COMPARISON OF FOREST STRUCTURE AND REGENERATION ON BENCH AND STEWART ISLANDS, NEW ZEALAND

THOMAS T. VEBLEN* and GLENN H. STEWART

Protection Forestry Division, Forest Research Institute,
New Zealand Forest Service, Christchurch

SUMMARY: The absence of introduced browsing animals from Bench Island, located 5 km east of Stewart Island, provides the opportunity to compare forest structure and regeneration in these two areas of similar vegetation with and without browsing animals. The population structures of the main canopy tree species, rata *(Metrosideros umbellata), kamahi (Weinmannia racemosa),* and rimu *(Dacrydium cupressinum),* are similar in the areas compared. However, on Stewart Island, browsing animals, mainly white-tailed deer *(Odocoileus virginianus)* and the Australian brush-tailed possum *(Trichosurus vulpecula),* have drastically reduced the abundance of subcanopy trees and shrubs such as *Pseudopanax simplex, P. crassifolius, Fucshia excorticata, Myrsine australis, Schefflera digitata, Coprosma lucida* and *C. foetidissima;* ferns such as *Phymatosorus diversifolius, Asplenium bulbiferum* and herbs like *Kirkophytum lyallii* have likewise been reduced. The regeneration of the tree fern *Dicksonia squarrosa* is also severely impeded by browsing, and the generally sparse character of the understorey vegetation on Stewart Island contrasts sharply with the nearly continuous cover on Bench Island. On Stewart Island, the more open main tree canopy and greatly reduced abundance of plants in the 15-140cm tier results in greater species frequencies in the 0-15 em tier, but browsing pressure impedes their further development. Introduced browsing animals have already significantly altered the structure and floristic composition of the rata-kamahi-rimu forests on Stewart Island and their effects are likely to be more severe in the future unless animal numbers are reduced.

INTRODUCTION

In New Zealand there are only a few areas where native forests have not long been subject to the influences of introduced browsing animals, and Stewart Island, lying *c.* 30 km south of the South Island, is no exception. At Paterson Inlet in the northeast of the island six red deer *(Cervus elaphus)* were liberated in 1901 and 22 in 1902 (Logan and Harris, 1967). There was a single liberation of Virginian or white-tailed deer *(Odocoileus virginianus)* in 1905 at Port Pegasus in the south from where they rapidly spread and became common throughout the island by the 1920s (Williamson, 1976). Australian brush-tailed possums *(Trichosurus vulpecula)* were released on Stewart Island in the 1890s and by the 1920s were also reported as common (Williamson, 1976). Presently, red deer are not numerous but both white-tailed deer and possums are common over much of Stewart Island (Williamson, 1976). However, on several of the small nearby islands with forest covers similar to that of Stewart Island no browsing animals are present. These circumstances provide a nearly unique opportunity in New Zealand for a comparative study of the vegetation of similar areas affected and unaffected by introduced browsing animals. The present report is the result of a preliminary study of the effects of introduced animals on the lowland mixed hardwood / softwood forests of Stewart Island. A long-term study of animal influences involving manipulation of deer and possum numbers and remeasurement of permanent plots and exclosures has also been recently initiated.

The areas selected for the present study are Bench Island (46°55'S, 168° 15' W) where no browsing animals occur and Chew Tobacco Bay (470°1'S, 168° 14' W) on Stewart Island where both white-tailed deer and possums are common. The four (two on each island) *c.* 0.4 ha areas of forest selected for study are all located on relatively flat terrain at least 200 m inland from the coastline and show no evidence of past direct human influence such as burning or logging. They are underlain by well developed clayey soils, rich in organic matter and at least 50 cm deep, which are derived from granitic rocks (Purey-Cust and McClymont,

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* N.R.A.C. Post-Doctoral Research Fellow.

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1978). Climatically both areas are characterised by usually cool temperatures and by evenly distributed abundant precipitation *(c.* 1500- 2000 mm per year) resulting in nearly constant high relative humidity (Purey-Cust and McClymont, 1978). Although some climatic or edaphic differences may exist between the two areas compared, the main habitat differences are the presence or absence of deer and possum. The forests of both areas are dominated mainly by southern rata *(Metrosideros umbellata*),* kamahi *(Weinmannia racemosa),* and rimu *(Dacrydium cupressinum);* the other main canopy tree species include miro *(Podocarpus ferrugineus)* and Hall's totara *(P. hallii).* The small tree/tall shrub stratum includes numerous species, the most abundant of which are *Pseudopanax simplex, P. crassifolius, Griselinia littoralis, Coprosma foetidissima,* and the tree fern *Dicksonia squarrosa.* This forest type, which corresponds to the rimu-kamahi association described by Cockayne (1909a) and the lowland podocarp-broadleaved forest described by Wells and Mark (1966), is characteristic of nearly all of Bench Island and is the most extensive forest type of Stewart Island at elevations below c. 300 m.

Along much of the coastline of Stewart Island dead patches of forest occur over a 40-80 m strip, extending even further inland along stream valleys. Dead standing stems indicate that the former forest was of the rata-kamahi-rimu type. Coastal die-back in the same forest type is also common on Bench Island which indicates that browsing animals are not the sole cause. However, on Stewart Island browsing animals are the likely explanation for the poor forest recovery following die-back and for the tendency towards forest replacement by fern and graminoids. Similarly, further inland regeneration of most tree species is also poor and in general palatable species are virtually absent from the browse zone. The purpose of this study is to ascertain the degree to which poor tree regeneration may be attributed to browsing animals and to assess their effects on the abundance and development of understorey species in the rata-kamahi-rimu forest type.

The approach

The objectives of this study include not only the quantitative comparison of floristic composition but also the comparison of forest regenerative processes. A general comprehension of the various species' modes of regeneration is a prerequisite to understanding the possible effects of introduced browsing animals on regenerative processes. Stand structure, or the frequency distribution of differently sized individuals in a given stand, commonly reflects the modes of regeneration of the constituent tree species. Three general regeneration patterns as reflected by stand structure are commonly recognised: (1) catastrophic, (2) gap-phase, and (3) continuous. Catastrophic regeneration refers to the establishment of most individuals of a given population over a short period of time immediately following the devastation of the previous vegetation by a catastrophic disturbance such as fire, vulcanism or mass movements; the result is the development of an extensive even-aged stand (e.g. Ashton, 1976). Gap-phase regeneration refers to attainment of main canopy stature only beneath small to intermediate-sized canopy gaps resulting, for example, from windthrow of a single large tree or small group of trees (e.g. Bray, 1956). Continuous regeneration refers to the development of highly shade-tolerant species beneath canopies lacking any obvious gaps so that there is a steady replacement of the older dying trees (e.g. Hett and Loucks, 1976); this steady replacement process contrasts with the infrequent periodic replacement typical of catastrophic regeneration and the frequent periodic replacement typical of gap-phase replacement. In interpreting modes of regeneration the spatial patterns of tree species occurring at different scales is an essential consideration. For example, extremely large patch size, with randomly or regularly distributed trees within the patches, is often characteristic of catastrophically-regenerated populations (e.g. Cooper, 1961). Similarly, clustering of a population at an intermediate scale is often indicative of gap-phase replacement (e.g. Williamson, 1975), while the most shade-tolerant continuously regenerating species are often intensively clustered in small patches due to either vegetative reproduction or poor dispersion of heavy seeds (e.g. Veblen, Schlegel and Escobar, 1980). Consequently, in this comparison of forest regeneration on Bench and Stewart Islands particular attention is given to the spatial distributions of tree populations.

Analysis of size-class frequency distributions is often used to determine if in a given area a tree species is persistent in that there are sufficient numbers of young individuals to assure the replacement of the older trees as they die, thus maintaining or increasing the size of the main canopy population of that species. This type of analysis is based on the assumption that larger diameter stems are generally older than smaller diameter stems. Determination of an age-diameter relationship for each species usually substantiates this assumption, but in any case it is prudent to

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* For botanical authors see Appendix 1.

use rather large diameter classes (e.g. 10 cm) to allow for considerable variation in the strength of the age-size relationship. Characterisation of a population as all-aged and continuously regenerating is often based on qualitative evaluation of its size-class distribution. The degree of deviation from the ideal distributions expected for continuously regenerating populations in which there is a steady recruitment of older individuals from the younger age-classes; may also be assessed quantitatively. The negative exponential distribution as a model for describing age or size depletion rates has long been used in the analysis of stand structure (Meyer, 1952). Hett and Loucks (1976), however, have recently demonstrated that for steady-state *(sensu* Whittaker, 1975) populations of tree species the power function model better describes their age or size-class structures. Both models were used in the present study, but since the power function was found to clearly be the more rigorous criterion of continuous regeneration, only the results of its application are reported. The power function model is

$$y = y_o x^{-b}$$

where y is the number in any age- or size-class x, y_o is the initial input into the population at time zero, and b is the mortality rate. In addition to species persistence by way of a continuous regeneration mode, persistence may be attained through gap-phase or catastrophic regeneration modes which do not necessarily result in size-class distributions well described by the power function model.

METHODS

Stand structure

Tree diameters at breast height (dbh) of all individuals 5 cm dbh were measured and numbers of saplings (trees < 5 cm dbh and ≥ 1.4 m tall) counted in two 0.39 ha plots (54 x 72 m) each on Bench and Stewart Islands. For ring counts, at least 20 cores were taken from a wide range of diameters of the dominant tree species in each study area. Although rings of kamahi and rata were too indistinct to count reliably, log-transformed regressions of the diameter-age data from the podocarps (rimu and miro) confirmed the assumption that diameter is a good predictor of age ($r = 0.84$ to 0.94, $p < 0.01$). The size-class distributions of the tree species in each stand was analysed by preparing size-structure diagrams to depict the frequency of saplings and of stems in 10 cm dbh size-classes beginning at 5 cm. To avoid an over-representation of the number of individual trees, only the largest stem of multi-stemmed trees was included in the analysis. Size-class distributions were evaluated qualitatively for individual tree species and quantitatively for the total distributions of main canopy species, of sub-canopy species, and of both categories combined. The quantitative evaluation of size-class distributions was based on the goodness of fit to the distribution described by the power function model; the linear transformation of the power function model used is

$$\log_e y = \log_e y_o - b \log_e x$$

In order to characterise the vertical component of stand structure, trees ≥ 5 cm dbh were classified into the following five relative canopy-height categories: emergent, upper main canopy, lower main canopy, below main canopy, and overtopped. Tree species which are limited mainly to the fourth and fifth categories are referred to as sub-canopy species.

Spatial pattern

Spatial distributions of tree populations in the 0.39 ha plots were assessed by mapping all stems ≥ 1.4 m tall in the 3 x 3 m contiguous quadrats forming blocks of 432 quadrats. This mapping permitted application of a variation of the nested quadrat technique described by Greig-Smith (1964); the measure selected for determining the departure from a random distribution is Morisita's (1959) index. The application of this measure has been described by Williamson (1975). Morisita's index is given by

$$I\sigma = q \sum_{i=1}^{q} n_i (n_i - 1)/N(N-1)$$

where q is the number of quadrats, n_i the number of individuals of the species in the *ith* quadrat and N the total number of individuals in all q quadrats. The index $I\sigma$, equals 1.0 when the population is randomly distributed, where random implies an independent distribution of individuals into quadrats with an equal probability of each individual being distributed in any one quadrat. If the individuals are clustered, $I\sigma$ is > 1.0 and if evenly distributed or hyperdispersed, $I\sigma$ is <1.0. $I\sigma$ was computed for different species and different size-classes for quadrats of increasing size starting with quadrats of 1 x 1 unit with each unit being 3 x 3 m. For quadrat sizes ≤ 9 x 9 units the original 3 x 3 m quadrats were grouped into perfect squares, thus avoiding fluctuations in $I\sigma$ due to change in the shape of the blocks of quadrats (Pielou, 1977). Larger blocks of quadrats were rectangles of 9 x 11, 9 x 13, 9 x 16, 9 x 19, 9 x 22, and 9 x 24 units. The size of each quadrat is reported as the number of 3 m units on one side of a square quadrat of equivalent area. Thus, blocks of 27 x 27 m and 27 x 39 m are indicated as quadrat sizes 9 and 10.8, respectively. In cases where the quadrat sizes are not evenly divisible into the total area, Iσ was computed for the largest sub-areas containing whole quadrats of a given size. In such cases, the average index was computed from the results obtained from different sub-areas of the total grid of 3 x 3 m quadrats which, in any event, did not vary significantly. Where the number of individuals is small, Iσ tends to vary erratically; thus Iσ was computed only for the more abundant main canopy tree species populations.

Canopy density

In the 0.39 ha plots each of the 432 3 x 3 m quadrats was assessed as occurring beneath a closed canopy, a gap at least 3 m in diameter, or an intermediate canopy condition. Six hemispherical photographs were taken of each type of canopy condition and a mean canopy density was determined for each canopy type; these canopy densities subtracted from unity and expressed as percentages are Andersonís (1964) "total site factors" which are proportional to the total potential diffuse and direct sunlight at a given site (i.e., compared with total sunlight in the open over the same period). Total site factors for each stand were computed by multiplying the mean values for each canopy type by their respective frequencies and dividing their sum by the total frequency.

Understorey sampling

The understorey vegetation in each 0.39 ha plot was sampled in a restricted random lay-out using three types of plots. In addition to plots located on the forest floor, if a log occurred within 3 m of every third randomly selected sampling point, the plot was located on the nearest part of the nearest fallen log (including prostrate live tree trunks); additionally a few random sample points fell directly on logs. If a tree fern occurred within 5 m of a random sampling point, the epiphytic vegetation on its trunk was sampled as if the tree fern were an understorey plot. The presence of all vascular plants in height strata of ≤ 15 cm and 15-140 cm was recorded in all three types of plots.

In each of the 432 3 x 3 m quadrats in each plot understorey species cover (exclusive of bryophytes, tree species and tree ferns) was assessed as being < 1 % or ≥ 1 %. The purpose of this assessment was to estimate the number of "bare" (< 1 % cover quadrats in each stand. All *Dicksonia squarrosa* (the only tree fern species present in the stands sampled) > 0.5 m tall were counted in each 0.39 ha plot and classified into height classes of 0.5-2 m and > 2 m.

RESULTS AND INTERPRETATION

Stand structure

The two stands studied on Stewart Island are characterised by emergent rimu and miro which

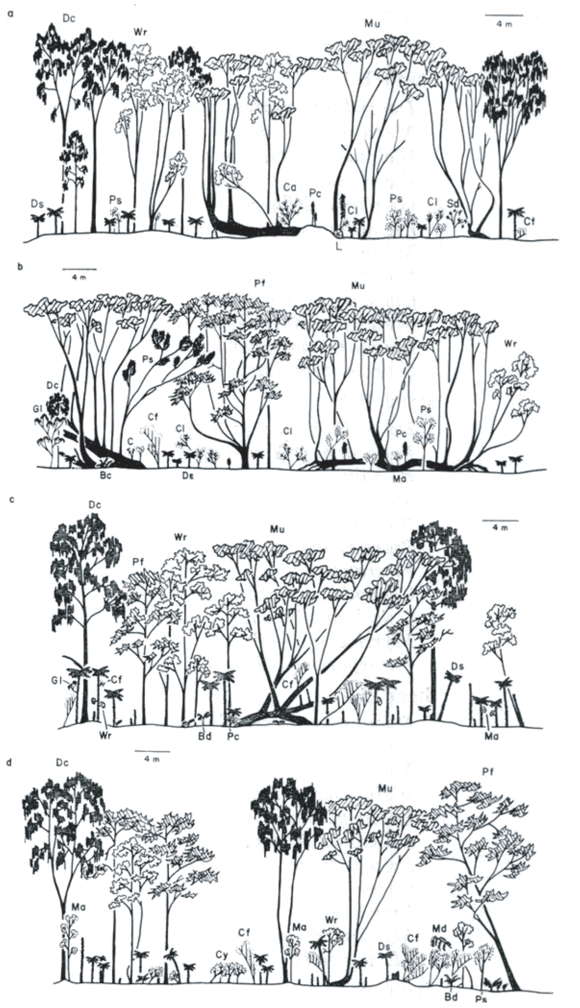

FIGURE 1. *Profiles of stand B-1 (a) and stand B-2 (b) on Bench Island and of stand S-1 (c) and stand S-2 (d)* on *Stewart Island. Dc,* Dacrydium cupressinum; *Wr,* Weinmannia racemosa; *Mu,* Metrosideros umbellata; *Pf,* Podocarpus ferrugineus; *Ds,* Dicksonia squarrosa; *Ps,* Pseudopanax simplex; *Cl,* Coprosma lucida; *Sd,* Schefflera digitata; *Cf,* Coprosma foetidissima; *GI,* Griselinia littoralis; *Be,* Blechnum capense; C, Coprosma sp.; *Bd,* Blechnum discolor; *Pc,* Pseudopanax crassifolius; *Ma,* Myrsine australis; *Cy,* Cyathodes juniperina; *Md,* Myrsine divaricata; *Ca,* Carpodetus serratus; *L,* log.

TABLE 1. *Numbers of stems ≥ 5 cm dbh in crown classes on Bench and Stewart Islands.*

	Crown Classes				
Stand And Species	Over-topped	Below main canopy	Lower main canopy	Upper main canopy	Emergent
Stand B-1					
Dacrydium cupressinum	12	3		24	1
Metrosideros umbellata			8	163	
Weinmannia racemosa	12	13	40	48	
Pseudopanax simplex	57	4	2	1	
Griselinia littoralis	3	1	1	2	
Pseudopanax crassifolius	3	2	3		
Myrsine australis	4	2			
Schefflera digitata	1				
Carpodetus serratus	2				
Melicytus lanceolatus	1				
Pseudopanax colensoi	2				
Senecio reinoldii	1				
Stand B-2					
Dacrydium cupressinum	1	2		2	
Podocarpus ferrugineus			1	7	
P. hallii	1			4	
Metrosideros umbellata		1	7	116	
Weinmannia racemosa	12	26	48	66	
Pseudopanax simplex	36	2	1	1	
P. crassifolius	1	3			
Carpodetus serratus	1				
Griselinia littoralis	1		1	2	
Myrsine australis	5	5	2		
Pittosporum colensoi	2	1			
Stand S-l					
Dacrydium cupressinum	2			3	16
Podocarpus ferrugineus	2	3	2	7	8
Metrosideros umbellata	3	3	2	42	
Weinmannia racemosa	30	62	46	48	
Leptospermum scoparium		8	6	2	
Griselinia littoralis	4	7	1	4	
Pseudopanax crassifolius	4	2	1		
Carpodetus serratus			1		
Pseudopanax simplex	71	9			
Myrsine divaricata	12	4			
M. *australis*	2	1			
Stand S-2					
Dacrydium cupressinum	3	6	5	17	25
Podocarpus ferrugineus		8		18	7
Metrosideros umbellata	1	2	3	9	3
Weinmannia racemosa	56	50	35	19	
Pseudopanax crassifolius	8	5	1		
Podocarpus hallii	2		1		
Pseudopanax simplex	47	8			
Myrsine divaricata	14	2			
Griselinia littoralis	2	2			
Myrsine australis	1				

extend several metres above a main canopy at a height of *c*. 20 m (Fig. 1 and Table 1). Although the two stands studied on Bench Island (B-1 and B-2) are characterised by the same mixture of dominant podocarps and broad-leaved species, their structures differ slightly from those on Stewart Island (S-l and S-2) in that the podocarps generally do not attain emergent stature. Thus, the tops of the forest canopies of stands B-1 and B-2 are more even in height than those of stands S-1 and S-2, perhaps reflecting a greater influence of wind on the Bench Island forest. All the stands studied are also characterised by numerous tree species which usually do not attain main canopy stature (i.e. sub-canopy species), the most abundant of which are *Pseudopanax simplex*. *P. crassifolius,* and *Griselinia littoralis*.

Size-class frequency distributions of rata are similar in all stands although total numbers are much greater on Bench Island (Fig. 2a). No rata saplings were present and only small numbers of 5-14 cm dbh stems occurred in all four stands. In general, the bell-shaped distributions for rata indicate populations of relatively even-sized individuals of main canopy stature (Table 1) in which there has been no recent establishment of new individuals. There is some inter-stand variation in the degree of even-sized tendency shown by rata, with stand B-1 being the most and stand S-2 the least even-sized. Similarly, in the case of kamahi there is a marked underrepresentation of saplings and in each stand this speciesí size-class frequency distribution is bell-shaped indicating tendencies towards populations of even-sized trees (Fig. 2b). In the absence of data on the relationship of dbh to age for both these species in these habitats, the degree to which even-sized size-class distributions reflect even-aged populations is not certain. However, where saplings are totally absent (rata) or rare (kamahi) the species are clearly not at present regenerating through seedling establishment and development into sapling and eventually tree-sized individuals. Since this lack of saplings characterises the dominant main canopy broad-leaved tree species on both Bench and Stewart Islands, the lack of regeneration cannot be attributed to deer or possum browsing.

Vegetative reproduction of rata by layering has been reported for Auckland Island by Cockayne (l909b) and is also important on Bench and Stewart Islands. Large trees lean over, sending adventitious roots downwards and epicormic shoots upwards and these become separate trees. Large (> 1 m diameter) prostrate trunks of rata with numerous epicormic shoots commonly extend 20 m or more along the

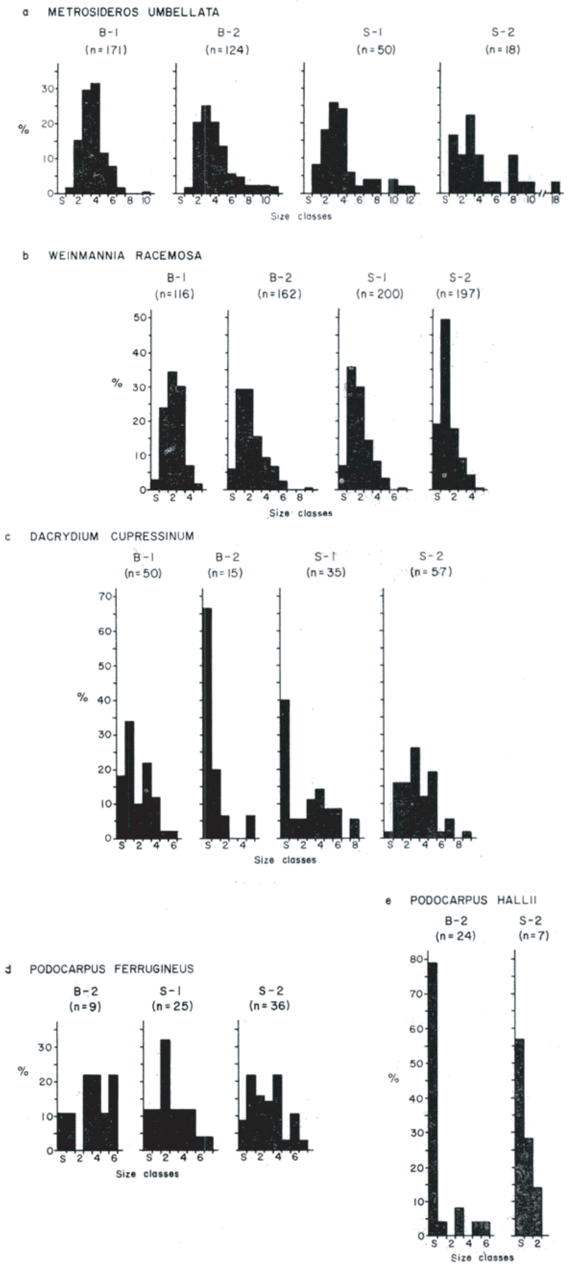

FIGURE 2. *Percentage frequency distributions in size-classes of main canopy tree species in stands B-1 and B-2 (Bench Island) and stands S-1 and S-2 (Stewart Island). The size-classes used are: S, trees < 5 cm dbh but at least 1.4 m tall (saplings); 1-18, trees by 10 cm dbh classes beginning at 5 cm,*

forest floor on both Bench and Stewart Islands. The stand with the least development of prostrate rata trunks is B-1 which is consistent with the younger age of rata indicated by the size-class distribution (Fig. 2a). In the collection of data, where adventitious roots connected boles to the ground the epicormic shoots were measured as separate trees; where no root-ground connection occurred, the shoots were regarded as limbs of the leaning main trunk. Thus, the lack of rata saplings and small stems in Fig. 2a also reflects the absence of new shoots produced by layering.

In the three stands where rimu is abundant (B-1, S-1 and S-2) small stems are present but are underrepresented in some of the smaller size-classes resulting in bimodal size-class distributions (Fig. 2c). This type of stand structure implies periodic regeneration, for example following the fall of large trees or small groups of trees. Similar size-class distributions have previously been interpreted as reflecting a regeneration gap for rimu related to climatic fluctuation (Wardle, 1963). However, when the composite size-class distribution from the four 0.4 ha plots is considered the size-class distribution of rimu is clearly all-aged (Fig. 2c). Similarly miro tends to be underrepresented in the sapling size-class and its size-class distribution is suggestive of intermittent regeneration on both Bench and Stewart Islands (Fig. 2d). Hallís totara in stand B-2 (Fig. 2e), the only stand in which it is abundant, likewise has a size-class distribution indicative of sporadic regeneration.

In contrast to the similar size-class compositions shown by the dominant tree species on both islands, important differences are evident for the sub-canopy tree species. *Pseudopanax simplex,* which is the most abundant sub-canopy tree species in all stands, is markedly underrepresented in the sapling size-class on Stewart Island, whereas on Bench Island saplings are abundant (Fig. 3a). Similarly, *Pseudopanax crassifolius, Myrsine australis,* and *Griselinia littoralis* as well as the combined less common species *(Melicytus lanceolatus. Fuchsia excorticata. Pseudopanax colensoi. Carpodetus serratus, Schefflera digitata. Senecio reinoldii,* and *Pittosporum colensoi),* are all represented by abundant saplings on Bench Island but not on Stewart Island (Fig. 3). In addition to the underrepresentation in the sapling size-class. the total numbers of these species are also generally less on Stewart Island. These differences in the abundance and size-class distributions of sub-canopy tree species on the two islands are taken as evidence that browsing has significantly retarded their regeneration on Stewart Island. The only exceptions to this pattern are *Leptospermum scoparium* and *Myrsine divaricata,* the former being absent and the latter rare on Bench Island.

Traill (1965), when writing of the forests as he remembered them before, and subsequent to, the influence of deer, has several pertinent comments on the sub-canopy tree species and understorey vegetation: "*Nothopanax* [now *Pseudopanax*] *colensoi,* and *Coprosma lucida* were doomed because deer developed the habit of chewing the bark as

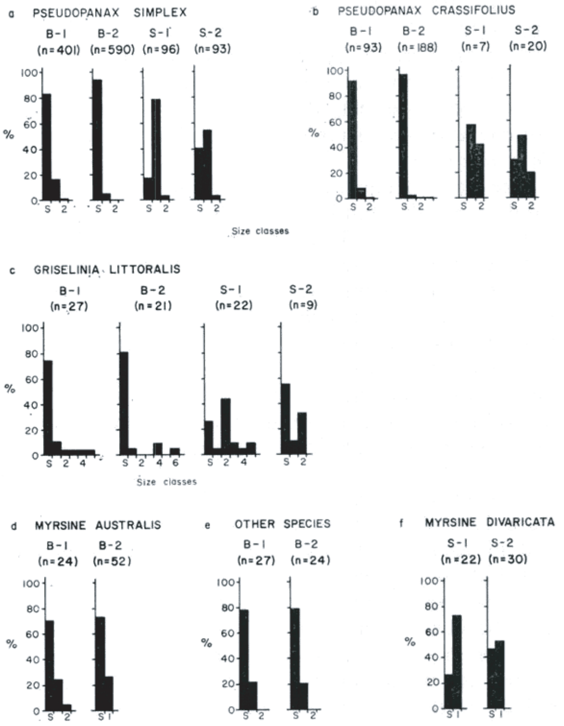

FIGURE 3. *Percentage frequency distributions in size-classes of sub-canopy tree species in stands B-1 and B-2 (Bench Island) and stands S-l and S-2 (Stewart Island). The size-classes used are: S, trees < 5 cm dbh but at least 1.4 m tall (saplings); 1-6, trees by 10 cm dbh classes beginning at 5 cm. The category "other species" includes Schefflera digitata, Pseudopanax colensoi, Pittosporum colensoi, Senecio reinoldii, Carpodetus serratus, Fuchsia excorticata, and Melicytus lanceolatus. Species not sufficiently abundant to show in the figure include: Myrsine divaricata in B-2 (1 stem), M. australis in stands S-l and S-2 (4 stems in each), Pseudopanax colensoi in the other species category in stands S-1 (2 stems) and S-2 (1 stem). and Leptospermum scoparium in stand S-l (20 stems).*

well as the leaves. They also began to push over the last named and I was puzzled to see so many broken ones till I realised what was happening." He also says when referring to the time of the deer liberation (1905): "At that time the bush of Stewart Island had a dense undergrowth of ferns, shrubs and young trees. This growth was so dense that even on dry days in the depth of winter anyone going into the bush for only a few chains usually got wet to the waist." This is certainly not the case now. Similarly, Cockayne (1909a) lists *Pseudopanax edgerleyi* and *P. simplex* as abundant and *P. colensoi, Myrsine australis, Coprosma lucida,* C. *rotundifolia* and *Pittosporum colensoi* as common in the rata-kamahi-rimu forests of Stewart Island. Today these species are relatively scarce on Stewart Island although all are present and most are abundant on Bench Island. Johnson (1972) also found that *Coprosma lucida* was severely reduced by deer in his comparative study of the Lake Manapouri shoreline and Buncrana Island (which was largely free of browsing mammals). Mark and Baylis (1975) report a similar influence on *Pseudopanax* spp. and *Coprosma* spp. by red deer following their invasion of Secretary Island, as do James and Wallis (1969) in their comparative study of an island free of browsing mammals with the mainland at Lake Waikareiti in the North Island.

When the dominant tree species are considered together (both podocarps and broad-leaved species), their size-class distributions are bell-shaped, indicating populations of largely even-sized stems (Fig. 4). However, when all the sub-canopy tree species are included, the whole size-class distributions for stands B-1 and B-2 approach the ideal distribution expected for a continuously regenerating population. In contrast, even when sub-canopy tree species are included, the Stewart Island stands show underrepresentations in the sapling size-class.

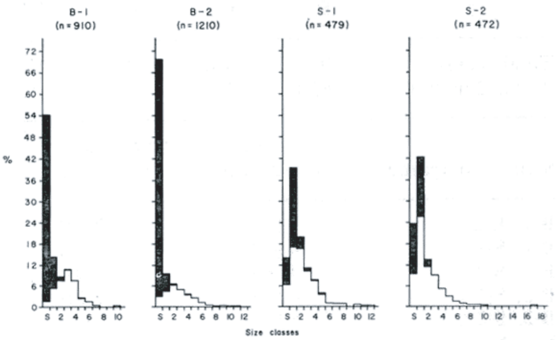

FIGURE 4. *Percentage frequency distributions in size-classes of total main canopy tree species (empty histograms) and total sub-canopy tree species (solid histograms) in stands B-1 and B-2 (Bench Island) and stands S-1 and S-2 (Stewart Island). Main canopy tree species include* Dacrydium cupressinum, Podocarpus ferrugineus, P. hallii, Metrosideros umbellata, *and* Weinmannia racemosa; *all other tree species are classified as sub-canopy species. The total number of main canopy and sub-canopy species is given by n. The size-classes used are:* S, *trees < 5 cm dbh but at least 1.4* m *tall (saplings); 1-18, trees by 10* cm *dbh classes beginning at 5 cm.*

TABLE 2. *Regression equations fitting the various size-class distributions to the power function model; n is the number of pairs of X (size-classes) and Y (numbers of stems in size-classes) variables.*

STAND AND TREE STRATUM	n	EQUATION	*r*	P<
B-1				
Dominant trees	9	$\log_e Y = 4.6856 - 0.5263 \log_e X$	-0.39	NS
Sub-canopy trees	5	$\log_e Y = 8.6492 - 2.2874 \log_e X$	-0.97	0.01
All trees	9	$\log_e Y = 8.3376 - 1.4615 \log_e X$	-0.86	0.01
B-2				
Dominant trees	12	$\log_e Y = 5.8878 - 0.8873 \log_e X$	-0.73	0.01
Sub-canopy trees	6	$\log_e Y = 8.7246 - 2.2823 \log_e X$	-0.97	0.01
All trees	12	$\log_e Y = 8.6790 - 1.\ 5640 \log_e X$	-0.95	0.001
S-1				
Dominant trees	12	$\log_e Y = 6.3273 - 1.1017 \log_e X$	-0.76	0.01
Sub-canopy trees	6	$\log_e Y = 5.6874 - 1.2028 \log_e X$	-0.77	NS
All trees	12	$\log_e Y = 7.3457 - 1.3333 \log_e X$	-0.83	0.001
S-2				
Dominant trees	12	$\log_e Y = 6.6267 - 1.1991 \log_e X$	-0.83	0.001
Sub-canopy trees	3	$\log_e Y = 5.1982 - 0.\ 7531 \log_e X$	-0.72	NS
All trees	12	$\log_e Y = 7.5877 - 1.4245 \log_e X$	-0.89	0.001

TABLE 3. *Total numbers of* Dicksonia squarrosa *stems > 0.5* m *tall and percentage 0.5-2.0* m *tall. Differences in the 0.5-2.0* m *height class were subjected to a chi-square test using the absolute frequencies and applying Yates' correction (Greig-Smith, 1964).*

	STANDS			
	B-1	B-2	S-1	S-2
Total stems	987	780	763	751
% 0.5-2 m tall	62.1	73.6	11.5	11.2

	STATISTICAL SIGNIFICANCE	
Stands compared	Chi-square	P <
B-1, B-2	25.5	0.001
B-1, S-1	456.3	0.001
B-1, S-2	458.3	0.001
B-2, S-1	603.8	0.001
B-2, S-2	605.5	0.001
S-1, S-2	0.2	NS

TABLE. 4. *Frequency of 3 X 3 m quadrats assessed as occurring beneath canopy gaps on Bench and Stewart Islands. Differences were subjected to a chi-square test using Yates' correction (Greig-Smith, 1964); the number of quadrats assessed in each stand was 432.*

	STANDS			
	B-1	B-2	S-1	S-2
Frequency	41	6	85	115

	STATISTICAL SIGNIFICANCE	
Stands compared	Chi-square	P <
B-1, B-2	26.0	0.001
B-1, S-1	17.2	0.001
B-1, S-2	41.7	0.001
B-2, S-1	74.7	0.001
B-2, S-2	112.1	0.001
S-1, S-2	5.5	0.025

All-aged forests of continuously regenerating populations, containing many stems (i.e. > 400) in nine to twelve size-classes, should have size-class distributions which closely approximate the power function model as indicated by correlation coefficients of –0.90 to –0.99 (c.f. Hett and Loucks, 1976). In all stands the size-class distributions of the dominant tree species either do not fit the power function model at the $p < 0.05$ significance level or fit it rather poorly ($r = -0.73$ to -0.83; Table 2). The greatest deviation from the power function model is for the dominant tree species of stand B-1 which is dominated by an even-sized, relatively young population of rata. The size-class distributions of the sub-canopy tree species are well described by the power function model in stands B-1 and B-2 ($r = -0.97$, $p < 0.01$ in both) but not in the Stewart Island stands. Thus, the fits for the total tree populations are much improved over those for the dominant species in stands B-1 and B-2 but only moderately improved in stands S-1 and *S-2*. For the total tree populations, only in stand B-2 is the size-class distribution well described by the power function model ($r = -0.95$, $p < 0.001$). In stand B-1 the poorer fit to the power function is due to the overrepresentation of mostly rata in the 25-34 cm size-class while in stands S-1 and S-2 it is attributable to the underrepresentation of both dominant and sub-canopy species in the sapling size-class (Fig. 4).

Relative to Bench Island, the proportions as well as absolute numbers of the tree fern *Dicksonia squarrosa* in the 0.5-2 m height class are low on Stewart Island (Table 3) which is a direct consequence of the deer browsing the new tree fern shoots. Traill (1965) also adds: ". . . the deer smashed down a lot of small tree ferns in places where these were growing close together. They appeared to be deliberately making open places to play in." As a consequence of epiphytic tree seedling establishment on the tree fern stems, the inhibition of tree fern regeneration may also affect the rate of tree seedling establishment.

The relative abundance of tree ferns> 2 m tall is substantially greater on Stewart Island than on Bench Island (Table 3). This may be due to the higher light levels beneath the main canopies, as discussed below, or may be related to less competition for other resources from the much reduced populations of sub-canopy species on Stewart Island.

Canopy density

An obvious structural difference between the Bench and Stewart Island forests is the relatively closed canopy of the former and the open, heterogeneous canopy of the latter. In stands S-1 and S-2 the frequencies of 3 X 3 m quadrats assessed as occurring beneath canopy gaps are much greater than in stands B-1 and B-2 (Table 4). Total site factors (Anderson, 1964), based on the analyses of hemispherical canopy photographs, are 33.4 and 25.7 per cent for stands B-1 and B-2, respectively, and 37.9 and 45.9 per cent for stands S-1 and S-2, respectively. Given the less dense main canopy on Stewart Island and hence higher" light levels, the reduced numbers of both sub-canopy tree species

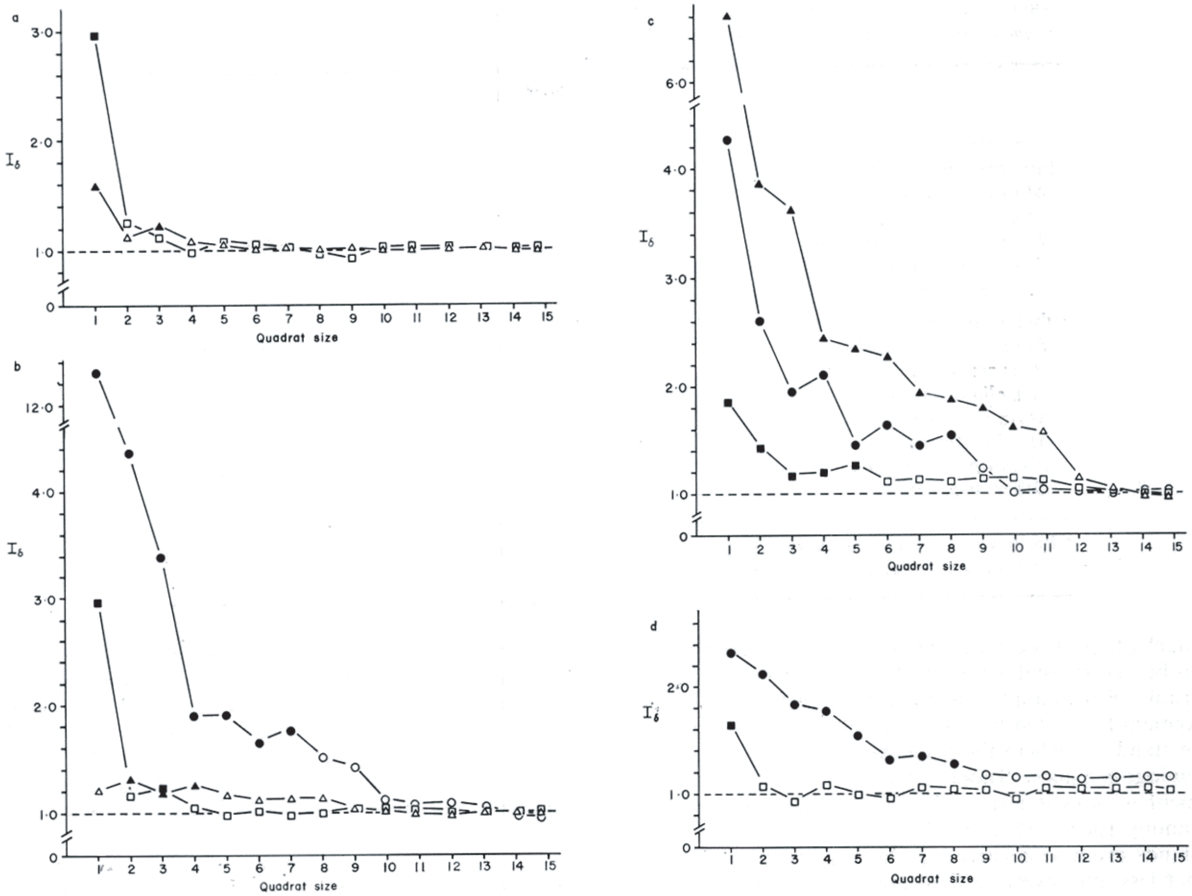

FIGURE 5. *Values of Morisitaís index,* la, *at different quadrat sizes in stands B-J (a) and B-2 (b) on Bench Island, and stands S-1 (c) and S-2 (d) on Stewart Island for* Metrosideros umbellata > *10cm dbh* (▲, △.*),* Weinmannia racemosa > *10cm dbh* (■, □), *and* W. racemosa *10cm dbh* (●, ○). *Filled symbols are* la *values significantly greater than 1.0 (P <0.05) according to an F-test of Morisita* (1959). *Quadrat size is given as side length of a square quadrat in units of 3m.*

and 0.5-2 m tall tree ferns are most logically attributed to browsing. While on Bench Island canopy gaps created by tree falls are quickly filled by sub-canopy tree species and tree ferns, canopy gaps on Stewart Island remain unoccupied due to the inhibitory effects of browsing.

Spatial pattern

Spatial patterns of young trees of a species may differ markedly from those of older trees which have long been subject to competition. Consequently, for kamahi and rata (the only species abundant enough to permit quantitative analyses of their spatial distributions) the spatial distributions of all individuals ≥ 1.4 m tall but with stems 10 cm dbh were assessed separately from individuals with stems > 10 cm dbh. The dashed lines in Figure 5 at Iσ = 1.0 represent random patterns. High la values correspond to patterns of individuals that are highly clustered at a given quadrat size. Thus, kamahi 10 cm dbh are highly clustered at the smallest quadrat sizes in all stands, except in B-1 where they were not abundant enough to analyse; they remain significantly clustered at quadrat sizes up to 7 x 7 units (441 m^2) in stand B-2 and up to 8 x 8 units (576 m^2) in stands S-l and S-2. Since only the largest stem of a multi-stemmed tree was recorded, the clustering at small quadrat sizes cannot be attributed to the common multi-stemmed habit of this species. On the other hand,

TABLE 5. *Percentage of saplings and stems ≥ 5 cm dbh established on logs and on tree ferns (in parenthesis) on Bench and Stewart Islands.*

	Stands B-1	 B-2	 S-1	 S-2
Main canopy species				
Metrosideros umbellata	26.3	25.8	33.3	27.8
Weinmannia racemosa	40.5	50.0	28.0 (4.5)	11.7 (5.1)
Dacrydium cupressinum	0.0	0.0	5.7	0.0
Podocarpus hallii	0.0	50.0	-	0.0
P. ferrugineus	-	0.0	0.0	0.0
Sub-canopy species				
Pseudopanax simplex	35.7	41.0 (0.2)	19.8 (5.2)	14.0 (4.3)
P. crassifolius	49.5	54.8	0.0	0.0
Griselinia littoralis	74.1 (3.7)	90.0	31.8 (22.7)	22.2
Myrsine australis	16.7 (4.2)	40.4 (3.8)	0.0	25.0
M. *divaricata*	-	0.0	0.0	0.0
Pseudopanax colensoi	25.0	100.0	0.0 (100)	0.0 (100)
Other species*	7.4	25.0	0.0	0.0

* Includes *Schefflera digitata. Pittosporum colensoi, Senecio reinoldii. Carpodetus serratus, Fuchsia excorticata. .Melicytus lanceolatus.*

much of the clustering at the small quadrat sizes appears to be due to establishment of kamahi groups on fallen trunks. For example, the intensity of clustering of small kamahi (indicated by higher 10 values) is much greater in stand B-2 where the percentage of stems established on logs is highest (Table 5). Clustering due to establishment on logs is also evident in the maps of the main canopy species (Fig. 6). Kamahi > 10 cm dbh in all stands are also clustered at the smallest quadrat sizes but less intensively so than are the small stems. Patch sizes of kamahi > 10 cm dbh are also much smaller than those of the smaller stems as indicated by 10 values approaching a random pattern for quadrat sizes> 2x 2 units (36m^2). Given the greater abundance of stems > 10 em dbh and hence greater potential for more intense clustering these results are highly significant. This pattern of 10 values is indicative of establishment in highly clustered patches up to c. 441 - 576 m^2 in extent and subsequent self-thinning which reduces both the intensity of clustering and patch size. In other words, kamahi establishes in small to intermediate size patches, especially favouring sites on logs beneath canopy gaps, and as the canopy gap is filled by both the upward growth of individuals beneath the gap and by the lateral development of large bordering trees, the patch becomes less dense and less extensive.

Rata >10 cm dbh were abundant enough to permit quantitative analyses of their spatial distributions in all stands except S-2. In stand S-1 rata >10 cm dbh are highly clustered at all quadrat sizes ≤ 10 X 10 units (900 m^2) (Fig. 5c). This large scale pattern is attributed to layering from extensive prostrate trunks of rata and is also reflected by the high percentage of stems established on logs (Table 5; Fig. 6). Clustering of rata> 10 cm dbh at small to intermediate quadrat sizes in stands B-1 and B-2 is also attributed to layering of large prostrate trees but this process is less advanced in these stands. Here, epicormic shoots from leaning rata trunks are common but this process of vegetative multiplication has not yet proceeded to the stage of abundant production of adventitious roots and hence of actual layering. The total lack of sapling sized stems and a very small number of 5-9 cm dbh stems of rata (one in S-1 and two in S-2) indicates that in all stands studied rata has not recently been regenerating other than by layering. However, on Bench Island data collected in a 20 X 20 m plot located beneath a large gap (*c.* 20 m in diameter) created by the fall of a large podocarp and several smaller trees indicate some development of rata from seedling into sapling and small diameter size-classes. Here, two saplings and five 5-14 cm dbh stems of rata had established; five stems in a plot this size corresponds to a density of 50 stems in the 0.39 ha plots, in which only two and four 5-14 cm dbh rata stems were recorded. Similarly, in this large and relatively old gap there was a total of 35 kamahi all ≤ 30 cm of which 37 % were saplings and 54% were in the 5-14 cm dbh size-class; at a plot size of 0.39ha the density of kamahi saplings in the gap would correspond to

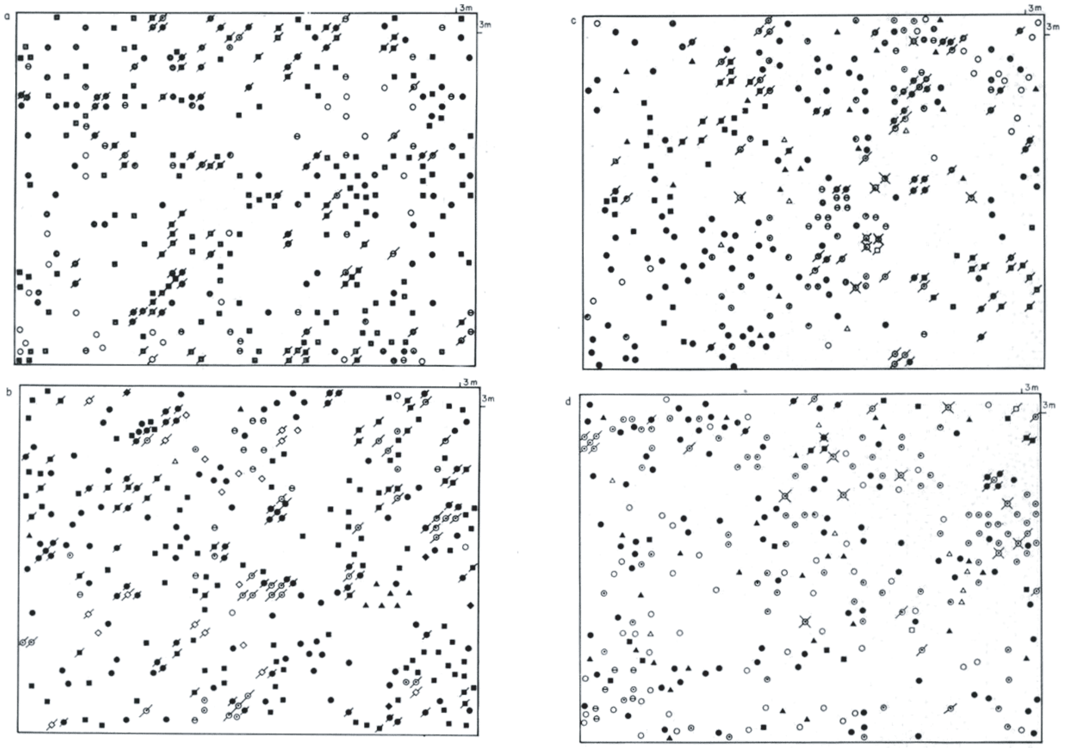

FIGURE 6. *Maps showing locations in stands B-1 (a) and B-2 (b) on Bench Island and stands S-1 (c) and S-2 (d) on Stewart Island of trees at least 1.4m tall of the following species:* Metrosideros umbellata *> 10cm dbh* (■), Weinmannia racemosa *> 10cm dbh* (●) *and ≤ 10cm dbh* (⊙), Dacrydium cupressinum *> 10cm dbh* (○) *and ≤ 10cm dbh* (⊖), Podocarpus ferrugineus *> 10cm dbh* (▲) *and ≤ 10cm dbh* (△), *and* P. hallii *> 10cm dbh* (◆) *and ≤ 10cm dbh* (◇). *Single slashed lines indicate establishment on logs or prostrate trunks and crossed lines indicate establishment on tree ferns.*

126, whereas only three and ten saplings were present in stands B-1 and B-2, respectively. In addition to the presence of saplings of dominant tree species in the gap a proliferation of sub-canopy tree species had occurred, resulting in densities 74 and 14% greater than in stands B-1 and B-2, respectively. Thus, rata and kamahi appear largely dependent on large canopy gaps for development from seedlings into small trees whereas the sub-canopy tree species depend less on large canopy gaps for their regeneration.

Although none of the podocarps were sufficiently abundant to permit quantitative assessments, their spatial distributions also indicate the establishment of regeneration beneath canopy gaps. For example, rimu ≤ 10 cm dbh is clustered at small to intermediate-sized quadrats in all stands as illustrated by the dense cluster of small rimu in the centre of plot S-I beneath a large canopy gap in association with *Leptospermum scoparium* (Fig. 6c and Fig. 7c). Similarly, where Hall's totara and miro are relatively abundant, stems 10 cm dbh and stems > to cm dbh are clustered in small to intermediate-sized patches (Fig. 6). Thus, both the podocarp and broad-leaved dominant tree species appear to regenerate in response to canopy gap creation. Which species occupies a given gap is probably the fortuitous result of seed and / or seedling availability at the time of gap creation. Once small to intermediate-sized stems of one species are established, the development of young individuals of other species would be impeded which is reflected

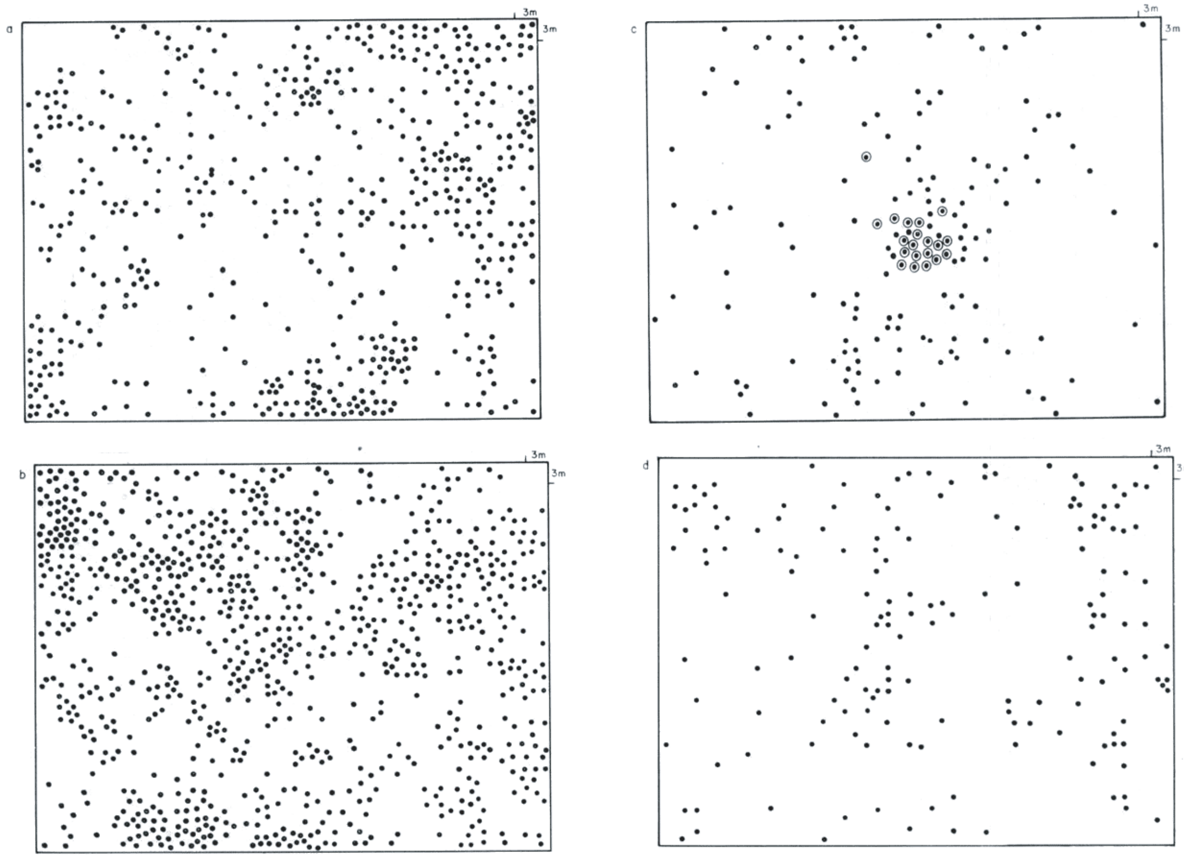

FIGURE 7. *Maps showing locations of all sub-canopy trees at least 1.4 m tall in stands B-1 (a) and B-2 (b) on Bench Island and stands S-1 (c) and S-2 (d) on Stewart Island.* Leptospermum scoparium *is indicated by circled dots and was present only in stand Sol.*

FIGURE 8. *Typical understorey in rata-kamahi-rimu forest on Bench Island.*

FIGURE 9. *Typical understorey in rata-kamahi-rimu forest at Chew Tobacco Bay, Stewart Island.*

TABLE 6. *Frequency of 3 x 3 m quadrats with < 1% cover by understorey species on Bench and Stewart Islands. Differences were subjected to a chi-square test using Yatesí correction (Greig-Smith, 1964); the total number of quadrats assessed in each stand was 432.*

	STANDS B-1	 B-2	 S-1	 S-2
Frequency	52	32	123	165

Stands compared	STATISTICAL SIGNIFICANCE Chi-square	 P <
B-1, B-2	4.8	0.05
B-1, S-1	35.1	0.001
B-1, S-2	77.2	0.001
B-2, S-1	63.7	0.001
B-2, S-2	114.6	0.001
S-1, S-2	8.8	0.005

by the tendency for the dominant tree species to form mutually exclusive patches (Fig. 6).

The sub-canopy tree species (considering all species together) occur in small to intermediate-sized patches (Fig. 7). Clustering is again probably a consequence of establishment on logs (small patches) and response to canopy gaps (small to intermediate-sized patches). The much reduced density of sub-canopy tree species on Stewart Island, attributed to deer browsing, is readily evident in Figure 7. Competition from these abundant sub-canopy tree species undoubtedly reduces the number of saplings of main canopy trees which survive beneath canopy gaps on Bench Island. Therefore, even over large areas of forest the size-class distributions of the main canopy species do not conform to the ideal expected for a continuously regenerating population.

Understorey vegetation

Several palatable species such as *Kirkophytum lyallii, Asplenium bulbiferum, Coprosma lucida,* and *Phymatosorus diversifolius* previously abundant on Stewart Island (Cockayne, 1909a) and presently abundant on Bench Island, are now rare or absent on Stewart Island.

The most visually obvious difference between the understories of Bench and Stewart Islands is the luxuriant nearly continuous plant cover in the former area and the abundance of relatively bare sites in the latter area (Figs. 8 and 9). This observation is confirmed by the data in Table 6 on frequency of 3 x 3 m quadrats which were assessed as having total understorey species cover values of less than 1 %. The frequencies of these bare quadrats are two to five times greater on Stewart Island. Given the lesser canopy densities, and hence higher light levels, the reduced understorey cover on Stewart Island is likely to be the consequence of severe browsing pressure.

Species percentage frequencies were determined separately for height classes of ≤ 15 cm and > 15 cm and for each of three types of site: forest floor, tree ferns and logs (Table 7). A major difference between the understorey vegetation of the two islands is the abundance of the fern *Phymatosorus diversifolius* on Bench Island and its scarcity on Stewart Island; on all three types of site it is by far the most frequent species on Bench Island. Cockayne (1909a) described *P. diversifolius* as abundant on the ground on Stewart Island when he studied the vegetation soon after the liberation of deer. Now, the only site in the Stewart Island plots in which *P. diversifolius* exceeds a frequency of 5 % is on the tree fern trunks where it is often above the browse-height of deer. Other than this species and the also highly palatable fern *Asplenium bulbiferum,* the frequencies of common species in the ≤ 15 cm height class are consistently and significantly ($P < 0.05$) more frequent on Stewart Island than on Bench Island on the forest floor sites (Table 7). This is generally true for woody species, ferns, and other herbs. The greater frequencies in the small height class are attributed to the more open main canopy as well as the opening up of the understorey in the 0.15-2.0 m height class by deer browsing on Stewart Island. Browsing and trampling of *P. diversifolius* prevents the development of an extensive cover by this species (as is characteristic of Bench Island) which, in turn, permits a much greater frequency diversity in the ≤ 15 cm layer on Stewart Island. Similarly, the reduction by browsing of the number of *D. squarrosa* tree ferns in the 0.5-2.0 m height class on Stewart Island permits greater light penetration to the forest floor. Despite the greater frequencies in the 15 cm layer on the forest floor, in the > 15 cm height class frequencies are greater on Bench Island. Thus, on Stewart Island a reduced main canopy and understorey permits more frequent establishment but browsing prevents the development in height of these plants. This is most evident when total frequencies of all species combined are considered; total frequencies in the ≤ 15 cm height class are over three times greater on Stewart Island yet total frequencies in the > 15 cm height class are over four times greater on Bench Island.

On both Bench and Stewart Islands epiphytes on the trunks which provide sites safe from deer browsing (at heights above *c.* 2 m) most of the

TABLE 7. *Percentage frequency of common species in 0.75* m^2 *plots on the forest floor, on* Dicksonia squarrosa *trunks, and on fallen logs on Bench Island (stands B-1 and B-2) and on Stewart Island (stands S-1 and S-2); only species which occurred in a total of ten or more samples in at least one study area are listed for a given substrate type. The ≤ and > symbols following each species indicate height classes of ≤ 15 cm and > 15 cm. Differences were subjected to a chi-square test using the absolute frequencies and applying Yates' correction (Greig-Smith, 1964). The number of samples is given by n.*

		FOREST FLOOR SITES				TREE FERN SITES				FALLEN LOG SITES			
		Bench Island	Stewart Island	Chi-square	P<	Bench Island	Stewart Island	Chi-square	P<	Bench Island	Stewart Island	Chi-square	P<
		n=174	n=200			n=190	n=232			n=70	n=44		
TREES AND SHRUBS													
Pseudopanax simplex	≤	10.9	68.5	124.5	.001	3.2	17.7	20.8	.001	18.6	72.7	30.9	.001
	>	6.3	0.5	8.4	.005	5.8	25.0	26.8	.001	20.0		8.3	.005
Coprosma foetidissima	≤	24.1	82.5	125.9	.001	4.7	26.3	33.5	.001	37.1	75.0	14.0	.001
	>	4.0	3.0	0.1	NS	1.1	26.3	50.4	.001	15.7		6.6	.025
Podocarpus ferrugineus	≤		42.5	93.3	.001						22.7	14.7	.001
	>		1.5	1.1	NS						2.3	0.1	NS
Griselinia littoralis	≤	10.9	28.0	15.9	.001	4.8	6.5	0.3	NS	21.4	20.5	0.1	NS
	>		1.0	0.4	NS	2.1	9.1	7.8	.01	4.3		0.6	NS
Myrsine divaricata	≤	1.1	26.5	45.7	.001						25.0	16.6	.001
	>	0.6	1.5	0.1	NS								
Dacrydium cupressinum	≤		16.5	29.7	.001								
	>		0.5	0.1	NS								
Cyathodes juniperina	≤		10.0	16.5	.001								
	>		9.5	15.5	.001								
Weinmannia racemosa	≤					17.4	26.3	4.3	.05	24.3	11.4	2.1	NS
	>					4.2	30.6	46.1	.001	1.4		0.1	NS
Myrsine australis	≤					2.1	4.3	1.0	NS				
	>					7.4	6.0	0.1	NS				
Coprosma sp.	≤									11.4		3.8	NS
	>									5.7		1.2	NS
FERNS AND FERN ALLIES													
Phymatosorus diversifolius	≤	37.9	2.0	76.6	.001	25.8	25.9	0.1	NS	81.4	4.5	60.9	.001
	>	71.3	1.0	202.5	.001	41.6	9.1	61.1	.001	80.0		66.0	.001
Blechnum capense	≤	0.6	3.0	1.8	NS						2.3	0.1	NS
	>	24.1		52.0	.001					15.7	2.3	3.9	.05
Asplenium bulbiferum	≤	7.5		13.3	.001					11.4		3.8	NS
	>	4.0		6.2	.025					2.9		0.2	NS
Hymenophyllum demissum	≤	12.6	74.0	138.8	.001	3.2	25.0	37.1	.001	28.6	65.9	13.9	.001
Grammitis billardieri	≤	0.6	14.0	21.6	.001	11.1	25.9	13.8	.001	4.3	34.1	15.9	.001
Dicksonia squarrosa	≤	5.2	19.5	15.8	.001					2.9	9.1	0.9	NS
	>	10.9	5.0	3.8	NS					11.4	2.3	2.0	NS
Tmesipteris tannensis	≤	0.6	8.0	10.2	.005	7.4	31.5	35.6	.001				
	>					3.7		6.6	.025				
Hymenophyllum ferrugineum	≤	0.6	7.0	8.4	.01	9.5	23.3	13.1	.001				
H. multi/Mum	≤		8.5	13.6	.001	2.1	11.2	11.8	.001				
Blechnum discolor	≤		2.0	1.9	NS								
	>		3.5	4.5	.05								
Rumohra adiantiformis	≤	1.1	5.0	3.3	NS	10.0	5.6	2.3	NS	5.7	13.6	1.2	NS
	>		2.0	1.9	NS	4.2		7.8	.01	7.1	9.1	0.1	NS
Hymenophyllum flabellatum	≤					8.4	45.7	68.8	.001				
H. revolutum	≤						4.3	6.5	.025				
H. dilatatum	≤									5.7		1.2	NS
OTHER HERBS													
Luzuriaga parviflora	≤	2.3	27.0	40.3	.001					8.6	40.9	15.1	.001
	>									1.4		0.1	NS

TABLE 7. *continued*

		FOREST FLOOR SITES				TREE FERN SITES				FALLEN LOG SITES			
		Bench Island	Stewart Island	Chi-square	P<	Bench Island	Stewart Island	Chi-square	P<	Bench Island	Stewart Island	Chi-square	P<
		n=174	n=200			n=190	n=232			n=70	n=44		
Ripogonum scandens	≤	1.1	7.0	6.4	.01								
	>	1.1		0.7	NS								
Chiloglottis cornuta	≤		8.5	13.6	.001								
Caladenia carnea	≤		9.5	15.5	.001								
Corybas oblongus	≤	0.6	6.5	7.5	.01								
Nertera dichondraefolia	≤	10.9	9.0	0.3	NS					20.0	11.4	0.9	NS
	>	0.6		0.1	NS								
ALL SPECIES*													
Total number of species		32	44	4.5	.05	15	18	0.4	NS	33	33	0.1	NS
Total of absolute frequencies ≤ /*n*		1.5	5.3	388.3	.001	0.9	2.1	107.1	.001	3.2	5.2	28.2	.001
Total of absolute frequencies> /*n*		1.4	0.3	119.6	.001	0.5	0.1	61.6	.001	2.2	0.3	72.5	.001

* Includes 28 additional species which occurred in fewer than ten samples in both areas for a given substrate type.

common tree and shrub species are more frequent on Stewart Island. Epiphytic establishment on tree fern trunks is occasionally a successful regeneration strategy for species such as kamahi, *Pseudopanax simplex, P. crassifolius, P colensoi, Griselinia littoralis,* and *Myrsine australis* as indicated by the presence of saplings and stems > 5 cm dbh still attached to tree fern trunks (Table 5). The greater frequencies of both epiphytic seedlings and of tree-sized individuals attached to *D. squarrosa* suggest that this regeneration strategy is more frequent beneath the more open forest canopies on Stewart Island. Among the ferns and fern allies, which are more shade-tolerant than most of the woody species, plants in the > 15 cm height class are more frequent on Bench Island; presumably due to deer browsing, the larger plants have been reduced on Stewart Island. Again, on Stewart Island the total absolute frequencies of plants ≤ 15 cm are more than twice as great, yet in the > 15 cm height class total frequencies are five times greater on Bench Island. The understorey species established on fallen logs as well as protrate living rata trunks 0.5-1.0 m above the forest floor are located in sites easily accessible to deer. Again, many species are more abundant in the ≤ 15 cm size-class on Stewart Island, but plants > 15 cm tall are seven times more frequent on Bench Island (Table 7). Considering the large percentages of the tree saplings and stems > 5 cm dbh established on logs, the lack of individuals > 15 cm tall on logs of species such as G. *littoralis, P. simplex,* and *W. racemosa* has serious implications for the future regeneration of these tree species under intense browsing pressure on Stewart Island.

CONCLUSIONS

On both Bench and Stewart Islands the size-class distributions of the main canopy tree species are similar; thus, it is unlikely that browsing animals on Stewart Island have greatly affected the population structure of the main canopy tree species. However, the dearth of tree seedlings> 15 cm tall in contrast to the abundance of seedlings ≤ 15 cm tall indicates that on Stewart Island browsing impedes seedling development which, in the long-term, will endanger maintenance of the main canopy tree populations. Rather than reflecting animal influences, the underrepresentation of rata and kamahi in the small diameter-classes on both Bench and Stewart Islands reflects their discontinuous modes of regeneration. Both species commonly regenerate vigorously on sites devastated by mass movements in Westland (Wardle, 1966, 1971), thus following a catastrophic regeneration mode. A gap-phase mode of regeneration is also indicated by the presence of small stems mainly beneath large wind throw gaps on Bench Island. While the catastrophic regeneration mode probably also occasionally occurs on Bench and Stewart Islands, in the stands studied gap-phase replacement is the more likely mode of regeneration for the main canopy species. Poor survivorship of rata and kamahi beneath canopy gaps leading to underrepresentation in the small size-classes on Bench Island is also attributed to intense competition with the numerous sub-canopy tree species. A similar explanation has been offered for underrepresentation of small individuals of the dominant species in some mesic species-rich northern temperate forests (Harcombe and Marks, 1978; Golden, 1979).

The fact that coastal die-back occurs on Bench Island in the absence of browsing animals demonstrates that such die-back is not necessarily caused by introduced browsing animals. Although the cause of the die-back is not positively known, the most likely explanation is exposure to salt-laden winds. Slight changes in storm frequency or intensity, not easily detected without long-term meterological observations of the sites affected, could account for the relatively sudden appearance of die-back over the past few decades. Nevertheless, recovery from die-back via epicormic sprouting of species such as rata and *Griselinia littoralis* will be less successful where possums are numerous. Similarly, the drastic effects of browsing animals, mainly of white-tailed deer, on successful establishment of sub-canopy trees, tree ferns, and understorey species, seriously impedes forest recovery following die-back on Stewart Island. Furthermore, the former abundance of many palatable species on Stewart Island (Cockayne, 1909a) and their abundance on Bench Island, compared to their current absence or scarcity on Stewart Island reflects a gradual depauperisation of the flora due to severe browsing pressure. The effects on the vegetation by browsing animals documented in the present comparative study are largely in accordance with the results from surveys of the forests of Stewart Island (Williamson, 1976; Ross, 1977). In general, the effects of browsing animals on the structure and floristic composition of the rata-kamahi-rimu forests of Stewart Island have already been significant and are likely to become more severe unless animal numbers are reduced.

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APPENDIX 1

FLORA OF BENCH ISLAND

* indicates species listed by Poppelwell (1918)

FERNS AND RELATED PLANTS

* *Asplenium bulbiferum* Forst. f.
* *A. flaccidum* Forst. f.
... *A. lucidum* Forst. f.
... *A. obtusatum* Forst. f.
* *A. polydon* Forst. f.
Blechnum banksii (Hook. f.) Mett. ex Diels
B. capense (L.) Schlect. ("minus" form and "procerum" form)
B. chambersii Tindale
* *B. durum* (Moore) Christen.
Cyathea smithii Hook. f.
... *Dicksonia squarrosa* (Forst. f.) Swartz
* *Grammitis billardieri* Willd.
* G. *heterophylla* Labill.
... *Histiopteris incisa* (Thunb.) J. Smith
... *Hymenophyllum demissum* (Forst. f.) Swartz
* *H. dilatatum* (Forst. f.) Swartz
H. ferrugineum Colla
H. flabel/atum Labill.
H. multifidum (Forst. f.) Swartz
* *H. revolutum* Col.
* *H. sanguinolentum* (Forst. f.) Swartz
* *Lastreopsis hispida* (Swartz) Tindale
* *Phymatosorus diversifolius* (Willd.) Pic. Ser.
* *Polystichum vestitum* (Forst. f.) Presl.
* *Pteridium aquilinum* var. *esculentum* (Forst. f.) Kuhn
Rumohra adiantiformis (Forst. f.) Ching
* *Tmesipteris tannensis* Bernh.
Trichomanes venosum R. Br.

TREES AND SHRUBS

Aristotelia serrata (J. R. et G. Forst.) W. R. B. Oliver
Carpodetus serratus J. R. et G. Forst.
... *Coprosma areolata* Cheesem.
C. *colensoi* Hook. f.
* C. *foetidissima* J. R. et G. Forst.
C. *lucida* J. R. et G. Forst.
C. *rhamnoides* A. Cunn.
* C. *rotundifolia* A. Cunn.
Dacrydium cupressinum Lamb.
Dracophyllum longifolium (J R. et G. Forst.) R. Br.
Fuchsia excorticata (J. R. et G. Forst.) Linn. f.
Gaultheria antipoda Forst. f.
* *Grise!inia !illoralis* Raoul.
* *Hebe elliptica* (Forst. f.) Pennell
* *Melicytus lanceolatus* Hook. f.
* *Metrosideros umbellata* Cav.
* *Myrsine australis* (A. Rich.) Allan
M. *divaricata* A. Cunn.
Olea ria arborescens (Forst. f.) Ckn. et Laing
* *O. angustifo!ia* Hook. f.
* *Pittosporum colensoi* Hook. f.
* *Podocarpus ferrugineus* G. Benn. ex D. Don
P. hallii Kirk
Pseudopanax colensoi (Hook. t.) Philipson
* *P. crassifolius* (A. Cunn.) C. Koch
* *P. edgerleyi* (Hook. f.) C. Koch
P. simplex (Forst. f.) Philipson
Pseudowintera colorata (Raoul) Dandy
Schefflera digitata J. R. et G. Forst.
* *Senecio reinoldii* Endl.
* *Weinmannia racemosa* Linn. f.

LIANES

* *Muehlenbeckia australis* (Forst. f.) Meissn.
* *Ripogonum scandens* J. R. et G. Forst.
* *Rubus australis* Forst. t.
R. cissoides A. Cunn.

HERBACEOUS PLANTS

* *Apium australe* Thouars
Caladenia carnea R. Br.
Cory bas oblongus (Hook. f.) Reichb. f.
C. *rivularis* (A. Cunn.) Reichb. f.
C. *trilobus* (Hook. f.) Reichb. f.
Dendrobium cunningham;; Lindl.
Disphyma australe (Sol.) J. M. Black
Drymoanthus adversus (Hook. f.) Dockrill
* *Earina mucronata* Lindl.
Gnaphalium involucratum Forst. f.
* *Hydrocotyle novae-zelandiae* DC.
* *Kirkophytum lyallii* (J. B. Armst.) Allan
Luzuriaga parviflora (Hook. f.) Kunth
Nertera depressa Banks et Sol. ex Gaertn.
* *N. dichondraefolia* (A. Cunn.) Hook. f.
Stellaria parviflora Banks et Sol. ex Hook. f.
* *Tillaea moschata* (Forst. f.) DC.
Urtica ferox Forst. f.

GRAMINOIDS

Carex appressa R. Br.
* C. *trifida* Cav.
Hierochloe fusca Zotov sp. nov
Juncus pallidus R. Br.
Luzula banksiana Meyer
* *Poa astonii* Petrie
* *Scirpus aucklandicus* (Hook. f.) Boeck
S. habrus Edgar
* *S. nodosus* (R. Br.) Rottb

ADVENTIVE SPECIES

Agrostis stolonifera L.
Cirsium arvense (L.) Scop.

Species listed by Poppelwell (1918), but not collected during present survey (Modern names in parentheses)
Asplenium scleroprium Homb et Jacq.
Blechnum penna-marina (Poir.) Kuhn.
Carex lucida Boott *(Carex flagellifera* Col.)
Erechtites scaberula Hook. f.
Hierochloe redo lens (Forst. f.) R. Br.
Tetragonia trigyna Banks et Sol. ex. Hook. f.
Senecio stewartiae J. B. Armst.