2		.	2.997
<u>WFS</u>								
a	68.8	14.6	1.0	4.4	0.0	1.7	9.5	3.187
b	77.5	16.4	1.1	4.9	0.0	.	.	2.829
<u>WUV1</u>								
a	79.5	10.8	0.5	1.5	0.0	1.2	6.6	3.851
b	86.2	11.7	0.5	1.6	0.0	.	.	3.553
<u>CBH</u>								
a: living	.	12.6	.07	0	4.3	22.1		5.039
dead	34.6	.	.05	0	1.3	23.9		
b: living	.	23.3	0.9	0	7.9	.		2.717
dead	64.1	.	1.3	0	2.5	.		
<u>Macquarie 45m</u>[a]								
a: living	.	7.6	3.1	0.07	0.14	20.1		8.406
dead	30.6	.	1.3	.	0.12	37.0		
b: living	.	17.6	7.3	0.2	0.33	.		3.610
dead	71.3	.	3.0		0.28	.		

a) Jenkin, 1972

a. <u>Mt Wilhelm</u>

An analysis of variance by ranks (Kruskal-Wallis test, Zar, p.139, 1974) of the total above ground (excluding pedestal) biomass indicated very significant variation between sample sites ($0.005 < p < 0.01$; Appendix 4.1). Non-parametric multiple comparisons (Zar, p.156, 1974); Appendix 4.2) indicated that site WUV1 (4300m) had a significantly higher total aerial biomass than did the other four lower sites ($p=0.05$) but at $p=0.01$ only half the sites showed significant differences from WUV1. At the higher level of significance, two overlapping groups are apparent among the latter four sites, a finding that indicates ambiguity in the data and the need for more samples before further statistical inference can be made. Either some intrinsic factor or random variation in the data could be responsible for the variation in the latter groups, and no emphasis will be put on differences in biomass between

WWF and WFS sites. The values of the samples from each of these two sites will be pooled and only their averages used in the discussion below.

Small sample sizes and large variances preclude meaningful statistical analysis of the source of WUV1's high aerial biomass. However, inspection of the data (Table 4.1) shows that while WUV1 has the largest weight of dead attached grass, it has the lowest weight of living grass ~~and of~~ herbs, and ~~an intermediate weight of~~ cryptogams of all three Mt Wilhelm sites. The highest altitude site thus has the highest above ground biomass largely because of the presence of more attached dead grass than at lower sites. Perhaps lower mean temperatures at the highest altitude site inhibit decomposition and decay of leaves.

At all sites, nearly three-quarters of the total plant mass is dead attached grass leaves (Table 4.2). The proportion of living aerial mass is similar at all sites with the small exception that woody plants were present only at WWF. Shoot to root ratios were large (7.9 to 12.2) (Table 4.1) and will be discussed as indicators of the relative stress experienced by aerial and subterranean organs (Bliss, 1971) in section 4.B.c, in which Mt Wilhelm and sub-Antarctic sites are compared.

The 'standing dead' portion of herbs and cryptogams was not calculated. The figures for each group are for living aerial mass only. That separation of living from dead was not made is unfortunate but, as less than 5% of total plant mass at any of the three sites is in these categories, only a small amount of information on community structure is lost.

A direct comparison of my data with those of Walker (1968) is not possible because our sites are not very similar. My sites are almost exclusively tussock grasslands with very few herbs or shrubs whereas his sites most similar to mine have a rich admixture of herbs and shrubs with tussock grasses. However, for 'forb rich grassland' he reports 0.51 to 0.88 Kg/m^2 dry weight of living plant mass and for 'tussock grassland' 0.34 to 0.59 Kg/m^2. The comparable values from my study are WWF = 0.721, WFS = 0.637, and WUV1 = 0.492 Kg/m^2, *i.e.* they lie within the range of values that Walker reported.

b. The sub-Antarctic

The data for the sub-Antarctic islands (Table 4.1) come from my own observation on Campbell Island and from Jenkin (1972) for Macquarie Island. Living and dead components of the biomass of herbs and woody plants are also available for these sites.

Total plant mass is higher at Macquarie Island (8.406 Kg/m^2) than at

Campbell Island (5.039 kg/m^2)(Table 4.1). The greater amount of dead attached grass and dead roots at Macquarie Island than at Campbell Island appears to be the main source of the difference between the sites. That Macquarie Island is on average cooler than Campbell Island (see Chapter 3) may result in lower rates of decay and decomposition at the former, causing more dead matter to accumulate at the cooler site than at the warmer one. Douglas and Tedrow (1959) and Mikola (1960) have shown that decomposition rates may be proportional to temperature, although there is not complete agreement in the literature on the subject (see Heal, 1972).

At Macquarie Island, there appeared to be six times more herb and ten times less woody plant biomass than at Campbell Island (Table 4.1).

The greater woody plant mass at Campbell Island than at the Macquarie Island site is indicative of a real difference between the islands. The shrub *Dracophyllum* is common and robust on Campbell Island, equalling or sometimes exceeding the tussocks in height, whilst the woody element at Macquarie Island is confined to the prostrate creeper *Acaena*. However, if woody plants are included with herbs, the two sites can be seen to be similar in aerial, non-grass, plant mass.

The proportionate distribution of plant mass (Table 4.2) shows similarities and differences between the two islands that follow those just noted for plant mass.

c. Comparison of regions :

Equatorial high montane and sub-Antarctic island grasslands

The tussock grasslands of sub-Antarctic islands appear to support a greater total plant mass than physiognomically similar grasslands on the high equitorial mountains (Table 4.1). The main source of the difference is the great root mass at the sub-Antarctic sites. The living root mass is at least 20 times greater and the dead mass at least 4 times greater on the sub-Antarctic islands than on the equatorial high mountain. It is more difficult to generalize about herb aerial mass, but it too may be greater in the sub-Antarctic although the available data are insufficient to substantiate this. The magnitude of the difference in root mass between the two regions is further emphasized in the shoot:root ratio. Values of 7.9 to 12.2 were found for Mt Wilhelm tussock grasslands and 0.8 to 1.6 for the Macquarie and Campbell Islands grasslands.

The significance of the shoot:root ratio in relation to the plant environment has been noted by Billings and Mooney (1968), Bliss (1971), and Wielgolaski (1972), and several determining factors of different ratios have been suggested by them. However, Wielgolaski (1972) supports Bliss'

(1970) claim that at least part of the reason for the low shoot:root biomass ratio in the arctic results from the greater accumulation of organic matter due to low temperatures. However, on Macquarie Island and Mt Wilhelm, the shoot:root ratios are little changed if calculated only on living plant mass (10.9 - 14.4 for Mt Wilhelm and 0.6 for both Campbell and Macquarie Islands).

Billings and Mooney (1968), Bliss (1971) and Wielgolaski (1972) are in general agreement that small values of the ratio (*i.e.* relatively more root than shoot) are indicative of less severe root environments than shoot environments, the converse also being true. This is borne out to some extent by what we know of the climates of Mt Wilhelm and Macquarie Island. In Chapter 3 it was noted that on Macquarie Island, air temperatures (at 1m above ground and in the tussock canopy) varied little diurnally or seasonally whereas soil temperatures beneath a low turf showed a distinct warm season lasting 7 months, with mean temperatures at all depths (-0.1 m to -1.0m) higher than 1 m air temperatures. On Mt Wilhelm it appears that soil temperatures below about five to ten cm are perpetually low, changing little diurnally and probably not very much seasonally either. In contrast, tussock canopy temperatures vary a great deal diurnally although not very much seasonally (see Chapter 3).

I do not believe, however, that the answer to the very different shoot:root ratios between regions in the humid, ever-cool, and seldom harsh environments of the equatorial high montane and sub-Antarctic is as simple as is implied above. For example, it is known that in many Festucoid grasses root growth occurs primarily after shoot growth, root growth being favoured by lower temperatures than are optimal for shoot growth (hence the alternation of growth between shoot and root with changing seasons in temperate climates) (Evans *et al,* 1964). If *Poa foliosa* were to grow like these grasses, one could suppose that the large root masses found in its tussocks are the result of growth during the long 'winter' months. There is some evidence that *P. foliosa* does, in fact, behave in this way; it reaches peak aerial production when soil temperatures are beginning to decline (Jenkin, 1972). The environmental factor that triggers the cessation of shoot growth is not known and is unlikely to be air temperature, given its aseasonal nature in these regions, but quality or quantity of incoming radiation, soil temperature, or a combination of these could be responsible. If temperature is important in triggering growth processes in the tussock, it must be a sensitive system. Not only is the range of temperatures small (except for diurnal changes of canopy temperatures in the equatorial plants), but the thermal insulating properties of the tussock form (Coe, 1969; Hopkins and Sigafoos 1951;

Scott, 1962) act to reduce the amplitude of any temperature fluctuation in the surrounding environment, such that growth points (apices, leaf bases) are well protected from extreme temperatures.

Wielgolaski (p.26, 1972) summarizes the reports of shoot:root ratios in northern tundra sites by saying that a gradient of increasing ratio appears to be related to geographical gradients of increasing temperature, decreasing water supply, and possibly nutrient conditions. A comparison of soil nutrients between the two regions of the current study (Table 4.3) shows that Macquarie Island soils from tussock grassland sites not affected by seals or poor drainage (Jenkin, 1972) are richer in nutrients than those examined by Wade and McVean (1969) on Mt Wilhelm.

Table 4.3: Nutrients of tussock grassland soils of Mt Wilhelm[1] and Macquarie Island[2].

		me/100g exchangeable bases								
		Ca	Mg	K	Na	Sum	pH	%C	%N	C/N
Mt Wilhelm:										
"*Deschampsia klossii* alpine tussock grassland"	a.	1.50	0.38	0.56	0.05	2.49	5.5	11.9	0.50	23.8
	b.	1.07	tr	0.47	0.18	1.72	5.8	3.1	0.17	18.2
Macquarie Island										
"*Poa - Stilbocarpa* grassland"	c.	.	.	.	.	.	4.4	13.9	1.19	11.7
	d.	6.11	8.50	1.45	5.42	~~22.48~~ 21.48	4.4	16.2	1.46	11.1

1. Wade and McVean, 1969, p. 27.
2. Jenkin, 1972, p. 26.
   a. relevé no. 190; b. relevé no. 232; c. sample no. 378/2274;
   d. sample no. 378/2274A.

There is between 2.4 and 8.6 times as much nitrogen (as % of dry weight) in the Macquarie soils as in the Mt Wilhelm soils and between 9.0 and 13.1 times as much total exchangeable cations in the former than in the latter soils. Jenkin (1972) indicates that airborne salts from the nearby ocean are present in precipitation and are probably a major source of many nutrients in Macquarie Island soils. Although no measurements of nutrients in precipitation are available from Mt Wilhelm, a similarly large aerial input is not expected due to the distance from the sea and the large amount of mostly orographic precipitation there. The organic matter content appears to be a little higher in the Macquarie soils than in the Mt Wilhelm soils but data from other sites presented by Jenkin (1972), and Wade and McVean (1969) suggest that it may be similar for the two regions.

Moisture content of the soils in these two areas has not been monitored but is probably high at most times with perhaps greater variation on Mt Wilhelm than at Macquarie Island. On Mt Wilhelm the height of the soil water table is closely correlated with the seasonal precipitation; during the 'dry' period the water table is low and during the 'wet' period the soil is water logged to the surface. If a similar relationship of water table to precipitation is true for Macquarie Island, then with the aseasonal rainfall coming in small amounts on most days of the year, the water table is expected to be at a more or less constant and high level (but not necessarily water logged to the surface).

At both Mt Wilhelm and Macquarie Island there is a large portion of the total as well as aerial plant mass in the 'dead grass' element. The proportion at Mt Wilhelm is about twice as large as at Macquarie Island. The conspicuous accumulation of dead plant matter may be a characteristic of grassy communities in cool climates. The data of Schamurin *et al.* (1972) for plant biomass of communities at the Tareya station (Taimyr) show graphically the enormous accumulation of dead vascular plant mass in a 'herb-grassy community' compared with that in four other tundra communities in the near vicinity that are not dominated by grasses.

The mass of plants other than grasses is very low in the tussock grasslands of both Mt Wilhelm and the sub-Antarctic sites. The highest values are 4.4% of total plant mass for bryophytes at WFS and 4.3% of total plant mass for living woody plants at CBH. These values are about one third or less of the living grass values. Plants other than grasses are generally confined to a shallow stratum against the ground (for most herbs and bryophytes), although some bryophytes live amongst the leaf bases in the tussock. The shrubs and ferns of CBH grew in spaces between tussocks, with crowns either beneath the grass canopy or intermingled with it (*e.g. Coprosma ciliata, C. cuneata*). Site selection criteria, however, are important in controlling the low levels of non-tussock plants in the data.

The dominance of bryophytes over non-grass vascular plants at Mt Wilhelm sites compared with the sub-Antarctic sites is puzzling since apparent bryophyte abundance did not affect selection of plots. On Macquarie Island bryophytes are particularly abundant in areas of water logged soils. On Campbell Island they are abundant in bogs, as epiphytes in dense shrubbery, and as a carpet beneath some shrub canopies. On Mt Wilhelm the situation is similar to that on Campbell Island but with the bryophytes extending into the tussock grassland. One difference that may be important is that the lower altitude tussock grasslands on Mt Wilhelm (WFS and WWF) replaced shrubs or forest communities after burning altered the vegetation an unknown time ago. It is possible that the bryophytes represent a remnant of the previous woody community or are seral after burning, but comprehensive and comparative ecological studies of the bryophyta are needed before these differences between regions are understood.

C. Structure

The physiognomy of a plant community is, as Greig-Smith (1964, p.135) says, 'the criterion least susceptible to exact description though it is a most useful characteristic...'. It is useful because it describes the distribution of plant mass in relation to space. It can be used as a basis of classifying communities or simply as a tool to describe their physical structures.

Tussock grasses can be classified only inadequately in the 'Life form' system of Raunkiaer (1934). Some tussock grasses are hemi-cryptophytes because their perennating buds are just below ground surface (*e.g.* some *Chionochloa* and *Poa* species of New Zealand (personal observation), *Stipa stenophylla* in Eurasia (Eyre, 1963), and tussocks in the Afroalpine (Hedberg, 1964)); others are chamaephytes with buds at the ground surface (*e.g.* some *Deschampsia klossii* of Mt Wilhelm and *Chionochloa* sp. of the Snowy Mountains, Australia, personal observations); others, particularly the taxa with pronounced pedestals, are a form of phanerophyte. These latter forms are the most difficult to assign. The buds grow either at or just below the upper surface of the pedestal which may or may not be deemed 'soil' since most of the plant's roots are found in it, although the pedestal also contains stems and leaf bases. Perhaps a new term should be introduced to describe the strongly pedestalled growth form when few or no roots penetrate beneath the pedestal (*e.g.* auto epiphyte).

Some of the tussocks in both regions studied in the present work were of the latter or phanerophyte categories. The mature tussocks were usually characterized by a pedestal of compact, living and dead plant parts which often rose above ground like a thick tree trunk, reminiscent of a pachycaulous plant. However, on steep slopes the pedestal sometimes became decumbent under its own weight. Pedestals could measure nearly one metre in diameter and over 1.5 m in height. Each was topped by a crown as wide as the tussock was high (Figure 4.1). However, the high altitude

FIGURE 4.1 *Poa foliosa* tussocks in full flower, December, 1971, Lusitania Hut, Macquarie Island.

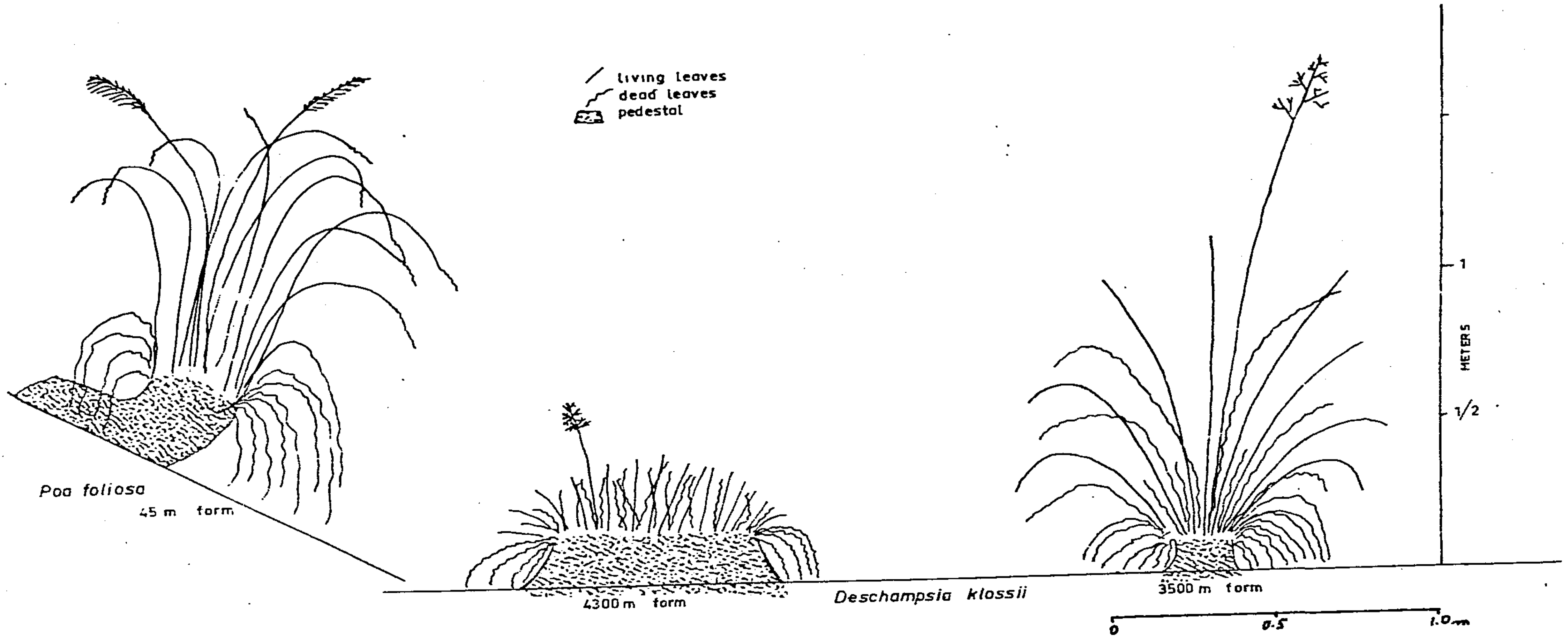


FIGURE 4.2. A schematic diagram of tussock form. The characteristic alpine and subalpine forms of *Deschampsia klossii* are shown. The *Chionochloa antarctica* although not shown is very similar to the Macquarie Island *Poa foliosa.*

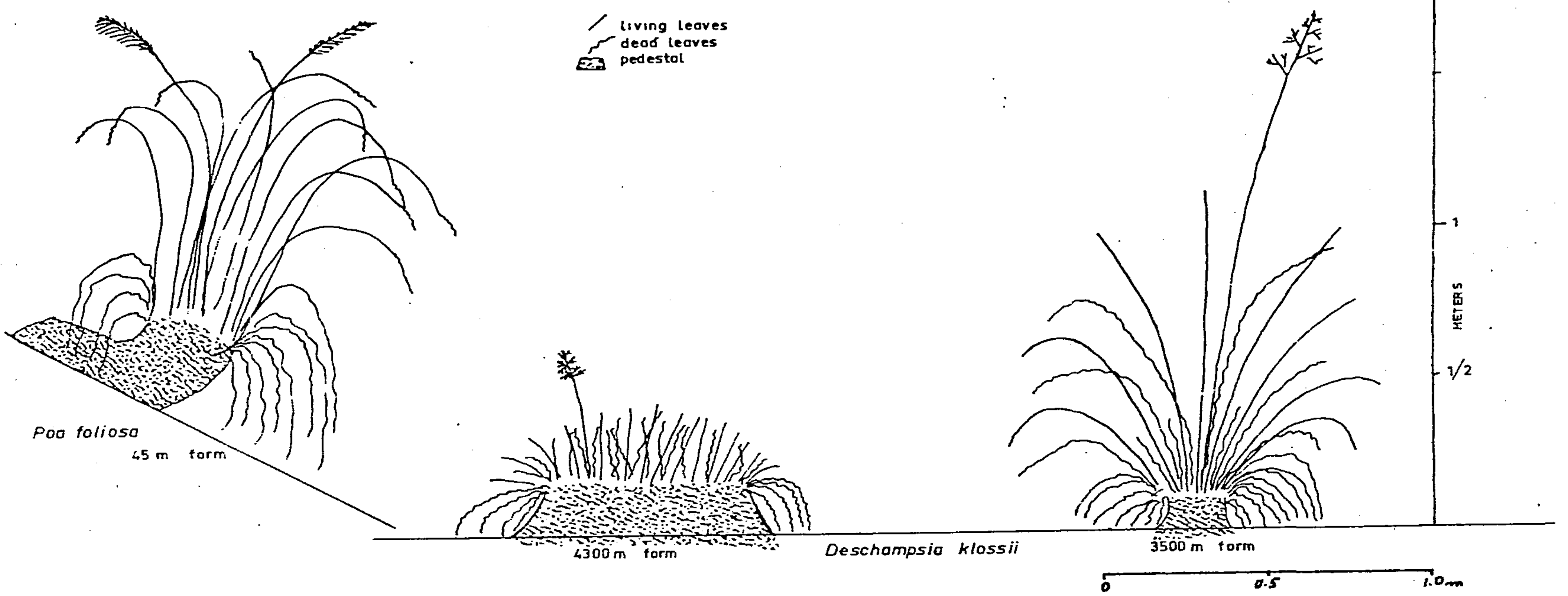


FIGURE 4.2. A schematic diagram of tussock form. The characteristic alpine and subalpine forms of *Deschampsia klossii* are shown. The *Chionochloa antarctica* although not shown is very similar to the Macquarie Island *Poa foliosa*.

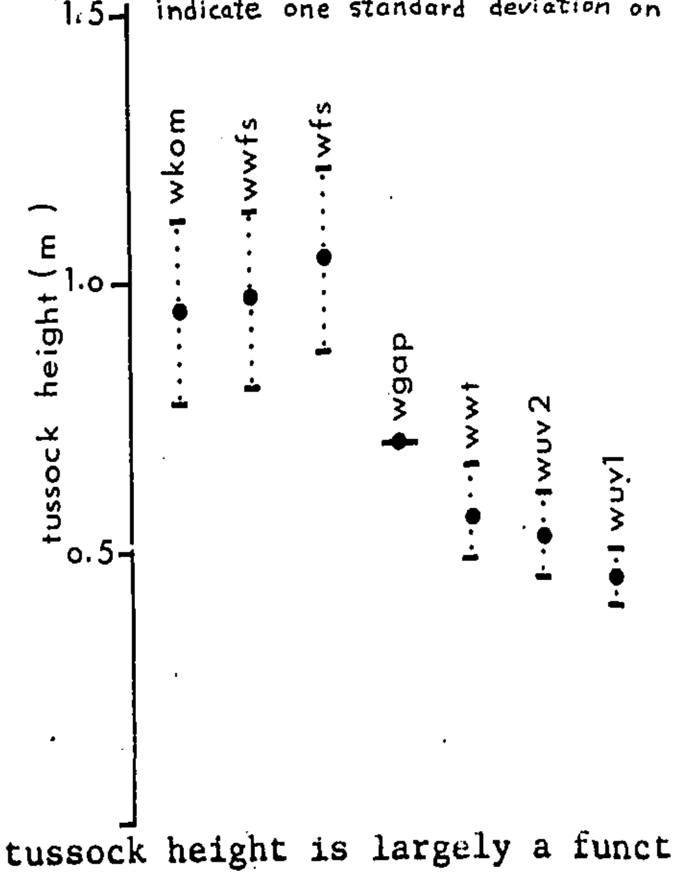
Deschampsia klossii had rigid, short leaves rather than long arching ones (Figure 4.2).

Hedberg (1968) and Troll (1961) have applied descriptive names to the unusual growth forms found in the high equatorial mountains. Both use the term 'tussock grass' (or its equivalent) but their diagrams do not indicate whether pedestalled tussocks are meant to be included in the term.

a. Tussock height and leaf length

From Kombuglomambuno (3200m) to WFS (3510m) in the Pindaunde Valley, tussock height (ground surface to the top of the canopy) was fairly constant at about 0.98m. It decreased from WFS to 0.46 m at WUV1 (4350m) (Figure 4.3). The slight variation in mean tussock height between 3200m and 3510m suggests that 0.98m is about the maximum mean attainable by *Deschampsia klossii*, perhaps because cell number is genetically controlled and maximum elongation is physically limited. Above 3510m tussock height appeared to decrease with increasing altitude, apart from the WUV2 site (4380m) having slightly taller tussocks than the WUV1 site (4350m).

Figure 4.3: Tussock height at Mt Wilhelm sites. ● = mean; bars indicate one standard deviation on either side of the mean.



Deschampsia tussock height is largely a function of leaf length; pedestal height (Table 4.4) contributes only 3.5% to 7.5% to the total (using data from Figure 4.1 and Table 4.4). Table 4.5 shows the modal frequency of length class of leaves sampled at each site. There appears to be a steady increase in length of the commonest class with decreasing altitude. In view of Coe's (1967) experiments showing the positive relationship between temperature and leaf elongation for some Afroalpine species, it seems reasonable to attribute variation in *Deschampsia* leaf length to differences in temperature which themselves are related to altitude.

Table 4.4: Tussock pedestal height, Mt Wilhelm and Macquarie Island.

Site	cm	N	% of tussocks without measurable pedestal
WWF	4.4 ± 6.0[1]	35	63%
WFS	6.6 ± 8.7	175	49%
WUV1	1.3 ± 3.3	225	90%
WUV2	2.3 ± 5.0	185	77%
Macquarie[2]	0 - 33	89	only young tussocks without pedestal

1. Error term is standard deviation of mean.
2. Data from Ashton, 1965.

Table 4.5: Modal leaf class lengths at Mt Wilhelm sites.

Site	Modal class (cm)
WWF	60 - 70
WFS	50 - 60
WGAP	40 - 50
WWT	30 - 50
WUV1	20 - 25
WUV2	20 - 25

That leaf size of grasses is related to leaf environment finds further support in the statement of Evans *et al.* (1964):

> Mature leaf size is markedly affected by environmental conditions. Since cell division in the intercalary meristems ceases when the leaf tip is first exposed to light, differences in mature leaf size must be largely due to differences in cell size rather than in cell number...

Stuckey (1942) has presented evidence that leaf length in a grass species growing under different environments is a function of cell size rather than cell number. Thus, if in genetically similar individuals leaf length is a function of cell elongation which is controlled by temperature, it may be that the lower the mean temperature, the less the cells can elongate and the shorter the resulting leaf. This hypothesis could be tested if leaves were collected from a range of altitudes on Mt Wilhelm and cell length and number determined per unit of leaf length.

Leaf diameters (Table 4.6) show very significant increases from a low of 0.106 cm at WUV1 to a high of 0.130 cm at WFS (t-test $p < 0.01$) (t-test applicable because sample size large and variances small and similar). As with leaf length, leaf diameter may well be controlled by temperature-dependent cell expansion.

Table 4.6: Leaf diameters at three Mt Wilhelm sites

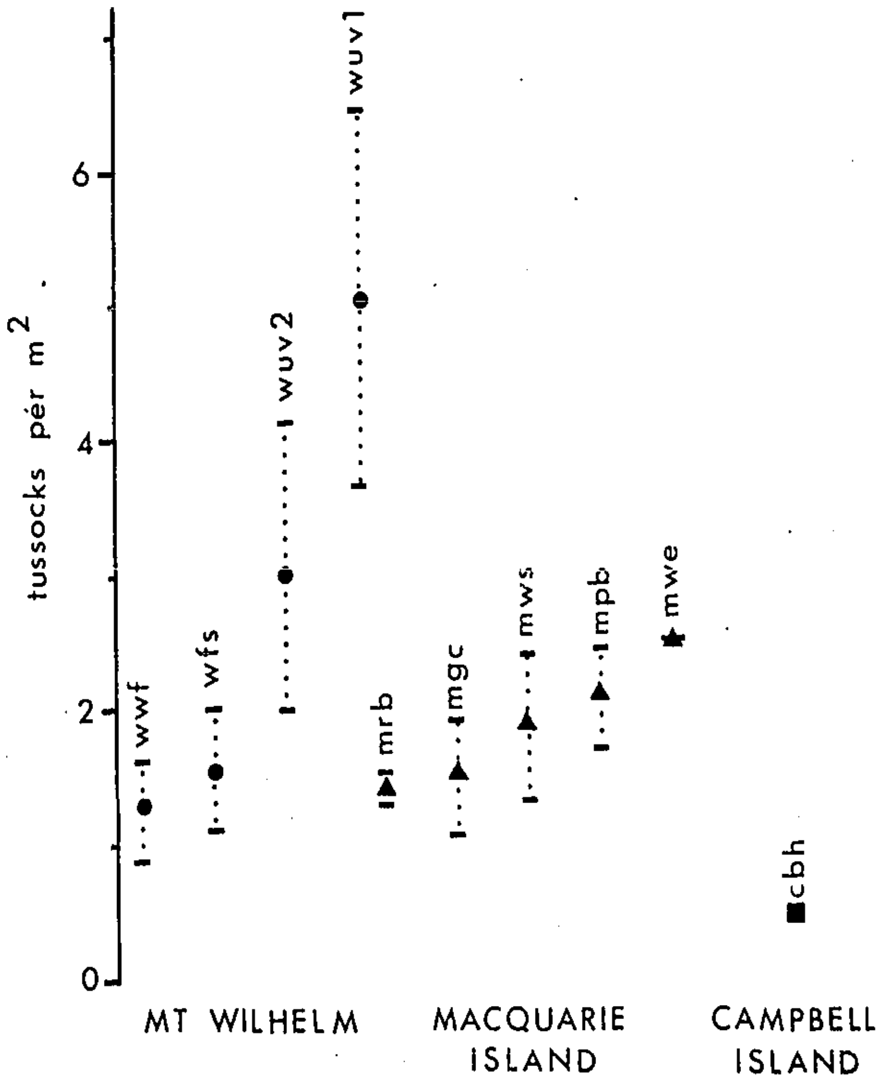
Site	Mean (cm)	St. Dev (mean)	N
WFS	0.130	0.015	150
WUV1	0.121	0.008	448
WUV2	0.106	0.006	649

Tussock height in the sub-Antarctic was fairly constant at 0.7 to 0.8 m at all sites studied, except MGC and MWS where the average was closer to 1.0m. Pedestals were larger (Table 4.4) on the southern island than on Mt Wilhelm, perhaps due to the greater accumulation of root mass, and they contributed a greater proportion to total tussock height (19-33% of total tussock height on Macquarie Island (Ashton, 1965) compared with less than 10% on Mt Wilhelm). In restricted areas on Macquarie Island where elephant seal wallowing is common, pedestal height may be greater due largely to the compaction and removal of peat from between tussocks.

b. Tussock density

The density of tussocks (number of tussocks per square metre is shown in Figure 4.4. Highest densities were found at the highest Mt Wilhelm sites and decreased with decreasing altitude. If density was strictly

Figure 4.4: Tussock density at Mt Wilhelm, Macquarie Island and Campbell Island sites.



a function of tussock size (*e.g.* diameter), one would expect density to vary randomly with respect to altitude such that various size-density combinations would be found at each altitude. Furthermore, if size-density changed with age (*e.g.* many small young to few large old tussocks or *vice versa*) one would not expect a clear relationship with altitude to be found.

Since temperature is the most obvious environmental factor related to altitude, it may be that low temperatures inhibit cell expansion resulting in shorter leaves and stems and therefore tussocks with smaller diameters, ultimately leading to more tussocks per unit area.

On Macquarie Island, tussock densities are similar to those at the lower altitude Mt Wilhelm sites and the density on Campbell Island is least of all (Figure 4.4).

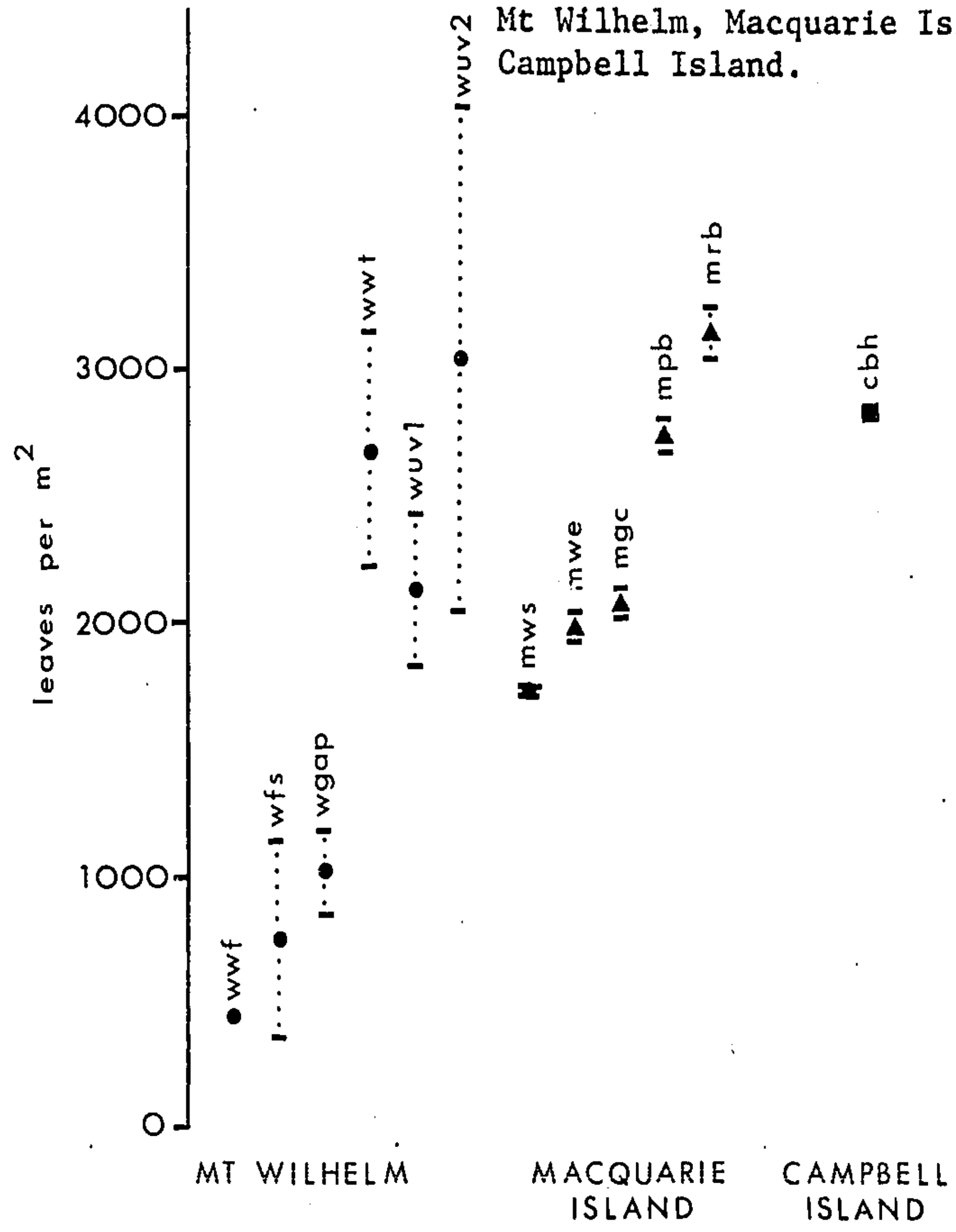
It is possible that the amount of radiant energy received by a site is more important than the average temperature of the site with regard to tussock density. Temperature is sometimes a good measure of energy received and thus one finds that tussock density increases as average temperatures (and therefore energy) decrease . Variations from the temperature:tussock density relationship are explicable in terms of special radiation conditions. Take for example the Macquarie Island sites. The two sites with the lowest density occur at the lowest altitude where temperatures are presumably higher than at greater altitudes. Of these two sites, tussock density is slightly lower at the north facing (*i.e.* sun facing) than the SSW facing site. Of the other three sites, the high altitude NNE facing MPB site has a tussock density that falls between those of two mid altitude SW and SSW facing sites and indicates that aspect as a factor determining radiant energy input can be more important than altitude in relating to tussock density.

Only detailed studies and experimental work can solve the problem of density differences. Soil nutrients and life cycle dynamics also need attention in searching for a solution. Ashton (1965) has studied regeneration patterns in Macquarie Island tussock grassland but has not discussed factors influencing tussock density. From Evans *et al.* (p.114-5, 1964), it appears that tillering is highest at low temperatures. If tussocks arise largely from vegetative regeneration, as Ashton (1965) suggests for *Poa foliosa*, there could be a causal relationship between temperature and tussock density.

c. Leaf and tiller density

Leaves were counted in tussocks of known horizontal dimensions (*i.e.* crown area) for six Pindaunde sites (Figure 4.5). Because the relation of crown area to ground area was not known for all sites, leaf density based on crown areas only was used. However, as there was nearly a 1:1 relation between crown and ground areas at sites from which both were available, the measures of leaf density per unit crown area probably approximate closely to those which would have been obtained in relation to ground area.

Figure 4.5: Tussock-grass leaf densities for Mt Wilhelm, Macquarie Island, and Campbell Island.



There was a remarkable increase in leaf density of seven times from the lowest site WWF to the highest site WUV2. There appear to be two density groups as shown in Figure 4.5 : a low and mid altitude group (3400m to 4190m) with densities of about 500 to 1000 leaves/m^2, and a high altitude group (4300m to 4380m) with densities of about 2000 to 3000 leaves/m^2. More complete samples taken over the whole range of altitudes at which *Deschampsia* grows on Mt Wilhelm could be expected to show a more or less continuously ~~de~~increasing leaf density with increasing altitude, barring exceptions caused by small variations in local environments. It was observed in the field that the high altitude group tended to have short, firm leaves and heavy, compact inflorescences while the lower altitude group had long, flexuose leaves and light, feathery, expanded inflorescences.

Leaf densities for Macquarie Island were calculated from the estimates of leaves per tiller and tillers per square metre at each site (Table 4.7). They ranged from $3152/m^2$ to $1991/m^2$. There is no obvious correlation of leaf density with site aspect, wind exposure, or presumed average temperature. The 2828 leaves/m^2 at the Campbell Island site lies within the range of values found for Macquarie Island. Leaf densities at both sub-Antarctic sites are similar to the high range of densities found on Mt Wilhelm.

Table 4.7: Tiller and leaf density (no./m^2) at Macquarie Island and Campbell Island sites.

	tillers			leaves
Site	mean	St. Dev (mean)	N	
MRB	516.7	133.8	3	3152
MPB	474.8	96.1	4	2754
MGC	367.5	49.5	4	2095
MWS	281.0	12.7	2	1742
MWE	331.8	64.4	4	1991
CBH	505.0	-	1	2828

The number of leaves per tiller at Macquarie and Campbell Islands is shown in Table 4.8. The fewest leaves per tiller occurred at CBH, but this value was statistically the same (t-test 1% level) as that for

Table 4.8: Number of leaves per tiller at Campbell and Macquarie Island sites.

Site	Mean	St. Dev (mean)	N
CBH	5.6	0.8	143
MGC	5.7	0.9	25
MPB	5.8	0.7	100
MWE	6.0	0.8	98
MRB	6.1	0.7	96
MWS	6.2	0.9	99

MGC and MPB. Most of the Macquarie sites had about the same number of leaves per tiller, although MPB and MGC had significantly fewer than MRB or MWS. The main reason for this difference lay in the presence of many tillers with seven or eight leaves each at the latter sites.

d. Leaf area index

The importance of the Leaf Area Index (LAI), first recognized by Watson (1947), has been reviewed in relation to other growth factors by Chang (1968).

LAI was estimated for three sites on Mt Wilhelm, one site on Campbell Island and five sites on Macquarie Island (see Methods, Chapter 2). These data are presented in Table 4.9.

Table 4.9: Leaf area indexes at Campbell Island, Macquarie Island, and Mt Wilhelm sites.

Site	Mean	St. Dev (mean)	N
CBH	5.5	0.8	29
MGC	3.4	1.1	20
MWE	2.7	0.9	20
MWS	2.4	0.7	20
MRB	4.4	1.4	20
MPB	3.9	1.0	20
WFS	1.6	0.6	7
WUV1	1.8	0.4	5
WUV2	2.4	1.0	5

On the basis of the site means in Table 4.9, LAI of tussock grasses, growing in virtually pure grass stands, appear to be lowest on Mt Wilhelm, intermediate on Macquarie Island, and highest on Campbell Island. Although samples were more or less randomly selected within sites, the sites themselves were not randomly selected. Thus strict statistical analysis of the LAI data is not admissible. However, if allowance is made in the interpretation of statistical tests for the bias built into samples selected, some implications may be gained from such analysis. I have performed a nested analysis of variance (Appendix 4.3) of the LAI data from both regions. Its indications are that there is unlikely to be a significant difference in LAI between regions ($0.25 < p < 0.10$) or between sites within regions ($p > 0.50$). Since sites were deliberately chosen as representative of good tussock development in each local area, the above analysis may be interpreted as showing that similar LAI's are attained by well developed tussock grasslands in both the equatorial high montane and the sub-Antarctic islands.

Detailed separate examination of the Mt Wilhelm and Macquarie Island LAI data provides little further information. A non-parametric, Kruskal-Wallis analysis of variance of ranks (after Zar, 1974) shows no difference between Mt Wilhelm sites ($p > 0.1$), while the results for Macquarie are ambiguous.

Jenkin (1972) gives a mid-winter (June) LAI of about 4.5 and January value of about 7.6 for Macquarie Island grassland (*Poa foliosa* and the giant herb *Stilbocarpa polaris*). He does not present the data for these two species separately nor is there any indication of the variability of each. Thus it is not known whether the apparent seasonal trend is largely due to winter die back of large *Stilbocarpa* leaves alone or whether the *Poa* also reduces its leaf area. Casual observations on Macquarie Island do not indicate any substantial die back in the tussock grass, but the behaviour of *Stilbocarpa* is puzzling. Jenkin notes that lowland *Stilbocarpa* dies back during the winter and reports that the large-leaved herb, *Pleurophyllum hookeri*, growing in 'herbfield', changes its leaf area by a factor of six from winter to summer. However, his series of photographs of high altitude plots containing *Stilbocarpa* indicate that it undergoes virtually no seasonal change in leaf area.

It appears, then, that LAI is variable but that the factors affecting it on the tropical montane and sub-Antarctic island grasslands are not well known. The apparent seasonal changes at Macquarie Island sites are especially puzzling (*e.g. Stilbocarpa* above).

e. Leaf longevity

Leaf longevity is not an aspect of structure but following the seasonal anomalies just noted in leaf area index, it seems appropriate now to treat the subject of duration of growth of individual leaves of tussock grasses in the two regions.

Although data on the rate of leaf appearance and leaf longevity are very incomplete, some are available from the two regions being compared here. On Mt Wilhelm, less than 5% of the 250 young leaves of *Deschampsia klossii* tagged in mid April, 1970, had died by the middle of November (*i.e.* nine ~~seven~~ months later), but all 650 leaves tagged by mid October, 1970 had died by the middle of the following July (*i.e.* between seven and 15 months later). From the 5% of leaves that substantially died back before mid-November, it is known that the leaves with shortest lives completed about 95% of their length growth at least two to three months before die back had spread more than 3 millimetres back from the leaf tip. Thus, the rest of the leaves must have remained entirely green at full length for more than 2 to 3 months. Possibly leaves die all at once, perhaps in response to some climatic factor, but visitors to Mt Wilhelm have never mentioned any marked seasonal change in the appearance of the tussock grasslands. Furthermore, the tussocks would require a very sensitive monitoring system to detect triggering environmental changes such as that found by Njoku (1964)(in Huxley and van Eck, 1974). As leaf appearance (*i.e.* when the leaf becomes visible outside the last enclosing sheath) is an asynchronous event in the population, it is likely that death may also be. Huxley and van Eck (1974) suggest that plant growth and development events that are asynchronous in a population of one species in a uniform environment indicate the presence of endogenous controlling factors in the species. A similar condition may thus exist in *D. klossii.*

From the few tagged *Deschampsia* leaves that died back more than 3 mm from the tip by mid November, it appears that death, particularly the early phases, progresses sporadically backwards from the leaf apex. Leaves remain green but do not elongate for several months and then a centimetre or two of the apical region turns brown. Another period of no die-back occurs, then a further short period of die-back, and so on. A very few leaves that began to die after only 2-3 months growth did die back more or less in a steady manner. This could mean that once a phase of irregular stops and starts has passed, death progresses steadily to the end. The pattern of death in these early-dying leaves, however, could be unique to their class and not true of longer-lived leaves.

Jenkin (p.83, 1972) states for Macquarie Island:

> 'Data from tagged shoots indicate that the longevity of individual *Poa* leaves is approximately six months over summer and ten months over winter.'

Whilst this statement (also made in Jenkin and Ashton 1970) is ambiguous and no examples are given to illustrate the meaning intended, it is nevertheless clear that leaves live for periods of less than one year. They therefore exhibit a similar short life span to tussock leaves on the high tropical mountains, contrasting with the two-three year functional lives of leaves of the tussock grass *Chionochloa rigida* in New Zealand (Mark, 1965).

There is no information on leaf longevity for *Chionochloa* *antarctica* from Campbell Island. What is known is that, while scarcely any new leaves appeared during February and March, die back did occur, suggesting that a pronounced seasonal cycle may be present in the *Chionochloa* phenology. On Macquarie Island in December-January, I recorded new leaf appearances of between 1.8 and 2.2 leaves per tiller, and Jenkin (1972) indicates tussock litter to accumulate most rapidly from April to June. If the same periodicity applies to Campbell Island tussocks, the few new leaves found there could simply be a result of sampling later in the season there.

The outstanding question is whether *Chionochloa antarctica* leaf longevity is more like that of its genetic relations living under a climatically different regime in New Zealand than that of tussocks of other genera living under similar climatic conditions. I would guess the latter to be most probable. *C. antarctica* is thought to be a native species of Campbell Island and can therefore be expected to be more adapted to conditions existing there than to conditions existing somewhere else. That Mark (1965) reports leaf longevity to range from two years per leaf for *Chionochloa rigida* tussocks in New Zealand growing between 260m and 1000m altitude to three years per leaf at 1500m altitude indicates that leaf longevity does vary within a genus from habitat to habitat. (Mark and Bliss, 1970, report that Zotov, 1970, has described the high altitude 'ecotype' of *C. rigida* as a separate species: *C. macra.*) Thus it would not be surprising if *C. antarctica* displayed a leaf life time different from that of related mainland New Zealand species.

It would appear that leaves live for greater lengths of time if their functional lives are broken by periods of enforced dormancy, *e.g.* by long periods of freezing temperatures (*Chionochloa* in New Zealand mountains). The implication, though unproven, is that death occurs after a leaf has functioned (as opposed to existed) for a certain maximal length of time.

The rate of appearance of leaves can be estimated for Mt Wilhelm sites. The mean periods of growth and rates of leaf initiation for seven sites are given in Figure 4.6 where it can be seen that both these attributes vary in a similar way with respect to site altitude, but a Spearman's rank correlation of the rate of appearance with the rate of growth is not significant ($r_s = 0.46$, $n = 7$, $0.10 < p < 0.25$).

For all seven Mt Wilhelm sites together, 302 new leaves appeared on tagged tillers (see Table 4.10). If the appearance of a new leaf is

Figure 4.6: Comparison of length of leaf growth period and rate of appearance of new leaves on *Deschampsia klossii*, Mt Wilhelm.

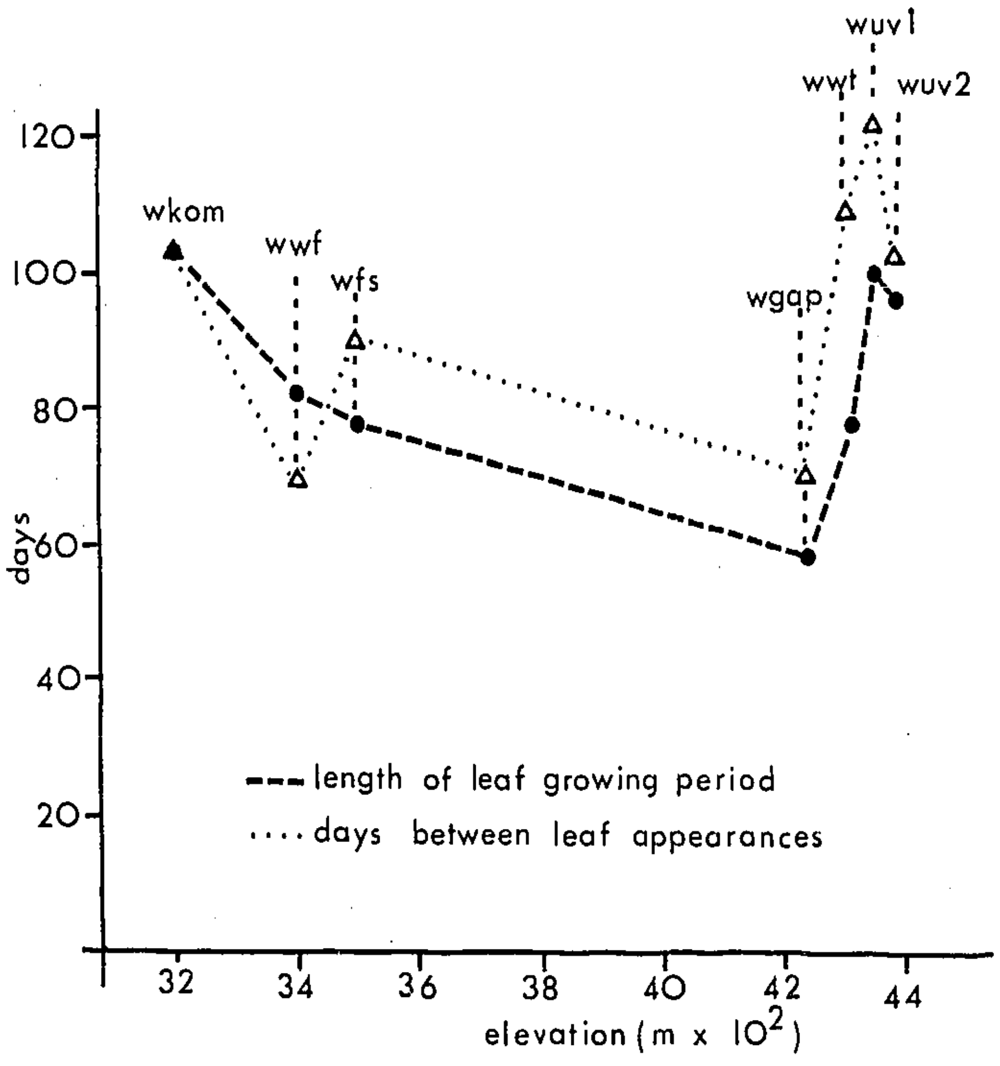


Figure 4.10. Leaf appearance in relation to die back of next oldest leaf, *Deschampsia klossii*, Mt Wilhelm.

Site	A	B	C	Sum	D
WKOM	33	9	2	44	$0.01 < p < 0.025$*
WWF	70	10	4	84	$p < 0.0001$**
WFS	33	17	4	54	$0.1 < p < 0.25$
WCAP	5	4	2	11	$0.75 < p < 0.9$
WWT	25	6	3	34	$0.01 < p < 0.025$*
WUV1	12	26	1	39	$0.1 < p < 0.25$
WUV2	17	15	4	36	$0.75 < p < 0.9$
Sums	195	87	20	302	$p < .0001$**

A: new leaf appeared before die back;
B: new leaf appeared after die back commenced;
C: new leaf and start of die back coincide;
D: probability of A and B being equal with C divided equally between them; chi-square test with 1 degree of freedom.

recorded as occurring before, after, or at the same time as three millimetres or more of die back is seen on the next older leaf (same criterion of cessation of growth as is used in the productivity study, Section d), it is found that 195/302 = 64.6% of the new leaves appeared before die-back started and only 28.8% after die-back started; for only 6.6% of observations did the two events coincide. If the 'ties' are equally distributed between the remaining two classes and a chi-square test of goodness of fit performed, it is seen that for a very significant ($p < 0.001$) number of times, new leaves appear before the next youngest leaf begins to die back ($\chi^2 = 19.3$, d.f. = 1). The timing of leaf initiation in the apex is not known nor is the relation of death of oldest leaf to appearance of new leaves.

If the leaf appearance and die back are examined for each site on Mt Wilhelm (Table 4.10), then sites WFS, WGAP, WUV1, and WUV2 are seen to show no significant differences between the rate of leaf appearance and the length of leaf growing period while the other three sites do show a significant difference between the times of these events (chi-squared tests, see Table 4.10).

With some sites showing and others lacking this relationship, it probably should be concluded that the rate of leaf appearance is only indirectly and not obligately correlated with the death of the next youngest leaf. More information will be needed before this situation is understood. Langer (1972), in discussing how grasses grow (pp 9-10), indicates that, while temperature is an important element in leaf appearance, the situation is complex and there is much variability between taxa.

f. Leaf weight - length relationship

The relationship of leaf weight to length may yield some information regarding the way in which the leaves grow, and hence permit further comparison of the tussock grasslands and their environments. To this end, a sample of eleven tussocks of *Deschampsia klossii* from Mt Wilhelm was collected in 1971 by J.M.B. Smith. The green leaves were divided into those with less than 3 mm of die back and those with 3 mm or more of apical die back. Each group was measured for length, subdivided into 10 cm length classes, then oven dried. The average weight per centimetre of length in each length class was determined. The graphs from these data are presented in Figure 4.7.

The trend in 'living' leaves is for weight/cm to decrease from the shortest leaves to the next one or more length classes. Presumably

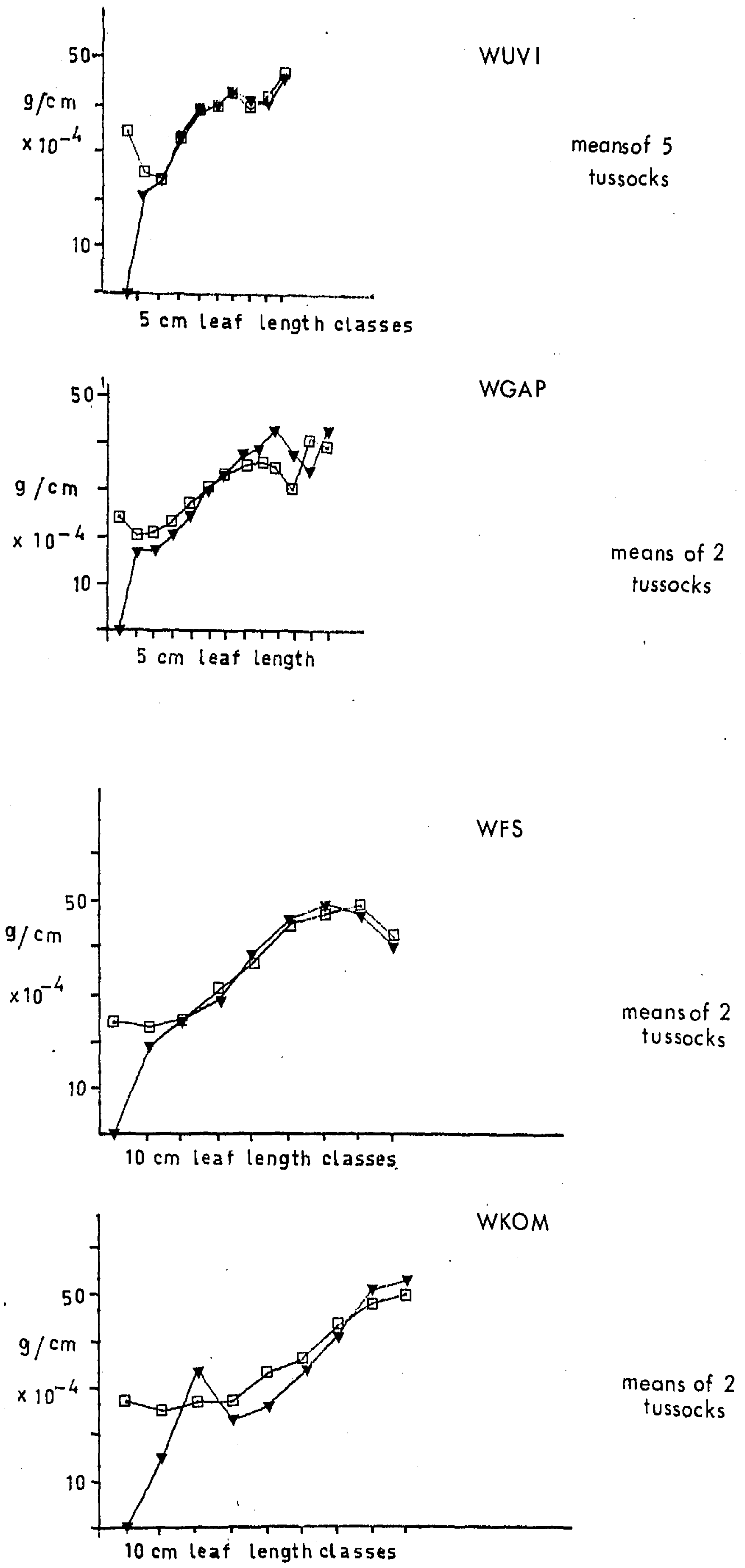


Figure 4.7. Weight (g) / cm of *Deschampsia klossii* leaves, Mt Wilhelm sites.

the drop in weight/cm is related to a rapid cell expansion phase of short leaves and the later increase in weight/cm to a period when expansion is completed or proportionately small and structural growth was predominant. Dying leaves showed very little evidence of lower weights/cm in the second and third length classes; this suggests that most leaves dying in the short leaf classes had completed expansion growth.

Data similar to those just noted were also collected in 1970. However, although chlorotic or brown leaves were rejected, the distinction between 'living' and 'dying' leaves was not made. These data are graphically presented in Figure 4.8. The low-weight, expansion phase is not evident, presumably because too few leaves of this type were present relative to non expanding leaves.

Leaf weight-length data for the sub-Antarctic sites are presented in Figure 4.8. Here leaves were divided into age classes based on position on the tiller from youngest to oldest. Only the green portion of leaves were measured and weighed (oven dry weight).

The most conspicuous aspect of the curves for *Poa foliosa* on Macquarie Island is the similarity of curves between sites for about the youngest two thirds of leaves on tillers. Weight/cm increases steadily and rapidly for all young leaves at all sites. Sites become differentiated on the oldest leaves. Sites of high wind exposure (MRB, MWE) and high altitude (MPB) have lighter old leaves than sites of low wind exposure and low to mid altitude (MGC and MWS). However, a two-way analysis of variance (Appendix 4.14) indicates no overall significant differences in weight/cm between sites ($0.05 < p < 0.$). No statistical test can be used to compare the weight/cm of the oldest leaf between sites. Understandably though, there are very significant differences of weight/cm between leaves of different ages ($p << 0.001$; *cf.* Figure 4.6).

A single tussock was sampled on Campbell Island (*Chionochloa antarctica*) in a manner similar to that for Macquarie Island and showed yet a third pattern of development. Weight/cm increased slowly at first, then more rapidly for older leaves. This pattern may result from the rather long period during which leaves of the *Chionochloa* remain enclosed in the sheaths and folded older leaves of tillers. As leaves gradually are exposed to full light, their weight increases.

It would thus seem that for tussock grasses in the equatorial high montane and the sub-Antarctic, leaf weight per unit length is genetically rather than environmentally controlled.

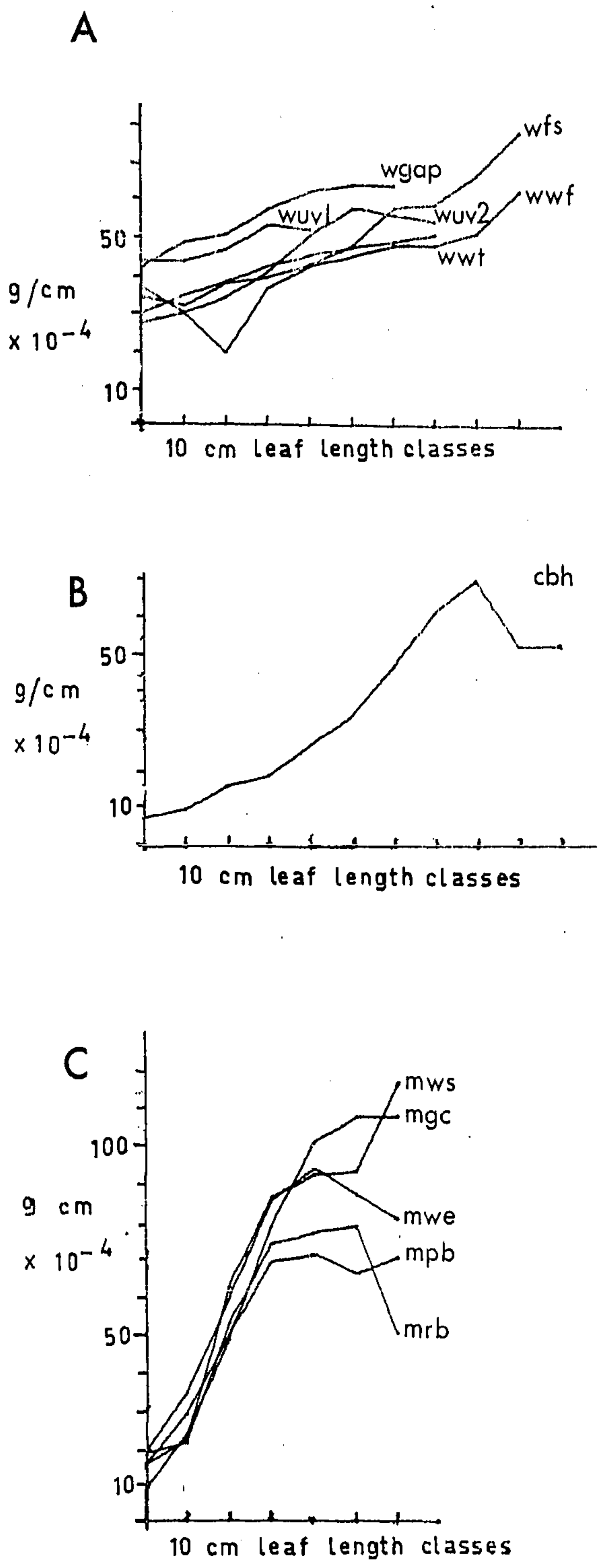


Figure 4.8. Weight (g) / cm of leaves of A: *Deschampsia klossii*, Mt Wilhelm sites; B: *Chionochloa antarctica*, Campbell Island site; and *Poa foliosa*, Macquarie Island sites;

D. PRODUCTIVITY

a. Introduction

In the preceding sections, information has been presented about the quantity and structure of living matter in tussock grasses. The spatial distribution of the aerial parts of the tussocks was examined in Section B to illustrate the types of adaptation to environment which these plants have developed. It is now intended to compare the rates of plant growth and associated efficiencies of energy utilization in the widely separated regions with which this study is concerned.

A selection of published productivity estimates for the sub-Antarctic, temperate alpine, arctic tundra, and a variety of other regions and vegetation types are shown in Table 4.11. It is clear that, of the communities in the list, the lowland tussock grassland of Macquarie Island (Jenkin, 1972) is the greatest annual producer of plant mass (3281 g/m^2/year). However, Lieth (1972) indicates that values up to 3500 g/m^2/year can be expected in rain forest communities and up to 4000 g/m^2/year in watery habitats.

Table 4.11: Published productivity estimates for sub-Antarctic, alpine, arctic, and other areas of the world.

Site	Vegetation type	Growing season (days)	g/m^2/day (growing season)	g/m^2/yr	Source
SUB-ANTARCTIC					
Macquarie Island (54°17'S)	*Poa foliosa* tussock grassland 45m	295	11.1	3281	Jenkin (1972)
	230m	295	3.2	949	"
	Pleurophyllum hookeri (herbfield) 9m	295	4.2	1248	"
	235m	295	1.7	489	"
South Georgia (54°17'S)	*Polytrichum alpestre* moss mat	*ca.* 80	5.9	468±22	Longton (1970)
Signy Island (65°15'S)	"	*ca.* 85	4.1	342	"
Galindez Island (Arg.)	"	*ca.* 53	7.6	403±25	"
South Georgia	*Pohlia wahlenbergia*	*ca.* 80	5.8-7.8	425-465	Clarke *et al.* (1971)

continued

Table 4.11 continued.

Site	Vegetation type	Growing season (days)	g/m^2/day (growing season)	g/m^2/yr	Source
South Georgia	*Tortula robusta*	*ca.* 80	*ca.* 2.0	*ca.* 160	Clarke *et al.* (1971)
NORTH TEMPERATE ALPINE					
Central Rocky Mts	Moist swales	?	.40-2.07	23.9-124.6	Anon. ex Bliss (1960)
	turf: slope and ridges	?	.19-1.12	11.2-67.6	"
Medicine Bow Mts Wyoming USA	wet *Carex-Deschampsia* meadow	60	1.87	112.4	Bliss (1956)
	cushion plants ridge	60	0.46	27.6	"
	Geum-Salix snowbank	56	0.65	36.2	"
	Sibbaldia-Carex Agrostis snowbank	56	2.30	128.5	"
Mt Washington, New Hampshire	*Carex bigelowii* meadow	64	3.24	208.1	Bliss (1960)
	rush-dwarf heath meadow	64	1.70	108.8	"
	rush-dwarf heath fellfield	64	1.25	80.1	"
Mountains of Wyoming	xeric tundra	?	1.2(min.)	61	Scott and Billings 1964 ex Jordan, 1971
	mesic tundra	?	11.1(max.)	464	
ARCTIC TUNDRA					
Cornwallis Island	*Salix* barren	60	0.05	3.0	Warren Wilson (1957)
Abisko Sweden	*Carex rostrata*	111	2.18	242.0	Pearsall and Newbould (1957)
Pt Barrow Alaska	*Dupontia fischeri*	60	3.16	190.0	Shank, ex Bliss (1960)
	Carex-Eriophorum marsh	60	2.37	142.6	"
Umiat Alaska	*Carex-Eriophorum*	70	0.85	59.7	Bliss (1956)

continued

Table 4.11 continued.

Site	Vegetation type	Growing season (days)	$g/m^2/day$ (growing season)	$g/m^2/yr$	Source
Labrador	Lichen woodland	?	?	10-22	Hustich (1951)
Yamal USSR	Lichen heath	?	?	40	ex Bliss (1960)
OTHER AREAS					
Minnesota	*Quercus* (closed)	?	?	7.3	Bray (1960)
Central	grassland (mature)	?	?	3.1	"
	Zea mays	?	?	8.8	"
	Soja max	?	?	1.6	"
	Typha (marsh)	?	?	13.6	"
	Nymphaea (pond)	?	?	1.1	"
equatorial regions	forests	365	2.9	1090	ex Jordan (1971)
warm temp. regions	forests	?	?	550	"
arctic-alpine	forests	?	?	100	"
subalpine	forests	?	?	350	"
Europe	gymnosperm forests	?	?	1320	"
	angiosperm forests	?	?	1050	"
Thailand	tropical rainforest mature	365?	8.15	2980	Kira *et al.* (1967)
Peurto Rico	tropical rainforest mature?	365	1.3	486	Jordan (1971)
Arizona	*Larrea tridentata* (desert scrub)	214	0.65	140	Chew and Chew (1965)

Annual net production of plant mass is only one way of expressing productivity. If mean net production per day, averaged over the growing season, is calculated the Thailand rainforest (Kira *et al.* 1967; 8.15 $g/m^2/day$) is seen to be only slightly above the daily production (7.8 $g/m^2/day$) of a bryophyte community in the sub-Antarctic (Clarke *et al.* 1971). Whereas the rainforest produces a net gain of 6.4 times more mass per year than the bryophyte community in South Georgia, it does so only

1.04 times faster on a daily basis, than the moss community. Alternatively, if the moss community grew for 365 days it would produce 96% of the net annual increment of the Thai forest. It thus appears that length of growing season is an important factor in controlling annual production of plants in favourable habitats in very different parts of the world.

b. Tussock aerial productivity

Net aerial productivity estimates (excluding stems which are thought to be 10% or less of aerial plant mass) for the tussock populations at the twelve sites studied are given in Table 4.12. The details of calculation are given in Appendix 4.4. The average daily growth rates range from a low of 0.35 g/m^2 at 3400 m on Mt Wilhelm, to 10.88 g/m^2 at 60 m on Macquarie Island. Only the Mt Wilhelm and Campbell rates fall in the range (0.5 to 5.0 g/m^2/day over the growing season) quoted by Bliss (1966) for temperate alpine communities (see also Table 4.11). It is not possible to estimate the variance of the productivity values in Table 4.12, so no statistical comparisons between sites can be made (Professor P.A.P. Moran, Dept. of Statistics, Australian National University, personal communication). However, from inspection of the data in Table 4.12 it can be seen that there is a distinct difference between the average rates of aerial net production determined for the New Guinea high mountain tussocks and those for the sub-Antarctic tussock grasses; the latter are 3.4 to 31.1 times higher than the former.

Table 4.12: Tussock productivity (g/m^2/day) at Campbell Island, Macquarie Island and Mt Wilhelm sites.

Site	Mean
CBH	4.12
MGC	7.79
MWE	6.62
MWS	10.88
MRB	10.26
MPB	9.70
WWF	0.35
WFS	0.69
WGAP	0.77
WWT	0.87
WUV1	0.71
WUV2	1.21

On Mt Wilhelm, tussock productivity tended to be higher at the higher altitude sites than at the lower ones. The differences between sites might be accounted for by local factors which promote or inhibit growth. It is interesting to note that *Deschampsia klossii*, in spite of having a lesser above ground productivity in a pyric-disclimax community at low altitudes than in a climatic climax community at high altitudes, has spread extensively on Mt Wilhelm to occupy large areas of burned land. In view of its lack of one of the major attributes, namely rapid growth (Smith, 1974), found in most invasive or alien plants, this spread is perhaps surprising. Mark (1965) found the high altitude form of *Chionochloa rigida* to grow faster but for a shorter length of time than did the low altitude populations.

At Macquarie Island, the variation in tussock productivity between sites is difficult to interpret but may be related to wind and aspect. Near sea level, the very wind exposed but northerly facing MRB site had a greater rate of production than the sheltered southerly facing MGC site. The MWE and MWS sites were both southerly facing and at mid altitudes (60m) but the latter had the higher rate and low wind exposure while the former had the lower rate and high wind exposure. Site MPB was at high altitude (222 m), had low wind exposure, was northerly facing, and had an intermediate production rate.

Before comparing Jenkin's (1972) and my productivity estimates for Macquarie Island, it is necessary to consider the 'growing season' for tussock grasses there and in the equatorial high montane region. To begin with, a clear definition of growing season is required. I shall use the following: growing season is the period of the year over which plants accumulate mass through photosynthesis. Potential growing season is the growing season estimated from a knowledge of the occurrence and duration of growth limiting environmental factors (*e.g.* frost, short days). Actual growing season is the growing season determined from observation of the cessation and rejuvenation of growth in plants.

'Growth' is taken to mean the positive net production of a plant over a period of time. Difficulties arise in using this definition because it is often impossible to determine when a plant is growing, especially if most 'growth' is manifest only in subterranean organs, or takes the form of storage of high energy matter rather than cell increase, or is at a very low level. Furthermore, the time period under consideration is important. For example, a plant may accumulate mass during the day in the form of sugar or starch from photosynthesis, but by sunrise the next day have respired the previous day's gains. Thus, over the period when photosynthesis can occur, there is a net gain in plant mass (*i.e.* growth), but over a 24 hour cycle there is no net gain. Can it be said then that no growth has occurred?

Very careful attention to the meaning of growing season is fundamental to its study in regions where climatic extremes are few or absent. Transference of ideas developed under very different climatic conditions can be misleading.

Jenkin (1972) has attempted to determine the growing season of plants on Macquarie Island. For *Poa foliosa* his calculations are based upon changes in estimates of above ground plant mass from harvesting new metre square quadrats at approximately 10-weekly intervals. From this analysis he concludes that, at his 45 m site (M1), the growing season of *Poa foliosa* is about 10 months: June to April. He notes that the data on plant mass at the M1 site is very variable. The period April-June during which 'no growth' apparently occurs represents one sample interval, between the start and end of which there are no significant differences (least significant difference test, $p = 0.05$) in plant mass. In fact, from his data it appears that at $p = 0.05$ only the December (HI) and January (H VII) means are significantly different from one another (using his least significant difference information), and at $p = 0.1$ the December harvest is only different from the October and January harvests. He has shown production of green leaf mass to reach a peak between March and April (Jenkin's Figure 3:4) at a time when living root mass might have been minimal (Jenkin's Figure 3:1). Root mass appears to increase through the winter until at least August when the last sample was taken. Although root mass data are acknowledged to be very variable, Jenkin does note that root development has been shown to follow leaf development in many Festucoid grasses (Evans *et al.* 1964, p.110-111). If this is the case with *P. foliosa* on Macquarie Island, we have the situation where leaf growth that is active for 10 months, peaks in the month that marks the beginning of the 'no growth' period and presumably is followed by the period of most active root development.

It would appear therefore that we do not have the necessary information to define a growing season for Macquarie Island grasslands. What we do know is that the season is long and that *Poa* grassland at 45 m altitude changes its total living mass but little on a seasonal basis. It is not beyond possibility that the growing season essentially spans the entire year, hesitating only during short, irregular occurrences of freezing temperatures.

For the high montane New Guinea tussock grasslands, there is even less information than for the sub-Antarctic Islands. We have the observations of several people that the equatorial high mountain tussock grasses look the same yellow-brown colour at all months of the year, which simply indicates that neither massive die back nor flush growth occurs. There are no obvious environmental factors which would limit growth, and flowering in *D. klossii* can occur almost anytime of the year, albeit predominately in the drier months (P.J. van Royen, personal communication). Whether an endogenous rhythmn is present will only be known if detailed study is done.

Comparison of my productivity estimates for Macquarie Island with those of Jenkin (1972) reveals both similarities and differences. It must be remembered that, whereas my data are for the mid summer months (therefore probably near maximal values) and based on a non-destructive sampling method, Jenkin's data (his Table 3:12, p.128) are average values for the entire year 'corrected to 365 days' and based on changes in biomass between successive harvests. His M1 site production rate of 8.99 g/m^2/day (for 365 days or 11.12 g/m^2/day over 295 day growing season) is not very dissimilar from the 10.26 g/m^2/day for my nearby MRB site. However, his M2 site value of 2.60 g/m^2/day (for 365 days or 3.22 g/m^2/day for 295 day growing season) is much lower than the 9.70 g/m^2/day value determined for my nearby MPB site (both at high altitude). These differences could be random chance variation, they could reflect intrinsic differences between sites despite their close proximity, they could result from the different methods used to collect the data, or any combination of these possible sources of variability.

That the differences are not consistent argues against their methodological origins. Jenkin's figures are annual averages whereas mine are near the seasonal maxima (December to January average). Thus his lowland annual value of 8.99 g/m^2/day is 88% of my lowland (MRB) site (10.26 g/m^2/day) while his highland annual value of 2.60 g/m^2/day is only 27% of my upland (MPB) site (9.70 g/m^2/day). His upland annual rate is 29% of his lowland whereas my upland value (MPB) is 95% of my lowland (MRB) value.

Jenkin (1972, p.51) presents climatic data indicating a more severe climate at the upland than lowland sites on Macquarie Island. At 235 m altitude snow falls are more common, last longer, and irradiance is lower due to more cloud cover than at 6 m altitude. That my upland and lowland mid summer production rates are similar indicates that differences between sites are minimal at this time of year (*i.e.* temperature and light are either not limiting or are equally limiting for all sites.) That my mid summer rates are similar to Jenkin's lowland values but very different from his upland values may indicate that the lowland rates change very little during the year but the upland rates vary a lot. A possible climatic cause may be found in the greater frequency and greater duration of freezing temperatures at upland than at lowland sites based on the observation of snow lie and freezing temperatures.

The relative contributions of leaves in different length classes to tussock production (aerial, excluding stems) is shown in Appendix 4.4 where the g/m^2/day/leaf class is expressed as a % of the total g/m^2/day. Leaves of intermediate length appear to contribute one half or more to the total leaf production, while short and long leaves, which are largely the youngest and oldest leaves respectively, make up less than half of the production. Because of the method of calculation used for Macquarie Island tussocks, it can be seen that the flush of growth of *Poa foliosa* during December and January made up 35-47% of the total production measured over that period. Such a flush of growth was not found in Mt Wilhelm tussocks during 7 months of observations. Nothing can be said in this regard for Campbell Island tussocks as they were observed for only 6 weeks.

c. Efficiency of aerial production

At least since the time when Lindeman (1942) focused attention on trophic dynamics of ecosystems, great effort has been spent in trying to express interrelationships of organisms and their environment in terms of energy exchange.

The estimated values for efficiency of short-term, aerial primary production for tussock grasslands in equatorial high montane and sub-Antarctic are given in Table 4.13. These are crude estimates because of the short term over which data were collected; nevertheless they should be comparable between sites. Moreover, for Macquarie Island my estimates are similar to those of Jenkin (1972).

The sub-Antarctic sites are strongly contrasted with the equatorial ones (MWS = 2.5%, WFS = 0.2%). Tussocks from the southern islands are about 10 or more times as efficient than those from the equatorial montane in their conversion of solar energy into plant mass. When Jenkin (1972, p.116) includes all above and below ground production, an efficiency of 4.45% is estimated. This is a high figure compared with many from other natural communities. Thus, Bliss (1962) reports 0.09% annual efficiency for alpine *Carex* meadow on Mt Washington, Bray *et al.* (1959) report 0.04 to 0.53% for some herbaceous communities in Minnesota, and Bliss and Mark (1974) report a low net aerial efficiency of 0.18 to 0.35% and root plus shoot

Table 4.13: Efficiency of aerial production at Mt Wilhelm, Macquarie Island, and Campbell Island.

1.	2.	3.	4.	5.
Site	cal/cm^2/day (leaves)	cal/cm^2/day (0.28-3.0)	cal/cm^2/day (0.4-0.7)a	% efficiency
WFS	0.323	389.2	175	0.185
WUV2	0.566	(")	(")	0.323
MWE	2.951	405	190	1.553
MWS	4.849	"	"	2.552
CBH	1.985	335.2	135	1.471

a. For WFS, WUV2, and CBH sites, column 4 values equal 45% of column 3 values, based upon data taken from Figure 3, Gates (1962). For Macquarie Island sites column 4 equals 47% of column 3 based on data from Jordan (1971). These percentages were chosen because the instruments used at Macquarie Island were similar to those used by Jordan, while at the other sites different instruments were used. The data of Gates were the only source of data on the proportion of photosynthetically active radiation for the instruments used.

efficiency of 0.46 to 0.79% for alpine communities in New Zealand. The sub-Antarctic tussock grasslands are at least as efficient in their utilization of solar energy as the sugar cane (1.43%) reported by Westlake (1963). In a survey of world vegetation, Jordan (1971) notes six out of thirty nine plant communities with a 'growing season' efficiency of greater than 1% and only four of these with an annual efficiency of greater than 1%. The six communities are (annual, then growing season efficiencies) annual herbs 1.77, 3.08 (New Jersey); maize 1.11, 2.91 (Minnesota); old field, swale 1.07, 1.31 (Michigan); mature tropical rainforest 1.15, 1.15 (Thailand); ragweed 0.85, 1.42 (Oklahoma); and broadleaf evergreen forest 0.78, 1.44 (Japan). The values I reported for *Poa* on Macquarie Island are for less than the growing season and could thus be expected to be higher than estimates over longer periods. However, that Jenkin's (1972) annual estimates are in the 2 to 4% range strongly suggests that *Poa foliosa* is a very efficient user of energy.

E. CARBOHYDRATES

a. INTRODUCTION

Intermittent attention has been paid to the subject of carbohydrate content of plants growing in cool climates and, in particular, at arctic and temperate alpine sites (Russell, 1940, 1948; McCarty and Price, 1942; Mooney and Billings, 1960, 1961, 1965; Fonda and Bliss, 1965; Bornkamm, 1970; and others). The primary objective of most of these studies has been to determine the way in which plants have adapted to growing in environments made severe for them by low or high light intensity, low temperature, and a short growing season. The common features of plant adaptation to such environments are a perennial habit and relatively large energy reserves in the perennating organs (*e.g.* roots, rhizomes, leaf or culm bases, stems, evergreen leaves). The annual cycle of carbohydrate production and utilization is characterized by the depletion of last year's reserves during rapid growth in spring, followed by replenishment throughout the rest of the growing season. To date, most studies have been done on plants which have a sudden burst of growth in spring. Little attention has, however, been given to plants which develop later in the season, although Mooney and Billings (1960) suggest that they may depend more upon current production for growth than do the early growing plants.

Russell (1948) speculates about the relationship to frost resistance (using the findings of Levitt, 1941 and Anderson, 1944) of the high proportion of soluble carbohydrates to starch, which he found in his Jan Mayen Island studies. He (1940) refers to the work of Hopkins (1924) which demonstrates that starch is hydrolyzed to sugar in potato tubers at temperatures of 4.5°C or less. As the mean summer temperature on Jan Mayen is 1.5°C, the high sugar levels may thus be accounted for. Russell's (1940) speculation that the same species (*Oxyria digyna*), when growing in warmer climates, may have relatively higher starch to sugar proportions was borne out by his own work in the Karakorum Mountains (1948) and by Mooney and Billings' (1961) work in the Medicine Bowl Mountains of Wyoming.

Carbohydrate analyses for starch and total sugars were done in the present study of tussock grass productivity in order to learn how these plants function under the unusual conditions of a long growing season in a cool climate. The Mt Wilhelm samples, which consisted of roots, leaf-bases, green leaves, culms and inflorescences, were collected at irregular intervals over a six month period, April-October, 1970. At each sampling time, a new tussock was used in order to eliminate changes in physiology which might be caused by the sampling procedure. Most samples were collected in the early morning (0730 - 0830 hr). A further series of three samples was collected during daylight hours one foggy day and two samples (early morning and midday) on a clear day in order to gauge the magnitude of diurnal change under different weather conditions. All samples, except culms and inflorescences, were collected from single, non-flowering tussocks (except for the 0915 hr sample on 3rd May 1970). Each sample consisted of several tillers in order to reduce between-tiller variation. Because of the small numbers available, three culms and three inflorescences were collected from different tussocks. A *Deschampsia* tussock at 4350m (WUV1) was sampled at 1500 hr on a cold, cloudy day (20/6/70). Root starch and sugar levels were comparable with the series from 3510 m (*ca.* 2.1% starch and 3.1% sugar). A similar lack of distinction for other organs was found between the two sites and no further mention will be made of the WUV1 data.

The Macquarie Island samples were collected from each of the five study sites and from another site near sea level. The latter site (LAB) was sampled at 1000 hr each day of the sampling period (11/1/72 to 15/1/72) in order to gauge the variation present at one site from day to day. All samples were collected during the first two weeks of January. Diurnal variation in sugar and starch content were measured over a 24-hour period at the LAB site. The weather during that time was dominated by strong winds, rain, and mist which, during the daylight hours, reduced the light intensity to about one third of the daily average for January. The samples from the five study sites and the 1000 hr LAB samples consisted of several tillers from one tussock at each site. Samples for the diurnal variation study were each composed of five tillers taken from one or other of the two tussocks selected for this study.

The Campbell Island samples were collected at 0900 hr and consisted of several tillers from one tussock. As they were collected in late February and early March, 1971, they may have contained levels of carbohydrate characteristic of the peak of summer growth. Both *Chionochloa antarctica* and *Poa littorosa* were included in these studies because of their differing roles in the vegetation before and after the introduction of grazing animals.

b. Roots

The roots of the *Deschampsia* are very abundant in the tussock pedestal and nearby soil. Each consists of a central vascular strand surrounded by large cortical cells that were devoid of starch grains in the sections examined microscopically. The average level of starches was determined as 2.24 ± 1.04% (standard deviation of mean) for all samples. The average sugar levels were 4.24 ± 1.93%. A nested analysis of variance of sugar levels in roots (Appendix 4.5) indicated no significant difference between sampling times ($0.1 < p < 0.25$) but highly significant difference between duplicate samples taken at one time ($0.0001 < p < 0.001$). An analysis of variance of starch levels (Appendix 4.5) showed no significant differences with time ($0.05 < p < 0.10$).

Mid summer root carbohydrates in *Poa foliosa* on Macquarie Island are generally low in comparison with levels found in Mt Wilhelm *Deschampsia* roots. With the exception of one site (MWS), mean sugar levels were below 1% in *Poa* and, with the exception of MWE site, mean starch levels were also below 1%. A nested analysis of variance of sugars (Appendix 4.6) indicated very significant differences between sites ($p < 0.005$) and no significant differences between samples ($0.10 < p < 0.25$). An SNK multiple range test (Zar, p.151, 1974) indicated that all but the MWS site sugar levels were similar ($0.005 < p < 0.01$).

Jenkin (1972, p.226) reports total carbohydrate values for *Poa foliosa* from Macquarie Island. For 3 December he gives 13.0% of dry weight and for 19 March 7.5% of dry weight for roots. The maximum total carbohydrates I measured (21 January) was about 4.41% at MWS, the remaining sites had values of 0.96 to 1.95% total carbohydrates in the roots. As Jenkin oven dried his samples before analysis, considerable changes in chemical composition probably took place as the plants warmed up before dying. Jenkin (p.207, 1972) notes that alcohol extracts of fresh material were also collected but, because analysis of these showed 'marked and, to date, unaccountable variation', he abandoned this analysis and did not present the results.

The Campbell Island tussocks sampled yielded root sugar levels of 2.0% for both *Poa littorosa* and *Chionochloa antarctica*, and 7.6% starch for *Poa* and 5.1% starch for the *Chionochloa* roots (Appendix 4.7). The Campbell Island roots had much greater quantities of starch than either Mt Wilhelm or Macquarie roots, but sugars were intermediate between those of the latter two sites.

c. Green leaves

The analysis for carbohydrates in green *Deschampsia* leaves produced the following results. 1) A nested analysis of variance of the sugar data (Appendix 4.8) indicated very significant differences due to time of sampling ($0.001 < p < 0.005$; extreme mean % = 2.48 and 10.94) as well as between duplicates at one time ($p < 0.0001$). 2) An analysis of variance of starch data (Appendix 4.8) indicated significant differences due to time of sampling ($p < 0.001$; extreme mean % = 0.82 and 2.41). The use of a Mann-Whitney U test (Zar, p.109, 1974) proved unsuccessful in separating (5% level) variation due to time into time of day or time of year for both sugars and starches (see section 3 below on leaf bases for technique). An SNK multiple range test of sugars (Zar, p.152, 1974) indicates ambiguity in the data and suggests the need for more samples.

The large differences between samples complicates the search for relationships between time and carbohydrate levels. The large inter-sample differences could be the result of a combination of factors, such as variation in amount of light received by individual leaves and variation in vigour (related to age?) of individual leaves, although through the use of composite samples it was hoped to minimise such differences.

The carbohydrate analysis of *Poa foliosa* from Macquarie Island (nested analysis of variance, Appendix 4.9) indicated that there were no significant differences in sugar levels between sites ($p > 0.25$; overall mean % = 0.75) but there were very significant differences between duplicate samples ($p << 0.005$). No significant differences were found between sites for starches. The analysis of diurnal changes in sugars indicated very significant differences between times of sampling. No similar analysis is possible for starches.

Green, Campbell Island, tussock leaves had sugar levels of about 2.0 to 2.5% (Appendix 4.7), which are similar to the lowest values found on Mt Wilhelm and roughly twice those found on Macquarie Island. Starch levels in both species on Campbell Island were higher (*Chionochloa* 3.4%, *Poa* 1.4%) than in the *Poa* on Macquarie, and *Chionochloa* had the highest level (3.4%) of any of the tussock leaves sampled.

d. Leaf bases

Deschampsia leaf bases on Mt Wilhelm show a mean sugar level of 17.3 ± 7.4% compared with less than 5% for most other organs. Starch levels in the sheaths were high (2.5 ± 1.1%) but not as conspicuously so as were sugars. An analysis of variance of starch levels in sheaths (Appendix 4.10) indicated very significant differences due to time ($0.002 <$

$p < 0.005$; extreme range of mean % = 1.42 to 4.96). A similar analysis of sugar data from sheaths (Appendix 4.10) indicated very significant differences due to time ($0.001 < p < 0.002$; extreme range of mean % = 5.44 to 25.75) as well as between duplicate samples ($p < 0.0001$). The highly significant differences between duplicate samples makes analysis of the time variation difficult, as it did with the green leaves. It is therefore not possible to examine the data for a correlation in sugar levels between samples of green leaves and sheaths.

An attempt to segregate the time of day variable from the time of year variable was made by using a Mann-Whitney test (Snedecor and Cochrane, p.130, 1967). This non-parametric test was chosen despite its relatively low sensitivity because samples were very small and therefore not certainly normally distributed.

To test for the effects of time of day, the data were divided into two groups without regard for time of year: a) samples collected over the period of rising air temperature (0730 hrs to 0915 hrs), and b) samples collected during the period of usually stable temperature (1100 hrs to 1645 hrs). A two-tailed test of the null hypothesis that the sugar levels were the same in both groups was rejected at $p = 0.0022$. Stated otherwise, there is a highly significant difference in sugar levels between the two groups. Figure 4.9 indicates this diurnal trend in sugar level and shows that levels are higher during the middle of the day than in the early morning.

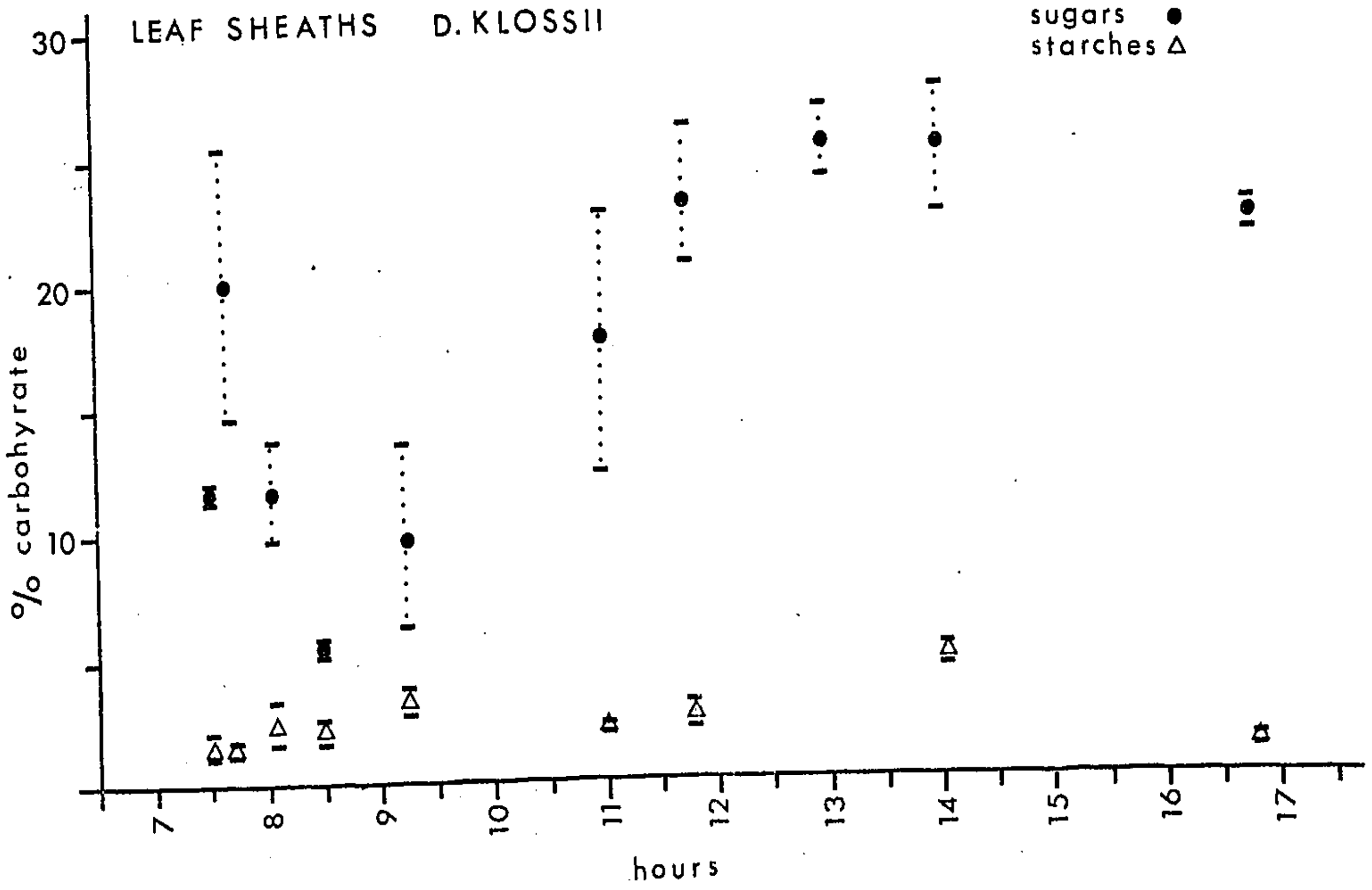


Figure 4.9: Diurnal variation in sugar and starch content of *D. klossii*, 3500 m, Mt Wilhelm, 1970. (Ranges are ± 1 standard deviation of the mean.)

To test for differences due to time of year the following procedure was used. As most data from different months came from samples collected in the morning, and as significant variation due to time of day was found, only samples collected before 1000 hrs were used. These were divided into two groups called a) dry season (June, July, August samples) and b) transition season (April, May, October). The null hypothesis that sugar levels in sheaths were the same during the two periods is accepted by the Mann-Whitney test ($p > 0.2$).

The Mann-Whitney test and the same criteria of grouping as used for sugars were applied to leaf base starch levels. No significant difference was found between times of year ($p = 0.147$; overall mean % = 2.45). The effect of time of day was not tested because samples were too few.

On Macquarie Island, I found very significant differences ($p << 0.005$) between sites (extreme range of mean % = 1.210 to 3.060) and no significant differences ($p > 0.25$) between duplicate samples of sugars in the leaf sheaths of *Poa foliosa* (Appendix 4.11). For starch levels there were significant differences between sites ($0.02 < p < 0.05$; overall mean % = 1.06)

Poa littorosa on Campbell Island had about 3.8% sugar and 1.3% starch in its leaf sheaths (Appendix 4.7). *Chionochloa* had 6.8% sugar and 3.6% starch. The Campbell Island tussocks thus appear to have more sugar than Macquarie Island tussocks, about equal levels of starch, but only ½ - 1/3 as much sugar as the Mt Wilhelm tussocks.

A series of samples was collected from leaves and sheaths of *Poa foliosa* on Macquarie Island at about 3-hourly intervals over a 24 hour period (Appendices 4.8 and 4.10). Heavy overcast conditions throughout the day probably reduced the photosynthetic rates of the grass, which, together with the high intersample variation, prevented the detection of diurnal patterns. The great differences in carbohydrate levels from one time to the next are not explicable in relation to time of day and probably relate to large inter sample differences.

e. Dead attached leaves

Analysis of sugars of dead, attached, standing leaves of *Deschampsia klossii* indicated no significant differences due to time ($0.5 < p < 0.75$; overall mean % = 0.174) but very significant differences between duplicate samples ($0.001 < p < 0.005$)(Appendix 4.12). For starches in dead leaves very significant differences were found between different sampling times ($p < 0.0001$); extreme range of mean % = 0.95 to 4.11). A Mann-Whitney test similar to that used with leaf sheaths for time of day showed a significant difference ($0.01 < p < 0.05$) between starch levels at different times of day, but the sample was considered too small to test for seasonal differences.

f. Stems

Carbohydrate analyses of stems were done only for plants from sub-Antarctic sites. On Macquarie Island significant differences were found between sites for starches ($0.02 < p < 0.05$) but not for sugars ($p > 0.25$; mean % starch = 0.85, and sugar = 0.65; Appendix 4.13). Very significant differences were found between sugar samples ($p < 0.005$); starches could not be so tested. On Campbell Island the two species of tussocks had 6-7 times more sugar in their stems (Appendix 4.7) than did *Poa foliosa* on Macquarie. The starch level of the stems of *Chionochloa* and *Poa foliosa* were similarly low (less than 1%) while *Poa littorosa* had 5.1% starch content in its stems.

g. Summary of Carbohydrate Results

Leaf sheaths were found generally to be the main site of sugar storage. No data on seasonal trends in carbohydrate levels in various parts of the tussock grasses are available for the sub-Antarctic (Jenkin, 1972, generally discounts his data because of variability). What is available from the montane grassland of Mt Wilhelm indicates no significant seasonal trends, although not providing absolute proof. Diurnal variation is very likely to occur because of the diurnal cycle of photosynthetic activity. On Mt Wilhelm, some evidence of this cycle was found, particularly in the leaf sheaths. If the sheaths are the main sites of carbohydrate storage and respond substantially to daily cycles of production and utilization, the amount of energy stored in the sheaths may be small compared with the daily amounts produced in the leaves. If this were so, it is possible that there would be no seasonal build-up of reserve energy for use either over a dormant period or for flush growth.

An experiment in which *Deschampsia* tussocks were clipped close to but above their growing points indicated that, while some tillers survive and produce new leaves (generally short, flat leaves and not the long involute normal ones), most tillers die. This tends to indicate that no general supply of carbohydrates is available for massive regrowth following defoliation. That the tussocks survive burning however, is indicative of their capacity to withstand some degree of defoliation and firing, at least relative to that of other species in the area.

Inter-duplicate variation in carbohydrate content was found to be high from collections in both the equatorial montane and sub-Antarctic tussock grasses. This variation was much higher than expected and considerably weakened the analysis. That there was no significant inter-sample differences in sugars in either roots (which had generally low levels) or leaf sheaths (which had high levels) of *Deschampsia klossii* suggests that methodological errors are an unlikely source of the large differences in the other samples. Therefore large scale heterogeneity of carbohydrate content appears to be characteristic of the living parts of the tussock species studied. The causes of this variability are not known and it has not been noted in other carbohydrate studies (*e.g.* Fonda and Bliss, 1966) done on arctic and alpine plants. If one looks to growth and development processes in tropical plants living in largely aseasonal climates rather than to processes known from plants growing under conditions of strong seasonality, a possible explanation is found for the high variability in carbohydrates in tussock grasses. Huxley and van Eck (1974) present growth and development data for 31 woody species growing near the equator in Uganda. These authors show that the growth events may vary from species to species, from individual to individual within a species, and even between branches of one individual when all are growing at the same essentially uniform site. They attribute such variation to endogenous factors that are at least somewhat influenced by climatic factors. The balance for any one plant or part of a plant may depend on the relative strength of exogenous and endogenous factors. Thus, for the tussock grasses in largely aseasonal climates, growth may be commencing, continuing, and ceasing for some members of the population at any given moment so that small samples taken from the population give very different results from one another. Any future sampling of these organisms must take this variability into account, although it is difficult to judge the state of growth or quiescence of a particular organ in tussock grasses.

In contrasting the high montane tropical tussocks with those of the sub-Antarctic, no clear distinction between regions is found on the basis of carbohydrate content; rather, species differences appear to dominate over regional ones.

It is interesting to speculate on the implications of differences in carbohydrate levels in the different organs of the two species of Campbell Island tussock grasses studied. The leaves, and particularly the leaf sheaths, of *Chionochloa antarctica* are much richer in carbohydrates than are the leaves and leaf sheaths of *Poa littorosa*. By contrast, the carbohydrate content of the stems and roots of the two species are the reverse of that of the aerial parts. Hence, when *Chionochloa* tussocks (or tillers) are grazed to a low level, there is much less carbohydrate reserve energy available to support the replenishment of lost photosynthetic surface than in grazed *Poa*.

When the history of these two species is viewed over the past 80 years one finds that, before sheep grazing began in 1895, *Chionochloa* was the dominant tussock of the middle altitudes and uplands and *Poa* was confined to the lowlands (Cockayne 1903). With sheep grazing, *Chionochloa*, which was more palatable to sheep, soon became confined to rocky, inaccessible steeps while *Poa*, which was less preferred by the sheep, spread widely.

In 1970, a large *Chionochloa* tussock clipped close to ground level but above tiller growing point, showed little regrowth after four weeks. Only 125/725 tillers in the tussock showed any signs of life after four weeks and regrowth was only 2-3 cm and very chlorotic. Mr D. Merton (personal communication) of the New Zealand Wildlife Service observed similar results on *Chionochloa* tussocks cut at Moubray Hill on Campbell Island during the same period as my own observation. In addition, he observed re-growth amounting to 20 cm of leaf on nearly all tillers of *Poa littorosa* tussocks at the same time in the same area. All leaves had been cut off the tussocks 18 days before the observations.

The rapid disappearance of *Chionochloa* and the spread of *Poa* under grazing could be closely linked with their respective carbohydrate storage patterns.

In this chapter, many aspects of the structure and growth of tussock grasses in the equatorial high montane and sub-Antarctic regions have been presented. An integration of this information will be found in the next chapter.

Several differences have been found in the growth of tussocks in the two regions under study. Standing crop and net above ground productivity are much greater in the sub-Antarctic than in the equatorial montane tussock grasslands but shoot:root ratios are less. Soils appear to be more fertile at the southern sites than at the equatorial ones. Efficiency of aerial production of tussocks is much higher on Macquarie Island than on Mt Wilhelm. In fact, the Macquarie Island efficiencies may be among the highest in the world for natural vegetation. Some tussock structural characteristics (height, cover, and leaf area index) indicate similarity between the regions perhaps because they are part of the quantitative physiognomic similarities which initially related these areas only subjectively. Leaf weight/length relationships and carbohydrate levels appear to be more strongly influenced by genetic composition of the plants than by environmental factors. However, great variation in carbohydrate content of duplicate samples and the irregular progress of leaf death, as well as of growth (leaf extension), tend to indicate a condition of asynchronous activity amongst individuals or parts of individuals that make up the tussock populations.

CHAPTER 5

INTEGRATION AND CONCLUSIONS

The present study began with the observation of the occurrence of similar tussock grass dominated vegetation in the remote and separate regions of the equatorial high montane and the sub-Antarctic. In the tradition of Humboldt, the father of empirical geography (Botting, 1973, p.40), I have gathered first hand observations and facts which will now be brought together to indicate some of the basic points of similarity and difference in these cool-climate tussock grasslands.

The apparent convergence of vegetation types with increasing altitude on the one hand and increasing latitude on the other is paralleled climatically in both cases by a decrease in mean temperature. In simplest terms, this similarity of vegetation in the two regions is seen as a result of the progression from forest to non-forest vegetation, with increasing altitude on Mt Wilhelm and with increasing latitude on the chain of islands: Snares, Auckland, Campbell, and Macquarie. The non-forest vegetation would be called tundra or alpine in the seasonally cold environments (*e.g.* the European Alps, the Rocky Mountains, the Arctic, and the New Zealand Alps) but in the seasonally isothermal regions (*e.g.* equatorial high montane and sub-Antarctic islands), where no severe climatic factor forces plants into dormancy, no widely accepted name is available.

The temperature change paralleling the forest to non-forest sequence in these regions is always from warmer to cooler. With increasing altitude the rarified atmosphere provides lessened insulation against radiation loss and air temperatures decrease; with increasing latitude, air temperatures decrease because of a) a reduction in radiation received due to the dissipation of the solar beam during its longer passage through the atmosphere, and b) its geographic dispersion due to the reduced angle of incidence at the earth's surface. The progression of thermal seasons is almost absent in equatorial regions, whatever the altitude; for example, daylength varies by less than one hour annually at Mt Wilhelm (Forsythe, 1954). With increasing latitude, seasons usually become increasingly more evident and at 50^{o}S latitude, daylength varies by more than eight hours during the year (*ibid*). However, the expected large differences in thermal seasonality are not found in the sub-Antarctic because the presence of almost continuous cloud cover moderates both irradiation and radiation loss. Additionally, the vast expanse of ocean, in relation to the small area of of the sub-Antarctic islands, has a strong ameliorating effect on the climate. Thus Macquarie Island is one of the most isothermal places on the earth (Troll, 1958).

The thermoisopleth diagrams for Mt Wilhelm (3510m) and Macquarie Island (4m) at 1.5m above ground provide evidence of remarkable isothermy, both diurnally and annually (Chapter 3, Figs 3.2, 3.6). An absolute temperature range of about 14.5°C is characteristic of both stations. In contrast with the thermal climate 1.5m above ground, plant canopy level thermoisopleth diagrams at 3510m at Pindaunde (Figs 3.6, 3.7) show an extreme development of daily temperature climates. A plant-level thermoisopleth diagram is not available for Macquarie Island; however, in view of Jenkin's (1972) data on leaf temperatures compared with 1.0m air temperatures (which he believes to represent near maximum differences on Macquarie Island), it is clear that the plant canopy thermal climate at Macquarie is not very different from that at 1.0m.

The soil environments of tussocks in both regions are predominantly cool, constantly wet, peats overlying basic rocks. The rhizospheres differ markedly, though, in the range of temperatures which normally occur. On Mt Wilhelm at 3510m, soil temperatures at 10-20 cm depths fluctuate between about 7°C and 8°C diurnally. The annual variation for any given hour is not known, but given the isothermy of air temperatures and the small variation in the sun's midday altitude, it is probably less than the diurnal range. On Macquarie Island, the annual range of 10 to 20 cm depth soil temperatures is 0°C to 14.4°C and 1.1°C to 12.2°C respectively, probably more than ten times the range on Mt Wilhelm. Diurnal cycles at Macquarie have not been measured, but are likely to be small in view of the small diurnal air temperature range. Furthermore, soil frost is quite frequent at 2.5 cm depth at 4350m altitude on Mt Wilhelm but extremely rare on Macquarie Island at 4m altitude. This difference probably reflects the greater incidence of clear nights at the former than at the latter place. The number of days with ground surface frost is also higher at Mt Wilhelm than at Macquarie Island.

Precipitation is high in both regions. On Campbell and Macquarie Islands, it is evenly distributed throughout the year, and falls of more than 25mm in a day are not common. On Mt Wilhelm, there is a precipitation maximum during December through March and a minimum during July and August. Droughts of up to six weeks duration are experienced in some years while rainfalls of greater than 50mm per day also occur. Snow can fall at any time of the year in both regions, particularly at high altitudes, but it seldom lies on the ground for more than one to three days on Mt Wilhelm or a week at high altitudes on Macquarie.

A final point of climatic contrast is between the persistent, strong, blusterous winds of the sub-Antarctic, and the gentle, daily oscillation of slope and valley winds in the equatorial high montane.

The sub-Antarctic climate described for Macquarie Island and that of the equatorial high montane found at Mt Wilhelm differ respectively in some attributes from those of other places within each region. Thus, there are the very humid Melanesian and Columbian high mountains where clouds are a regular and common feature. As on Macquarie Island, one result of this cloudy, moist condition is a small range of temperature and a reduced radiation exchange environment. In contrast are the isolated, East African peaks which, while having an ever-humid climate on Lauer's (1952) criteria, experience much more extreme radiation climates than the former mountains, presumably because the air is drier, especially at night. Even drier and harsher radiation climates are found in the Bolivian and Peruvian high Andes (Troll, 1949, 1959). Variation in the sub-Antarctic region is seen in the results of a comparison of the climates of Kerguelen Island and Macquarie Island. Kerguelen has an average relative humidity of about 75% and 248 days per year with ground surface frost (Meinardus, 1923), whereas Macquarie Island, with average RH near 90%, has only 107 days with ground surface frost (Australian National Antarctic Research Expedition Reports, 1967-70). The mean temperatures are lower on Kerguelen than on Macquarie Island and thus probably cause the vegetation of Kerguelen at low altitudes (Werth, 1928) to be more similar to that of the high plateau than to the lowland vegetation of Macquarie Island.

In summary, it can be said that, in general, the sub-Antarctic and equatorial high montane climates are very much alike in their perpetual coolth and wetness, but differ greatly in wind and daily temperature change at plant level. All these factors may well be of importance to plant growth; for example, the relationship of wind and low temperature to transpiration, leaf area, and root mass. Arnold and Monteith (1974) have shown that seedling leaf elongation in the grass *Festuca ovina* in England is correlated with mean daily temperature and independent of daily amplitude, at least up to ± $9^{o}C$ over the range $0^{o}C$ to $32^{o}C$. They argue that, if limiting temperatures do no exist and if plant response times to temperature change are negligible, microclimate may be of only secondary importance in plant development and growth. In the sub-Antarctic and equatorial high montane where plant level frosts are frequent occurences, limiting temperatures occur and the conclusions of their work may not apply. Controlled environment experiments will be necessary to evaluate the role of various factors in controlling tussock grass growth in the sub-Antarctic and equatorial high montane.

The observations and conclusions from the study of tussock growth in Chapter 4 are briefly summarized in Table 5.1 to indicate points of similarity between the two regions. Where I have felt that the genetic constitution of the species involved may be of greater importance than environmental factors, this has been indicated in the Table. The classification of a feature of tussock grass growth as genetic is based upon differences being found between all three tussock species or, at least,

Table 5.1: Summary of similarities and differences between tussock grasslands of the sub-Antarctic and the equatorial high montane. (G = supposed genetic basis)

	variable	similar between regions	dissimilar between regions
Gross characteristics			
biomass:	total	.	x
	shoot:root ratio	.	x
	large amt. dead grass	?G	.
structure:	life form	x	.
	leaf and tiller density	x (at high range)	.
	tussock density	x	.
	LAI	x (note puzzling Macquarie situation)	.
	leaf longevity	x (short)	.
	leaf weight/cm	.	G
Productivity:	daily and annual	.	x
	efficiency	.	x
Carbohydrates:	roots	.	G
	green leaves	.	G
	leaf bases	G	.
	inter sample variation	x	.
Environment:	soil nutrients	.	x
	diurnal air temperatures	.	x
	soil temperatures	.	x
	radiation	.	x
	wind	.	x
	mean isothermy	x	.
	low mean temperature	x	.
	precipitation: high	x	.
	seasonal	.	x
	cloud	x (in some ways)	x
	humidity	x (in some ways)	x

between the Campbell Island and Macquarie Island species which exist in fairly similar environments. The classification does not apply however, where similar results from all species are found. In such cases they may reflect the influence of similar environmental factors in both regions, and differences between the Mt Wilhelm tussocks and the two sub-Antarctic ones may correlate with environmental differences between the regions.

The main points of similarity in Table 5.1 relate to structure (*i.e.* leaf and tussock density, accummulation of dead grass, leaf area index, and primary site of carbohydrate storage), and to a long growing season and short lifespan for individual leaves. The similarities of structure understandably bear out the initial observations of physiognomic unity. The characteristics of long growing season (that may be virtually a year long although it has not been proven so) and a short life span relate to a point of dynamic similarity in the way that tussock grasses grow. These characteristics, together with the 'evergreen' nature of tussocks, suggests that there is a rapid turnover of leaves. However, a long growing season and rapid leaf turnover are not universal characteristics of tussock grasses. Mark (1965) reports leaf lives of *Chionochloa* from New Zealand of up to 3 years and these tussocks, like those of *Sclerodactylon macrostachyum* (Benth). A. Camus on the tropical atoll of Aldabra (personal observation) and the *Eriophorum* spp. of Alaska (Hopkins and Sigafoos, 1951), all grow in seasonally arid climates that may restrict growth for part of the year.

Various aspects of growth (*i.e.* total biomass, shoot:root ratio, productivity, and efficiency of production) for which differences between regions were found (Table 5.1) are probably environmentally rather than genetically controlled. All of the growth differences relate to the very high biomass and productivity of the tussock in the sub-Antarctic compared with the much lower values from the equatorial high montane. That Jenkin (1972) and I arrived at similar productivity values for lowland sites by using very different techniques supports the case for the values being correct and not subject to gross experimental error. The main source of difference in total biomass comes from the large quantity of roots at both sub-Antarctic sites compared with the small values obtained from the equatorial high montane. The more favorable nutrient regime of the sub-Antarctic tussocks compared with those of Mt Wilhelm may be an environmental factor of primary importance here. However, genetic adaptation to the existing environment by both sub-Antarctic species in excess of that of *Deschampsia klossii* to the Mt Wilhelm environment cannot be ruled out at this stage. Whatever the ultimate cause for the growth differences, the equatorial high montane efficiencies and productivity are comparable to the values from arctic and alpine sites (Bliss, 1966) but the Macquarie Island values rank amongst the highest from natural vegetation in the world.

For the world's terrestrial plant communities, Lieth (1972) lists maximum primary productivity at 3500 g/m^2/year and this value was found for 'tropical rain forest' and 'rain green forest'. For temperate and tropical grassland, he quotes maxima of 1500 and 2000 g/m^2/year respectively. With equations (his Figs. 3 and 4) using mean annual temperature and annual average precipitation, he has produced maps of world primary production. These equations have been applied to the data from Campbell Island, Macquarie Island, and Mt Wilhelm (Table 5.2). Following Lieth's application of Leibig's law of the minimum, the smallest calculated value has been taken as the best estimate of production and compared with the actual values of dry matter production. The actual and calculated values for the upland Macquarie Island (235m), Campbell Island (CBII) and upland Mt Wilhelm (WUV2) sites agree reasonably well (using the variability shown in Lieth's Figures as an estimate of expected error). Production estimated from temperature data gives the lowest values for the Macquarie Island and Mt Wilhelm sites, whereas estimates based on precipitation give the lesser value for the Campbell Island site. The actual annual production values of the lowland Macquarie Island (45m) and the lowland Mt Wilhelm sites are

Table 5.2: Measured and calculated annual production (g/m^2) estimates for the sub-Antarctic and equatorial high montane. Calculated values come from Lieth's (1972) equations where the lesser values only are used.

site (1)	measured (2)	temp. estimate (3)	rainfall estimate (4)	ratio of (2) with the lesser of (3) and (4) (5)
Mt Wilhelm				
WFS	128	1205	2696	0.1
WUV2	442	797	–[a]	0.5
Campbell Isd.				
CBII	1506	1120	926	1.6
Macquarie Isd.[b]				
235m	949	883	1465	1.1
45m	3280	959	1378	3.4

a. no rainfall data available.
b. data from Jenkin, 1972.

very different from the calculated estimates. The Macquarie Island site value is 3.4 times greater than the estimated minimum and the Mt Wilhelm site value is only a tenth of its estimated minimum. In both cases the calculated estimates based on temperature give the lower value. Do the measured values for these sites truly reflect their production level or do the differences between them and the estimates based on Lieth's equation represent the degree of error in the field estimates?

For the Mt Wilhelm (WFS) site, the production value estimated from temperature is smaller than that estimated from rainfall, and temperature rather than precipitation may therefore be the factor limiting growth here. Since production at the cooler, higher site (WUV2) is reasonably well estimated from temperature data by the equation, it seems that temperatures at the lower site may be limiting by being above the optimum for growth for *Deschampsia klossii*. Given that *D. klossii* is native to high altitudes and invades at lower altitudes only after fire, this suggestion seems reasonable. Warmer temperatures at the lower altitude may have the effect of increasing respiration more than photosynthesis in a manner similar to that found by Mooney and Billings (1961) for arctic populations of *Oxyria digyna* when grown under conditions warmer than those under which they had evolved.

The lowland Macquarie Island site experiences a long growing season that is estimated to be 295 days (Jenkin, 1972) but which may well be nearly 365 days; there are however no conclusive data on the latter point. The high annual production is matched by high daily production as measured by both Jenkin (1972) and myself. The high daily rates are not entirely surprising as similar rates have been found for other communities in this region, for example, for bryophytes on South Georgia (Clarke *et al.*, 1971; see Table 4.11). The southern bryophyte communities have low annual production compared with lowland Macquarie Island, probably because of the much shorter growing seasons experienced by the former; for instance, the growing season at South Georgia is only 80 days. Were the growing season there as long as that on Macquarie Island, the South Georgia bryophytes might produce annually as much matter as a tropical rain forest or the lowland Macquarie Island tussock grasslands (*i.e.* 7.8 g/m^2/day of growing season x 365 days = 2847 g/m^2 annually for mosses). Perhaps the prodogious growth of bryophytes in moss, elfin and cloud forests that occur in cool, ever humid cloudy places represents just this kind of situation. It seems that the lowland *Poa foliosa* grassland on Macquarie Island exists in an environment to which the grass is very well adapted. Under conditions of low temperature and light, with neither water nor nutrients especially limiting, growth is excellent.

Chionochloa antarctica from Campbell Island was not found to have the same high production as *Poa foliosa* (but leaf sheath production was underestimated at Campbell Island), suggesting that the *Chionochloa* is less well adapted to its environment than *P. foliosa*. Insofar as *C. antarctica* is the most southerly representative of its genus, it might be argued that the optimal conditions for growth in this genus are found further north than Campbell Island where growth might be limited by low energy input. However, it should be noted that the actual production value for Campbell Island is close to that estimated from Lieth's equations and that the latter indicate that precipitation rather than temperature may be the factor controlling growth.

The explanations that have been offered to account for the differences and similarities between actual and estimated production values in Table 5.2 suggest an hypothesis that relates level of production to the degree of adaptation of the species concerned to its environment. It seems likely that, at least in such cases as *Deschampsia klossii* on Mt Wilhelm, temperature is an aspect of the environment to which adaptation is important for production. Current research suggests that there are plants with temperature thresholds for growth at 5°C or lower (H. Nix, C.S.I.R.O., personal communication). At this threshold, photosynthetic production and cell growth are optimally linked. Increases in temperature or light intensity (energy supplied), far from increasing growth, reduce it. If *Poa foliosa* had such characteristics, a high level of production on Macquarie Island would be expected. On the other hand, *Chionochloa antarctica*, belonging to a genus that may have evolved in warmer conditions than prevail on Campbell Island, might have a higher thermal/light optimum than occurs there and so have reduced production. Obviously more data need to be collected before the adaptation-production hypothesis can be adequately tested.

It is interesting to compare the upper limits to net plant production in natural communities and managed crop lands. Stewart (1970) summarises high productivity for tropical crops and reports daily averages up to 24 g/m^2/day over the whole year, *i.e.* about twice the maximum values I have been able to find in the literature for natural communities. Is the value of about 10 g/m^2/day near the maximum for undisturbed communities? Is the difference between it and the greater values for crops a measure of limits placed upon the generally more complex, self-perpetuating systems of nature? The role of nutrients as limiting factors to plant growth is certainly one element restraining growth in natural communities; it is overcome by the addition of fertilizer to the new 'man made' crops to help them to reach their high yields.

Two final points of comparison of growth of tussocks between the sub-Antarctic and equatorial high montane can be made.

1) An estimate of plant investment in leaf mass per unit of leaf area is shown in Table 5.3 which is based on data from Tables 4.1 and 4.9. In Table 5.3 it is seen that the sub-Antarctic tussocks invest about twice as much of each plant's mass in leaf area as do the equatorial high montane tussocks. This may be related to the perpetually low levels of irradiance caused in the sub-Antarctic by persistent high cloud cover and the consequent difficulty of light interception by the leaves. Levels of light intensity are intermittently higher at the equatorial site where sunny mornings are a common feature. A difference in light intercepting properties by leaves of tussocks in the two regions is also seen in their morphology. The Mt Wilhelm *Deschampsia klossii* tussocks have narrow, cylindrical, leaves while the sub-Antarctic *Poa foliosa* and *Chionochloa antarctica* had broad, flat ones.

Table 5.3: Leaf area compared with leaf dry weight and root dry weight for equatorial high montane and sub-Antarctic sites.

site (1)	leaf area/m^2 (2)	g/m^2 green leaves (3)	g/m^2 live roots (4)	LA/g green leaves (5)	LA/g roots (6)
WUV1	1.8	0.378	0.045	4.8	40.0
WFS	1.6	0.346	0.054	4.6	29.6
CBH	5.5	0.634	1.116	8.7	4.9
Macquarie 45m (Jenkin,1972)	7.2	0.637	1.686	11.3	4.3

2) There is between six and nine times as much leaf area per gram of roots per m^2 ground in the equatorial high montane tussocks as in the sub-Antarctic tussocks (Table 5.3). This compares with 3.0 to 4.5 times more leaf area/m^2 at the sub-Antarctic than the equatorial site.

Expressed another way, it takes at least six times more roots to support an equal area of leaf in the sub-Antarctic than in the equatorial high montane. Possibly this is because the strong persistent winds and large leaf area in the sub-Antarctic result in relatively high transpiration that can only be met by a large root network. However, resolution must await further studies because we do not know the stomatal response of the sub-Antarctic tussocks to strong winds with high relative humidity. *Deschampsia klossii* on Mt Wilhelm has tightly inrolled leaves with sunken stomata deeply buried in narrow, pappillose channels - very well designed to reduce stomatal water loss.

In concluding this thesis, I return briefly to the question posed at the beginning. Why are there tussock grasses? It has been disappointing that, in the comparison of tussock grasslands from the sub-Antarctic and equatorial high montane regions, no clear overriding generalizations have appeared. Details of structure have, not surprisingly, shown similarities between regions. However, growth characteristics have proven to vary considerably from place to place. Pearsall (1950) has written about the relationship between soil water and its movement to the formation of tussock swards in *Molinia caerulea*, Kershaw (1963) has speculated on the role of nutrients in causing clumping in grasses, and Hedberg (1964) and Troll (1960) have attributed tussock and other growth forms common to the sub-Antarctic and equatorial high montane to constantly low temperatures. I have observed the change from tussock to sward in *Poa foliosa* on Macquarie Island as wind exposure becomes extreme just below windward ridge crests. On Mt Wilhelm I have seen the tussock form of *Deschampsia klossii* become progressivley less compact and tussock-like the further it grows into wet boggy areas. Tansley (1949) reports that *Nardus* adopts a sward form rather than a tussock form under the pressure of grazing and I have observed something similar with *Sclerodactylon* tussocks grazed by tortoises on Aldabra atoll. Thus in some species at least the tussock form is clearly seen to be a plastic adaptation to environmental extremes.

Because the tussock habit can arise from the proliferation of a single plant or from the clumping and subsequent proliferation of several plants (Ashton, 1965; Kershaw, 1963), it seems that the form itself must confer some advantage on the plants which express it. Further research along the lines suggested below might indicate what the advantages are.

a) The relative energy expenditure between leaf and stem production and maintenance in tussock and sward growth forms. (I expect proportionately more leaf and less stems in tussocks than in swards but I have no data to support this.) We might find that leaf production is less costly than stem production and that by producing more and longer leaves and fewer shorter stems, *i.e.* a tussock, the same leaf area and ground cover can be achieved more economically than through the production of swards.

b) A study of the factors that promote tussock growth in species that are not obligate tussocks and in species which form tussocks from several separate individual plants. This study should include determining the microenvironmental conditions that may favour tussock forms over sward forms. For example, is there a more favourable thermal regime for growth in the well insulated base of a tussock than in the base of a sward?

c) The study of the role of waste leaf disposal and utilization by swards *versus* tussocks. Does the tussock form permit a more efficient mechanism for disposing of large volumes of dead leaves than does the sward form? What is the relationship between litter accummulation and nutrient cycling?

Finally, one aspect of the tussock form which may confer an advantage in those localities where woody plants (low trees or shrubs) give way to tussock grassland, is the height of canopy that the tussock form permits. Above or beyond timberlines where strong woody stems cannot be produced and thus no longer permit woody species to overshadow competing plants, it is herbs, grasses and sedges that dominate (Wardle, 1971, p.392). Of these latter plants, those that can grow tallest and cover the ground are the most successful. Tussock grasses and giant herbs are growth forms which have been evolved in the sub-Antarctic and equatorial high mountains to occupy this habitat which, though cool, does not possess those limitations characteristic of the alpine and tundra, namely long periods of freezing temperatures, abrasion from wind blown ice and sand during the dormant season, and late melting snow packs.

POST SCRIPT

Since the completion of this thesis, two publications have become available in Australia and are of sufficient importance to require their mention in a post script. The first is the volume *Primary Production and Production Processes, Tundra Biome* (Bliss,L.C. and Wielgolaski, F.F. eds, University of Alberta Printing Services, Edmonton, 1973.) Of the many relevant papers of importance to comparative primary production studies, I will note only some of those concerned with the sub-Antarctic region. High biomass of bryophytes on the British sub-Antarctic islands is noted by N.J. Collins (pp177-184)(this complements the earlier work of Clarke et al., 1971). The bi-polar comparison of growth in *Phleum alpinum* (T.V. Callaghan, pp 185-190) indicates the effect on growth of a short growing season in the arctic and the much longer growing season in the sub-Antarctic, and emphasizes the genetic adaptations of plants to their specific, natural habitats. The studies reported from the northern hemisphere, tundra zone, reinforce the known dominating influence of short summers and long winters on production, i.e. a short burst of growth often with much storage of energy in perennating organs.

The second work I want to briefly mention is that of A.F.Mark (1975, Photosynthesis and dark respiration in three alpine snow tussocks (*Chionochloa spp.*) under controlled environments, *New Zealand Journal of Botany 13:*93-122). In this study Mark reports that one species (that which occurs at the highest altitude) was capable of attaining maximal net assimilation rates very shortly after temperatures rose above 0°C. This is a capacity which could be of great advantage to an evergreen plant in an environment made severe by periodic frost. However, Mark also notes that while the response just noted was found following a single, either long or short period of freezing, it was not found in plants subjected to several cycles of night freezing - daytime thawing. If the tussock grasses described in this thesis should have physiological responses similar to those reported by Mark, then the differences in production rates between the sub-Antarctic and high equatorial montane, that I have reported, may be more understandable. For example, the high incidence of night frost throughout the year on Mt Wilhelm, together with low production there, contrasts with the lower incidence of frost and high production on Macquarie Island, where, furthermore, frost is largely confined to the winter months. Therefore, it might be the high frequency of night frost and low nutrient status that limits production on Mt Wilhelm, despite the largely aseasonal nature of the climate. Autecological studies, such as that of Mark, could now be extended to other tussock species.

Appendix 4.1: Total aerial biomass at Mt Wilhelm sites analysed by Kruskal-Wallis analysis of variance by ranks (from Zar, 1974, p.139).

Ho: the biomass is the same at all 5 sites.
Ha: the biomass is not the same at all 5 sites
data = Kg/m^2, ( ) = rank.

Site	WWF1	WWF2	WFS1	WFS2	WUV1
	2.786(15)	1.824(4)	3.327(22)	2.800(16)	3.200(20)
	2.664(14)	2.090(6)	1.769(2)	2.150(7)	4.591(25)
	2.948(18)	2.441(11)	2.514(12)	2.652(13)	3.463(24)
	2.376(8)	1.820(3)	1.746(1)	2.422(10)	2.830(17)
	3.353(23)	2.388(9)	1.859(5)	3.311(21)	3.073(19)
	$n_1=5$	$n_2=5$	$n_3=5$	$n_4=5$	$n_5=5$
	$R_1=78$	$R_2=33$	$R_3=42$	$R_4=67$	$R_5=105$

$N = 25$
$H = 12.281$
$V = 4$
$X^2\ 0.05,4 = 9.488$
reject Ho $0.005 < p < 0.01$

Appendix 4.2: Non-parametric multiple comparison of total biomass from Appendix 4.1 (method is that of Zar, 1974 p.156). The table indicates the probability level at which the null hypothesis of Appendix 4.1 can be rejected.

	WWF1	WWF2	WFS1	WFS2
WWF1	.	.	.	.
WWF2	$.01 < p < .025$	.	.	.
WFS1	$.025 < p < .05$	$.01 < p < .025$	.	.
WFS2	$.01 < p < .025$	$.01 < p < .025$	$.025 < p < .05$	.
WUV1	$.001 < p < .005$	$.01 < p < .025$	$.001 < p < .005$	$.01 < p < .025$

In summary: at $p = .05$ level, WUV1 is significantly different from the four other sites. The latter falls into 2 overlapping groups indicating a Type 2 error in the attempt to segregate the sites into similar groups.

at $p = .01$ and $p = .005$ WUV1 is significantly different from 2 sites (WWF1 and WFS1) while all other sites fall into a single group.
(Note one sample was selected randomly from each of WWF2 and WFS2 and rejected in order that sample size be equal for all five sites - a requirement of the test.)

Appendix 4.4: Calculation data for Mt Wilhelm aerial productivity of tussocks. ( ) enclose estimated data.

site	leaf class	cm/day/lf	g/cm x10^{-5}	lvs/m^2	g/m^2/day x10^{-3}	g/m^2/day as % of total
WWF	10-19.9	(.385)	267.3	17.1	17.598	4.99
	20-29.9	.395	295.5	16.1	18.792	5.33
	30-39.9	.398	189.9	25.2	19.046	5.40
	40-49.9	.545	361.7	32.2	63.475	18.01
	50-59.9	.395	424.9	44.3	74.351	21.09
	60-69.9	.568	450.0	43.8	111.953	31.76
	70-79.9	.385	481.9	16.6	30.798	8.74
	80-89.9	(.385)	483.6	6.5	12.102	3.43
	90-99.9	(.385)	517.6	1.0	1.993	0.57
	100-109.9	(.385)	628.4	1.0	2.419	0.69
					352.527	

This is a crude estimate because lvs/m^2 comes from only one tussock (an average size one in terms of no. of lvs. but as this is the most variable factor, the final estimate g/m^2/day is only a rough one).

site	leaf class	cm/day/lf	g/cm x10^{-5}	lvs/m^2	g/m^2/day x10^{-3}	g/m^2/day as % of total
WFS	10-19.9	(.456[c])	335.3	4.6	7.127	1.04
	20-29.9	.456	313.6	21.1	30.103	4.39
	30-39.9	.312	376.7	31.7	37.302	5.44
	40-49.9	.384	392.1	52.6	79.129	11.53
	50-59.9	.407	427.3	82.4	143.288	20.89
	60-69.9	.389	480.7	66.9	125.021	18.22
	70-79.9	.561	583.9	53.9	176.429	25.72
	80-89.9	(.664[a])	593.9	15.9	62.773	9.15
	90-99.9	.767	674.0	4.1	20.969	3.06
	100-109.9	(.767[b])	787.7	0.6	3.849	0.56
					685.990	

a = average of 70-79.9 and 90-99.9 classes cm/day/lf.
b = same as 90-99.9 class
c = same as 20-29.9 class

site	leaf class	cm/day/lf	g/cm x10^{-5}	lvs/m^2	g/m^2/day x10^{-3}	g/m^2/day as % of total
WGAP	10-19.9	.215	419.0	39.4	35.493	4.63
	20-29.9	.234	484.8	47.2	53.545	6.98
	30-39.9	.290	507.5	101.5	149.383	19.47
	40-49.9	.316	574.4	183.9	333.798	43.51
	50-59.9	.256	624.5	89.3	142.766	18.61
	60-69.9	(.256)	642.8	18.3	30.114	3.93
	70-79.9	(.256)	(642.8)	13.4	22.051	2.87
					767.150	

Only a crude estimate of productivity : lvs /m^2 from only 2 tussocks and g/cm from 1 tussock.

continued.

Appendix 4.4 continued.

site	leaf class	cm/day/lf	g/cm x10^{-5}	lvs/m^2	g/m^2/day x10^{-3}	g/m^2/day as % of total
WWT	10-19.9	.152	294.9	169.7	75.968	8.71
	20-29.9	.156	343.4	247.8	132.618	15.20
	30-39.9	.195	381.7	287.3	213.842	24.52
	40-49.9	(.195)	423.1	271.2	223.752	25.65
	50-59.9	(.195)	453.5	174.4	154.226	17.68
	60-69.9	(.195)	476.7	55.2	51.312	5.88
	70-79.9	(.195)	492.8	15.2	14.607	1.67
	80-89.9	(.195)	513.4	5.9	5.907	0.01
					872.231	

A very crude estimate of productivity. Only 2 tussocks sampled for lf/m^2, one had large overhang with long leaves; no long leaves in growth sample; abundance of long lvs not known.

WUV1	0- 9.9	(.125)	434.8	155.4	84.46	11.91
	10-19.9	.125	435.0	337.7	183.624	25.89
	20-29.9	.145	467.7	378.7	256.685	36.19
	30-39.9	(.145)	532.1	227.5	175.526	24.75
	40-49.9	(.145)	519.0	11.8	8.88	1.25
					709.175	

Although 3/5 of cm/day values are estimates, 61% of production comes from 2 classes with original data.

WUV2	0- 9.9	(.125)	363.6	132.3	60.130	4.98
	10-14.9	.125	296.5	142.5	52.814	4.38
	15-19.9	.117	339.9	234.8	93.376	7.74
	20-24.9	.170	407.5	319.6	229.577	19.02
	25-29.9	.192	508.6	331.4	323.616	26.81
	30-34.9	.204	580.3	205.3	243.037	20.14
	35-39.9	.201	562.6	116.8	132.080	10.94
	40-44.9	(.201)	546.0	65.9	72.323	5.99
					1206.954	

continued...

Appendix 4.4: Productivity data from Macquarie Island.

	1st leaf	2nd leaf	3rd leaf	4th leaf	5th leaf	6th leaf	7th leaf	8th leaf	$\sum_1^8$ lf= g/d/ tiller	new lvs produced during sample		$\bar{x}$ no. of new lvs	estm. new lvs g/d	grand total g/d	tillers /m^2	g/d/m^2
										g/cm of 4th leaf	$\bar{x}$ cm /d					
Razorback																
(1) $\bar{x}$ cm/day^a	6175	6923	6168	4530	1283	246	22	–			7157					
N	4	15	20	11	7	4	8	–								
(2) $\bar{x}$ g/cm^a	18	21	53	74	77	79	50			74						
N (lots of 25)	4	4	4	4	4	2										
(3)=(1)·(2)= g/d^b	1112	1454	3269	3352	988	194	11		10380				9470	19850		
(3) as % of total	5.6	7.3	16.5	16.9	5.0	.98	.06						47.7			
												1.788			516.7	10.26
Garden Cove																
(1) $\bar{x}$ cm/d^a	7401	8515	7350	4909	1175	15	0				6610					
N	7	24	16	11	6	8										
(2) $\bar{x}$ g/cm^a	81	234	487	786	1012	1082	12175			786						
N (lots of 25)	1	1	1	1	1	1										
(3)=(1)·(2)= g/d^b	600	1993	3580	3859	1189	16	0		11235				9955	21189		
(3) as % of total	2.8	9.4	16.9	18.2	5.6	0.08							47.0			
												1.916			367.5	7.79
Wireless Exposed																
(1) $\bar{x}$ cm/d^a	7324	7670	5876	2625	937	20	0				6379					
N	9	35	24	13	12	7										
(2) $\bar{x}$ g/cm^a	180	342	596	854	942	871	806			854						
N (lots of 25)	4	4	4	4	4	4	4									
(3)=(1)·(2)= g/d^b	1318	2623	3502	2242	883	17	0		10585				9370	19955		
(3) as % of total	6.6	13.1	17.6	11.2	4.4	0.09							47.0			
												1.720			331.7	6.62

continued.

Appendix 4.4 continued.

	1st leaf	2nd leaf	3rd leaf	4th leaf	5th leaf	6th leaf	7th leaf	8th leaf	$\sum^{8}$ lf= g/d/ tiller	new lvs produced during sample		x no. of new lvs	estm. new lvs g/d	grand total g/d	tillers /m^2	g/d/m^2
										g/cm of 4th leaf	x cm /d					
Wireless																
Sheltered																
(1) $\bar{x}$ cm/d^a	9723	9198	9222	8535	6213	2231	385	87			7208					
N	1	3	20	43	39	37	17	8								
(2) $\bar{x}$ g/cm^a	15	22	63	86	93	93	117	84		86						
N (lots of 25)	4	4	4	4	4	4	3									
(3)=(1)·(2)= g/d^b	1459	1987	5801	7366	5747	2086	451	73	24968				13735	38703		
(3) as % of total	3.8	5.1	15.0	19.0	14.9	5.4	1.2	0.19					35.5			
												2.208			281.0	10.88
Perseverance																
Bluff																
(1) $\bar{x}$ cm/d^a	7596	6869	7193	5597	2641	457	94				6149					
N	2	11	36	44	37	22	13									
(2) $\bar{x}$ g/cm^a	15	29	50	69	71	66	71			69						
N (lots of 25)	4	4	4	4	4	4	4									
(3)=(1)·(2)= g/d^b	1109	1978	3589	3873	1878	302	66		12795				7642	20437		
(3) as % of total	5.4	9.7	17.6	19.0	9.2	1.5	0.3						37.4			
												1.796			474.7	9.70

a = x10^{-4}

b = x10^{-6}

continued...

Appendix 4.4: Productivity data from Campbell Island.

lf class	0-9.9	10-19.9	20-29.9	30-39.9	40-49.9	50-59.9	60-69.9	70-79.9	80-89.9	90-99.9	100
a cm/day	.3261	.2746	.2865	.3023	.2917	.2998	.2842	.2889	.1641	.2054	.1965
b g/cm $x10^{-5}$	77	100	162	187	268	347	476	620	705	526	(526)
c = a·b = g/day $x10^{-5}$	25.1	27.5	46.4	56.5	78.2	104.0	135.3	179.1	115.7	108.0	103.4
c's as % of d	2.6	2.8	4.7	5.8	8.0	10.6	13.8	18.3	11.8	11.0	10.6

$d = \Sigma c = 979.2 \times 10^{-5}$

e = tiller/tussock = 668

f = d·e = g/d/tuss = 6.5411

$h = m^2$ ground/tuss = 0.6304

$i = f \cdot h = g/m^2/day = 4.1235$

concluded.

Appendix 4.5: Carbohydrates in *Deschampsia klossii*, Mt Wilhelm, 3510m, 1970. Values are % of oven dry weight. a. and b. are duplicate samples from the same site.

ROOTS

Date	Time	Sample	Sugar Determination		Starch
			1.	2.	
3/6	0730	a	1.905	1.905	2.38
		b	3.497	2.119	2.73
21/4	0745	a	7.188	6.885	4.92
		b	3.085	3.085	1.83
15/4	0830	a	3.845	4.419	0.43
		b	4.745	3.858	1.04
3/5	0915	a	6.565	4.565	1.84
		b	4.225	2.767	2.95
13/9	1100	a	1.191	-	2.75
		b	1.048	1.227	1.52
3/6	1145	a	1.198	1.198	1.76
		b	2.505	2.505	1.99
3/5	1300	a	8.238	7.479	2.80
		b	5.932	5.932	3.42
3/5	1645	a	4.799	4.588	1.88
		b	4.205	5.157	1.65

1-way nested Analysis of variance (sugars) (excluding 13/9 sample)

source of variation	degrees of freedom	sum of squares	mean square
time	6	54.93	9.16
samples	7	34.19	4.88
determination	14	9.88	0.71

F(time) = 1.8770, f 6,7
F(sample) = 6.8732, f 7,14

conclude: no significant variation due to time ($0.1 < p < 0.25$) but very significant differences due to sample ($0.0001 < p < 0.001$)

Summary of 1-way analysis of variance (starch)

source of variation	sum of squares	degrees of freedom	mean square
total	15.2453	15	
times	9.9057	3	3.3019
error	5.3396	8	o.6675

conclude: no significant difference between sites ($0.05 < p < 0.10$)

Appendix 4.6: Carbohydrates in *Poa foliosa*, Macquarie Island. Values are % of oven dry weight. a. and b. are duplicate samples from the same site.

ROOTS

				Sugar Determination		Starch
Date	Time	Sample		1.	2.	
11/1/72	0900	MGC	a	0.396	0.600	0.35
			b	0.631	0.418	0.56
12/1/72	0905	MWE	a	0.145	0.145	2.03
			b	0.433	0.103	1.45
12/1/72	0850	MWS	a	3.108	4.355	0.68
			b	3.079	2.822	0.82
13/1/72	0900	MRB	a	0.257	0.257	1.41
			b	1.173	1.055	0.45
14/1/72	0905	MPB	a	0.000	0.000	0.87
			b	0.505	0.678	0.91

1-way nested Analysis of variance (sugar)

source of variation	degrees of freedom	sum of squares	mean square
sites	4	27.773	6.943
samples	5	1.710	0.342
determinations	10	0.930	0.093

F(sites) = 20.301, f 4,5;
F(samples) = 3.677, f 5,10

conclude:
- variation between sites very significant ($p < 0.005$)
- variation due to sample not significant ($0.1 < p < 0.25$)
- only slight variation between determinations.

Summary of 1-way analysis of variance (starch)

source of variation	sum of squares	degrees of freedom	mean square
total	2.4879	9	
sites	1.0873	4	0.2718
error	1.4005	5	0.2801

F(sites) = 0.9704 ($p > 0.5$)
conclude: no significant difference between sites.

Appendix 4.7: Carbohydrates in *Chionochloa antarctica (C.a.)* and *Poa littorosa (P.l.)*, Campbell Island. Values are % of oven dry weight. a. and b. are duplicate samples from the same site.

				Sugar Determination		Starch
Date	Time	Sample		1.	2.	
		GREEN LEAVES				
9/3/71	0920	*C.a.*	a	1.189	1.169	1.26
			b	2.645	2.716	5.60
"	0900	*P.l.*	a	2.768	2.818	1.67
			b	2.195	1.997	1.14
		SHEATHS				
"	0920	*C.a.*	a	6.993	6.993	4.43
			b	6.292	6.290	2.79
"	0900	*P.l.*	a	3.263	3.070	1.09
			b	3.906	4.107	1.61
		STEMS				
"	0920	*C.a.*	a	3.818	3.181	0.68
			b	4.180	4.342	0.56
"	0900	*P.l.*	a	3.494	3.341	5.09
		ROOTS				
"	0920	*C.a.*	a	2.220	2.386	5.10
			b	1.498	1.688	5.15
		P.l.	a	2.105	1.558	7.59

Appendix 4.8: Carbohydrates in *Deschampsia klossii*, Mt Wilhelm, 3510m, 1970. Values are % of oven dry weight. a. and b. are duplicate samples from the same site.

GREEN LEAVES

Date	Time	Sample	Sugar Determination 1.	Sugar Determination 2.	Starch
3/6	0730	a	2.34	2.40	2.33
		b	2.57	2.62	2.49
21/4	0745	a	11.07	10.49	0.88
		b	11.24	10.96	1.69
3/5	0915	a	7.57	7.41	2.13
		b	6.59	6.59	1.80
13/9	1100	a	2.45	2.43	0.90
		b	5.75	5.75	0.83
3/6	1145	a	6.45	6.56	1.51
		b	4.83	5.05	1.70
3/5	1300	a	5.84	5.56	2.89
		b	5.89	5.63	2.40
12/8	1400	a	5.73	5.73	0.94
		b	7.29	7.09	0.69
3/5	1645	a	3.12	3.12	1.67
		b	4.36	4.22	1.83
15/4	0830	a	4.64	–	1.66
		b	4.40	–	1.85
16/7	0740	a	5.00	4.54	1.71
		b			2.04

1-way nested <u>Sugar</u> <u>Analysis of variance</u> (sugar; excluding 15/4 & 16/7 samples)

source of variation	degrees of freedom	sum of squares	mean square
time	7	186.9	26.7
samples	8	17.9	2.2
determination	16	0.4	0.025

F(time) = 12.1364; f 7,8 $(.001 < p < .005)$
F(sample) = 88.00; f 8,16 $(p < .0001)$

Summary of 1-way analysis of variance (starch)

source of variation	sum of squares	degrees of freedom	mean square
total	6.9826	19	
times	6.3306	9	0.7034
error	0.6520	10	0.0652

F(times) = 10.7884 $(p < 0.001)$

conclude: very significant differences in starches between different times at which samples were collected.

Appendix 4.9: Carbohydrates in *Poa foliosa*, Macquarie Island. Values are % of oven dry weight. a. and b. are duplicate samples from the same site.

GREEN LEAVES

				Sugar Determination		Starch
Date	Time	Sample		1.	2.	
11/1/72	0900	MGC	a	0.905	0.885	0.77
			b	0.797	0.937	0.78
12/1/72	0905	MWE	a	0.608	0.608	0.70
			b	0.594	0.528	1.17
12/1/72	0850	MWS	a	1.060	0.959	0.68
			b	0.690	0.690	0.78
12/1/72	1020	LAB	a	0.515	0.515	1.16
13/1/72	0950	MRB	a	0.474	0.078	0.81
			b	0.419	0.314	1.01
13/1/72	1010	LAB	a	0.320	0.320	0.55
14/1/72	0905	MPB	a	2.792	2.792	0.82
			b	0.707	0.306	0.86
14/1/72	1015	LAB	a	0.397	0.366	1.20
15/1/72	0800	LAB		0.511	0.373	1.28
"	1010	"		0.562	0.530	1.07
"	1100	"		0.493	0.360	1.27
"	1300	"		0.720	0.629	0.70
"	1400	"		0.622	0.522	0.64
"	1700	"		0.476	0.588	2.79
"	2000	"		0.468	0.606	1.29
"	2300	"		0.150	0.187	1.24
16/1/72	0200	"		0.401	0.311	0.98
"	0500	"		0.503	0.616	3.58
"	0805	"		0.565	0.587	1.49

1-way nested Analysis of variance (sugar) (excluding LAB samples)

source of variation	degrees of freedom	sum of squares	mean square
time	4	3.958	0.99
samples	5	5.337	1.067
determinations	10	0.182	0.018

F(sites) = 0.9278, f 4,5
F(samples) = 59.27, f 5,10

conclude:
- variation due to sites not significant ($p > 0.25$)
- variation due to samples very significant ($p << 0.005$)
- only slight variation between determinations

continued

Appendix 4.9 continued.

Summary of 1-way analysis of variance (starch)

source of variation	sum of squares	degrees of freedom	mean square
total	0.1967	9	
sites	0.0605	4	0.0151
error	0.1363	5	0.0273

F(sites) = 0.5545 ($p > 0.5$)

conclude : no significant differences between sites.

Summary of 1-way analysis of variance (diurnal changes in sugars)

source of variation	sum of squares	degrees of freedom	mean square
total	0.4308	21	
times	0.3755	10	0.0375
error	0.0553	11	0.0050

F = 7.4593 ($0.002 < p < 0.005$)

conclude : very significant difference in sugar levels between sampling times.

Appendix 4.10: Carbohydrates in *Deschampsia klossii*, Mt Wilhelm, 3510m, 1970. Values are % of oven dry weight. a. and b. are duplicate samples from the same site.

LEAF SHEATHS

Date	Time	Sample	Sugar Determination		Starch
			1.	2.	
3/6	0730	a	11.52	11.52	1.95
		b	11.54	12.12	1.20
16/7	0740	a	15.60	14.89	1.32
		b	25.41	24.15	1.51
21/4	0745	a	10.14	9.79	1.65
		b	13.66	13.56	2.98
15/4	0830	a	5.79	5.61	1.70
		b	5.27	5.08	2.55
3/5	0915	a	6.46	6.94	2.89
		b	13.16	13.16	3.72
10/10	1100	a	22.24	22.24	2.35
		b	13.31	13.31	2.19
3/6	1145	a	20.66	21.93	2.23
		b	25.55	24.29	3.07
3/5	1300	a	24.55	24.13	-
		b	26.98	26.65	-
12/8	1400	a	23.28	23.28	5.30
		b	27.96	27.11	4.62
3/5	1645	a	22.87	23.06	1.50
		b	22.01	22.37	1.39

1-way nested Analysis of variance (sugars)

source of variation	degrees of freedom	sum of squares	mean square
time	9	2012.4	223.6
samples	10	224.4	22.4
determinations	20	53.6	2.7

F(time) = 9.9821, f 9,10
F(sample) = 8.2963, f 10,20

conclude: very significant variation due to time $(0.001 < p < .002)$ and also due to sample $(p < 0.001)$.

Summary of 1-way analysis of variance (starch)

source of variation	sum of squares	degrees of freedom	mean square
total	22.6408	17	
time	20.1485	8	2.5186
error	2.4923	9	0.2769

F(time) = 9.0956 $(0.002 < p < 0.005)$

conclude: very significant differences between times of sampling.

Appendix 4.11: Carbohydrates in *Poa foliosa*, Macquarie Island. Values are % of oven dry weight. a. and b. are duplicate samples from the same site.

LEAF SHEATHS

Date	Time	Sample		Sugar Determination 1.	Sugar Determination 2.	Starch
11/1/72	0900	MGC	a	3.089	2.942	1.12
			b	3.106	3.106	1.00
12/1/72	0905	MWE	a	2.356	2.156	1.30
			b	2.466	2.407	1.20
12/1/72	0850	MWS	a	1.874	1.632	0.54
			b	1.776	1.776	1.08
13/1/72	0900	MRB	a	1.101	1.101	0.89
			b	1.421	1.227	1.03
14/1/72	0905	MPB	a	1.815	1.997	0.90
			b	2.004	1.644	1.50
15/1/72	0800	LAB		2.459	2.564	1.17
"	1100	"		1.997	1.752	1.53
"	1300	"		3.237	3.093	0.71
"	1700	"		2.606	2.705	3.74
"	2000	"		2.046	2.017	1.36
"	2300	"		1.190	1.247	1.17
16/1/72	0200	"		1.253	1.504	0.95
"	0500	"		2.762	2.700	3.89
"	0805	"		1.862	1.862	1.18

1-way nested Analysis of variance (sugar)(excluding LAB samples)

source of variation	degrees of freedom	sum of squares	mean square
sites	4	7.706	1.927
samples	5	0.098	0.020
determinations	10	0.162	0.016

F(sites) = 96.35, f 4,5
F(samples) = 1.25, f 5,10

conclude: - very significant variation between sites ($p << .005$)
- no significant variation between samples ($p > 0.25$)

Summary: 1-way analysis of variance (starch changes)

source of variation	sum of squares	degrees of freedom	mean square
total	2.4626	11	
sites	2.1148	5	0.4230
error	0.3478	6	0.0580

F = 7.2924 ($0.02 < p < 0.05$)
conclude: significant difference between sites.

Appendix 4.11 continued.

Summary: 1-way analysis of variance (diurnal sugar changes)

source of variation	sum of squares	degrees of freedom	mean square
total	19.3165	17	
time	19.2303	8	2.4038
error	0.0862	9	0.0096

F = 250.4 (p << 0.001)

conclude: very significant differences in sugar levels between sampling times.

Appendix 4.12: Carbohydrates in *Deschampsia klossii*, Mt Wilhelm, 3510m, 1970. Values are % of oven dry weight. a. and b. are duplicate samples from the same site.

DEAD ATTACHED LEAVES

Date	Time (hr)	Sample	Sugar Determination 1.	Sugar Determination 2.	Starch
15/4	0830	a	0.248	0.181	0.95
		b	0.117	0.254	0.95
21/4	0745	a	0.0	0.0	1.25
		b	0.0	0.0	1.00
3/5	0915	a	0.783	0.460	0.58
		b	0.220	0.139	0.60
3/5	1300	a	0.165	0.121	3.73
		b	0.109	0.366	4.50
3/5	1645	a	0.342	0.164	2.54
		b	0.061	0.061	2.35
3/6	0730	a	0.058	0.196	2.20
		b	0.0	0.0	2.75
3/6	1145	a	0.018	0.124	1.85
		b	0.161	0.093	1.44
16/7	0740	a	0.130	0.165	-
		b	0.460	0.342	2.52
12/8	1400	a	0.177	0.301	0.10
		b	0.098	0.152	-
WUV1 20/6		a	0.266	0.173	1.94

1-way nested Analysis of variance (sugar)

source of variation	degrees of freedom	sum of squares	mean square
time	6	0.2	0.033
samples	7	0.3	0.043
determinations	14	0.1	0.007

F(time) = 0.7762, f 6,7
F(sample) = 6.0423, f 7,14

conclude: no significant variation due to time ($0.5 < p < 0.75$) but very significant variation due to samples ($0.001 < p < 0.005$).

Summary: 1-way analysis of variance (starch)

source of variation	sum of squares	degrees of freedom	mean square
total	18.2169	13	
time	17.6357	6	2.9393
error	0.5813	7	0.0830

F = 35.3980 ($p < 0.0001$)

conclude: very significant difference between times of sampling.

Appendix 4.13: Carbohydrates in *Poa foliosa*, Macquarie Island. Values are % of oven dry weight. a. and b. are duplicate samples from the same site.

STEMS

Date	Time	Sample		Sugar Determination		Starch
				1.	2.	
11/1/72	0900	MGC	a	0.926	1.029	0.59
12/1/72	0905	MWE	a	0.731	0.521	0.89
			b	0.338	0.565	0.86
12/1/72	0850	MWS	a	0.000	0.342	0.61
			b	2.233	2.046	0.83
13/1/72	0900	MRB	a	0.138	0.000	1.22
			b	0.296	0.345	1.15
14/1/72	0905	MPB	a	0.274	0.180	0.69
			b	1.043	0.623	0.78

1-way nested Analysis of variance (sugar)(excluding MGC sample)

source of variation	degrees of freedom	sum of squares	mean square
sites	3	1.924	0.641
sample	4	4.336	1.084
determinations	8	0.227	0.028

F(sites) = 0.591, f 3,4
F(sample) = 38.714, f 4,8

conclude: no significant variation between sites ($p > 0.25$); very significant variation between samples ($p < .005$); only slight variation between determinations.

Summary: 1-way analysis of variance (starch)

source of variation	sum of squares	degrees of freedom	mean square
total	0.3105	7	
sites	0.2793	3	0.9310
error	0.0311	4	0.0078

F = 11.9359 ($0.02 < p < 0.05$)
conclude: significant difference between sites.

Appendix 4.14 : Leaf weight (g x10^{-4})/cm for five Macquarie Island sites.

the data

	MWS	MGC	MWE	MPB	MRB
1st	15	8	18	15	18
2nd	22	23	34	29	21
3rd	63	49	60	50	53
4th	86	79	85	69	74
5th	93	101	94	71	77
6th	93	108	87	66	79
7th	117	(122) (122)	81	71	50

The Analysis of variance (two-way without replication)

source of variation	ss	DF	MS
Total	34893.54	34	
sites	2082.11	4	520.53
leaf	28943.94	6	4823.99
remainder	3867.49	24	161.15

sites

$$F \text{ sites} = \frac{520.53}{161.15} = 3.23 \qquad (.05 < p < 0.1)$$

$$F \text{ leaf} = \frac{4823.99}{161.15} = 29.94 \qquad (p << .001)$$

conclude: no significant variation between sites but highly significant variation between leaves.

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