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PHYSICAL INFLUENCES ON FOREST TYPES AND DEER HABITAT, NORTHERN FIORDLAND, NEW ZEALAND

Summary: Forest types of the Wapiti, Doon and Glaisnock catchments, ranked in order of proportion of preferred food species for deer, paralleled a gradient of landform stability. Seral forests and low altitude silver beech forests were preferred deer habitat because they contained the largest proportions of highly preferred species. They often occurred on unstable landforms such as debris cones, colluvial sideslopes, and terraces with recent and compound soils, assumed to be of high nutrient status. In contrast, mountain beech and high altitude silver beech forests supported lower proportions of highly preferred food species and were poor deer habitat. They occurred on more stable landforms such as bedrock sideslopes, ridges and benches with poorly-drained, infertile soils. The Wapiti/Doon catchments contained a greater abundance of more stable landforms than the Glaisnock and therefore provided poorer deer habitat in the predominant mountain beech forests.

Keywords: browsing damage; red deer; wapiti; habitats; landforms; soil development; site factors; beech/hardwood forest; Fiordland; *Cervus elaphus nelsonii*; *Cervus elaphus scoticus*.

Introduction

Red deer (*Cervus elaphus scoticus*), have become established in a diverse range of habitats in New Zealand from sea level to the alpine regions (Logan and Harris, 1967). Forest, shrubland and grassland are all utilised but a preference is shown for areas with a mixture of vegetation types (Wodzicki, 1961; Howard, 1965).

In northern Fiordland, a 1969/70 survey showed that the forests that were most used by introduced red deer and wapiti (*Cervus elaphus nelsonii*) were complex silver beech forests of mid slopes and terraces (C3), and seral forests (P1, P2) (Table 1; Wardle, Hayward and Herbert, 1971). In contrast, subalpine scrublands (S types) and mountain beech forest types (especially M2, M3) were the least used.

Although many factors (e.g., slope, physiography, hunting pressure) affect deer distribution, the preference of red deer and wapiti for certain forest types largely reflects food preferences and availability (e.g., Wardle, Hayward and Herbert, 1973; J. Wardle, 1974). In northern Fiordland, the complex silver beech forests and seral forests contained high numbers of deer-preferred food species such as the small trees and shrubs *Griselinia littoralis*², *Pseudopanax simplex*, *P. colensoi*, *Myrsine divaricata*, *Coprosma foetidissima*, the fern *Polystichum vestitum*, and the herb *Astelia nervosa* (Wardle *et al.*, 1971; J. Wardle, 1984; Stewart, Wardle and Burrows, 1987). In contrast, subalpine scrublands and mountain beech types contained fewer preferred food species.

Table 1: Forest and scrubland types of northern Fiordland (after Wardle *et al.*, 1971)

Class	1 - subalpine scrub
	S1 - short <i>Hebe-Dracophyllum</i> scrub
	S2 - tall <i>Senecio</i> scrub
	S3 - Silver beech- <i>Dracophyllum</i> scrub
Class	2 - complex forests dominated by silver beech
	C1 - Silver beech- <i>Archeria-Senecio</i> forest
	C2 - Silver beech- <i>Coprosma</i> forest
	C3 - Silver beech-pepperwood- <i>Blechnum</i> forest
	C4 - Kamahi-silver beech- <i>Cyathea</i> forest
Class 3	- complex forests with a large mountain beech component
	M1 - Silver beech-rata-kamahi-mountain beech forest
	M2 - Mountain beech- <i>Phyllocladus</i> forest
	M3 - Mountain beech-manuka- <i>Dacrydium</i> forest
Class	4 - mixed scrub-hardwood forest
	P1 - <i>Lacebark-Polystichum</i> forest
	P2 - Silver beech-lacebark- <i>Polystichum</i> forest
	P3 - <i>Mahoe-pate-Cyathea</i> forest
Class	5 - simple mountain beech-silver beech forests
	E1 - Mountain beech-silver beech-kamahi forest
	E2 - Simple silver beech forest
	E3 - Simple mountain beech forest

Forests with high numbers of preferred food species tend to be those that occur on sites where disturbances such as flooding and downslope drift intermittently rejuvenate soils (P. Wardle, 1960, 1985; J. Wardle, 1984; Rose and Burrows, 1985). Conversely, mountain beech types with low numbers of preferred species frequently occur on poorly-drained, more stable sites (J. Wardle, 1984). It has

²Nomenclature follows Allan (1961), Moore and Edgar (1970), and Edgar (1973).

been suggested that inherent differences in fertility between these sites may explain the differences in forest composition (e.g., Wardle *et al.*, 1971; Rose and Burrows, 1985).

The morphological and chemical properties of soils reflect a trend of increasing soil development with time (Stevens and Walker, 1970; Smith and Lee, 1984). On stable landforms (e.g., bedrock sideslopes, benches, ridges) in climates with high rainfall the fertility of mineral soils decreases as they develop (e.g., from recent towards gley podzols) (Stevens and Walker, 1970; O'Connor, 1980; Basher, Tonkin and Daly, 1985). Infertile, poorly drained organic soils are also common on the strongly indurated bedrock of these landforms (cf. Poole *et al.*, 1951). Conversely, relatively fertile recent or compound recent soils occur on landforms of young surface age that are frequently disturbed by mass movement and fluvial action (e.g., debris cones and terraces) (Stewart and Harrison, in press).

It is therefore possible that we can relate use of forest by deer to the underlying physical environment. A resurvey of northern Fiordland forests in 1984/85 provided an opportunity to concentrate on physical site factors and how they influenced the vegetation composition and distribution that was established in the 1969/70 survey. Our objective was to determine whether landform type or stage of soil development, in combination with forest type, could be used to predict areas of high deer use. We used two approaches:

1. The original 1969/70 survey data were re-analysed by ordination.
2. Additional environmental data (in particular, on soils and landforms), were collected in 1984/85.

Use of a forest type by deer may also depend on the distribution of preferred species within it. The variability in composition in one forest type (C3: Silver beech-pepperwood-*Blechnum* forest) was therefore related to variation in the physical environment. This type was one of the most affected by deer in 1969/70, and occurred over a range of landforms and soils.

Study Area

The 'Wapiti Area' of Fiordland National Park is part of a deeply dissected upland rising to over 1800 m. It is characterised by generally narrow-floored valleys and fiords with steep sides which can rise 300-1000 m, sometimes almost vertically (McKellar, 1982). The major rock types are highly indurated gneiss, granite and granodiorite which are strongly resistant to

weathering (Wood, 1960). Successive glaciations have resulted in valley-in-valley topography, the remnants of which are indicated by ice-smoothed ridges, glacier-cut benches, and low saddles.

In post-glacial time landforms have been frequently disturbed by erosion/deposition, or reworking by rivers. Debris flows frequently peel vegetation and regolith from sideslopes, and larger scale slumps and rock avalanches sometimes block valley systems to form lakes (e.g., Lake Thomson). In addition, many large scale erosion features have probably been triggered by tectonic activity associated with the numerous faults throughout the region.

Soils are infertile, strongly developed, and are mapped as upland and high country podzolised yellow-brown earths and podzols (New Zealand Soil Bureau, 1968a). Prevailing westerly winds, interrupted by the main mountain axis, cause a declining west to east rainfall gradient across northern Fiordland. Rainfall in the west (Milford Sound) averages 6000-8000 mm per year and in the east (Te Anau) 1000-1300 mm (New Zealand Meteorological Service, 1983). The Wapiti Area, close to the Southern Alps, is likely to be at the wetter end of this gradient. Precipitation is heavy throughout the year but is generally greater in the summer months. In winter, much of the precipitation above treeline (c. 900 m) falls as snow.

Methods

Species composition and physical characteristics

In 1984/85, 526 variable area plots were located in the Wapiti, Doon, and Glaisnock catchments as part of a wider study on the recovery of forest understoreys after a reduction in deer numbers. The eight forest types common in the Wapiti/Doon and four in the Glaisnock were sampled. Areas of forest in each type were subjectively chosen to cover a range of altitudes and landforms, and plots randomly located in each. Forest type (*sensu* Wardle *et al.*, 1971) and the landform on which it occurred were recorded on each plot. Seven major landform types were recognised in the study area (Fig. 1).

At each plot a line was run out from a randomly located point to a specified radius (0.55, 0.90, 1.25, 1.80, 2.50 or 3.10 m) until at least 10 individuals of woody species in the browse tier (30-180 cm) were counted. If the target count of 10 was not reached at the maximum radius (3.10 m), sampling was terminated.

Woody species were grouped into three preference categories as foods for deer (Table 2 in Stewart *et al.*,

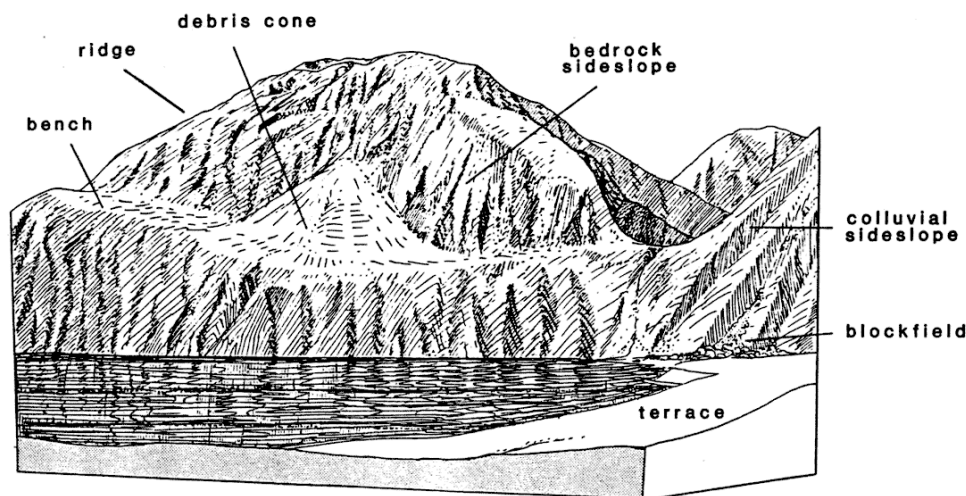


Figure 1: Schematic diagram of a northern Fiordland landscape showing the seven recognised landforms.

1987). Stem densities for each preference category and the percentage of each category in different forest types and on different landforms were calculated.

Soil description

It was not possible to survey soils extensively in the time available. Therefore 32 soil profiles were described in eight forest types in the Wapiti catchment in the vicinity of Lakes Hankinson and Thomson³. These were used to infer variation in soils between forest types. Soil pits were dug to bedrock or to a maximum depth of 1 m. Soil profiles were described following the terminology of FAO (1974) with the addition of the subscript j, denoting weak expression of a qualifying suffix (Canada Soil Survey Committee, 1978). On the basis of horizonation and depth to bedrock the described soils were classified according to the New Zealand Genetic classification (see Table 2, New Zealand Soil Bureau, 1968b). Eighteen of the soil profiles were described in the silver beech-pepperwood-*Blechnum* forest (C3) selected for detailed study.

Ordination of 1969/70 survey data

The distribution of species and forest types in relation to environmental factors was assessed by ordinating the presence/absence species data from the 1053 plots measured on the original 1969/70 survey, using

Detrended Correspondence Analysis (DECORANA, DCA; Hill, 1979; Hill and Gauch, 1980). The final DCA matrix groups plots with similar composition, and species with similar distribution in the plots (Gauch, 1982). These patterns often reflect underlying environmental gradients. Each sample or plot retains the forest type name (e.g., C1, C2, C3) given by Wardle *et al.* (1971) (Table 1).

Results

Forest type/landform/soil relationships

In the Wapiti/Doon catchments forest types were closely related to landforms (Fig. 2). Mountain beech types (M types) occurred almost exclusively on stable erosional landforms: bedrock sideslopes, ridges and benches. These landforms were characterised by shallow organic or strongly developed soils over bedrock (Table 2). Species such as *Dacrydium biforme*, *Leptospermum scoparium*, and *Phyllocladus alpinus* were found on these soils where poor drainage had led to gleying and leaching had resulted in podzolization (Table 2).

Silver beech types occurred on a range of less stable landforms characterised by recent soils and yellow-brown earths. High altitude silver beech types (C1, C2), were primarily found on bedrock sideslopes. Silver beech-pepperwood-*Blechnum* forest (C3) was

³Detailed soil descriptions are held at the Forestry Research Centre, FRI, P.O. Box 31-011, Christchurch.

Table 2: Soil types and landforms in forests of the Lake Hankinson/Thomson area, northern Fiordland. * = one soil pit dug per description unless otherwise indicated. † = a compound soil profile. ¹Horizonation sequences are: yellow-brown earth, Ah, Bw, C; podzolised yellow-brown earth, Ah, Ej, Bw, C; gley podzol, Ah, Eg, Bs (Bfe), C; shallow gley podzol, Ah, Eg, R; shallow peat, O, R; recent/recent, Ah, C, 2Ah, 2C; recent/yellow-brown earth, Ah, C, 2Ah, 2Bw, 2C; yellow-brown earth/yellow-brown earth, Ah, Bw, (C), 2Ah, 2Bw, 2C; yellow-brown earth/gley podzol, Ah, Bw, (C), 2Ah, 2Eg, 2Bs, 2C.

Forest Type	Landform	Soil Type ¹
Lacebark- <i>Polystichum</i> forest (P1)	debris cone	recent/recent*
Silver beech-lacebark- <i>Polystichum</i> forest (P2)	terrace	recent/recent
	debris cone	recent/yellow-brown earth
	debris cone	yellow-brown earth
	debris cone	recent/recent
	terrace	yellow-brown earth (9)
	terrace	podzolised yellow-brown earth (2)
	terrace	gley podzol (2)
	debris cone	yellow-brown/gley podzol
	debris cone	yellow-brown earth
	colluvial sideslope	yellow-brown/yellow-brown
block field	gley podzol	
Silver beech- <i>Coprosma</i> forest (C2)	bench	yellow-brown earth
Silver beech- <i>Archeria-Senecio</i> forest (C1)	bedrock sideslope	gley podzol
	bedrock sideslope	shallow gley podzol
Silver beech-rata-kamahi-mountain beech forest (M1)	bench	gley podzol
	bench	shallow gley podzol
	bedrock sideslope	shallow gley podzol
Mountain beech- <i>Phyllocladus</i> forest (M2)	bench	shallow peat
	bedrock sideslope	gley podzol
	bedrock sideslope	shallow gley podzol
Mountain beech-manuka- <i>Dacrydium</i> forest (M3)	bedrock sideslope	shallow peat

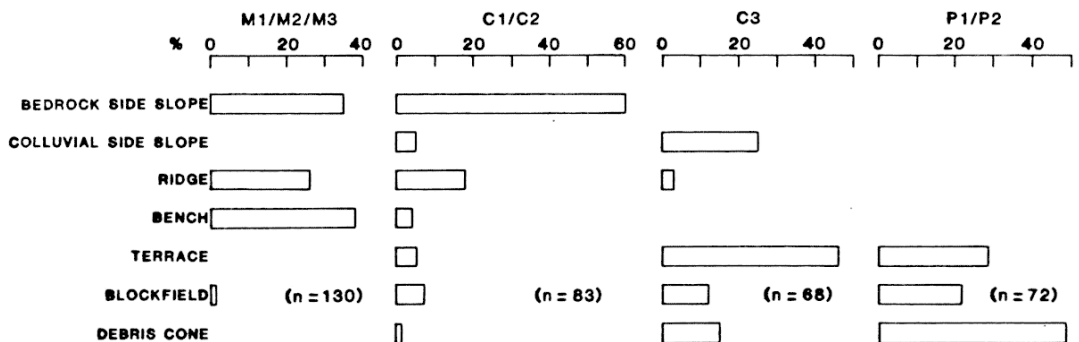


Figure 2: Percentages of different landforms under different forest types in the Wapiti/Doon catchments, northern Fiordland. n = number of variable area plots sampled.

present on colluvial sideslopes, but at lower elevations occurred on terraces, block fields and debris cones. A large range of soils had developed on these landforms, from recent soils to well-developed yellow-brown earth soils and occasional gley podzols (Table 2). The large number of compound soils at different stages of development reflected different rates of deposition.

The most active, frequently disturbed landforms where recent or compound soils predominated supported seral communities (P1/P2). These landforms were terraces, blockfields and debris cones.

In the Glaisnock catchment forest/landform relationships differed to those in the Wapiti/Doon. High altitude silver beech forests (C1/C2) occurred predominantly on colluvial sideslopes, not on bedrock sideslopes as in the Wapiti/Doon (Fig. 3). Because steep slopes were more common and terrace and debris cone systems were less common than in the Wapiti/Doon, over 50% of plots in silver beech-pepperwood-*Blechnum* forest (C3) were located on colluvial sideslopes. A few C3 plots were located on more active landforms such as terraces, and all P2 plots occurred on block fields and debris cones.

Forest understorey composition

(a) Wapiti/Doon

The proportion of woody species highly preferred by deer was low (2-4%) in the browse tier of mountain beech types (M1/M2/M3) that occurred on well-developed and often shallow soils on stable landforms such as benches (Table 2, Figs. 2 and 4). Similarly, highly preferred species were low in silver beech types (C1/C2) on well developed soils of stable landforms such as bedrock sideslopes and ridges (Figs.

2 and 4). The highest proportions of highly preferred species occurred in low altitude silver beech forest (7%, C3) and seral forests (8/15%, P1/P2) (Fig. 4). Highly preferred food species therefore occurred on recent and compound soils of depositional, frequently disturbed landforms such as terraces and debris cones (Table 2, Fig. 2). They also occurred on landforms such as block fields, and in C3 forests on colluvial sideslopes and ridges (Fig. 2).

Moderately preferred species predominated in M1, CI and C2 types on well developed soils on erosional landforms (Figs. 2 and 4). Least preferred species occurred primarily in M2, M3, P1 and P2. They were therefore characteristic of both well developed soils on stable landforms and frequently disturbed recent soils. In the P types and C3 forest *Pseudowintera colorata* was the most common species of low preference, and in M2 and M3, *Phyllocladus alpinus* and *Dacrydium bifforme*.

(b) Glaisnock

The distribution of preferred plants in the Glaisnock differed from that in the Wapiti/Doon. In the Glaisnock, mountain beech types were rare and almost all plots (except 5 plots in M1 not considered here) were located in C and P types.

Highly preferred species in silver beech types (C1/C2/C3) comprised larger proportions of all stems (7-10%) than in the Wapiti/Doon and occurred primarily on colluvial sideslopes (Figs. 3, 5). As in the Wapiti/Doon, the highest proportion of highly preferred species occurred on the frequently disturbed debris cones of seral (23%, P2) types. Least preferred species were rare in all types

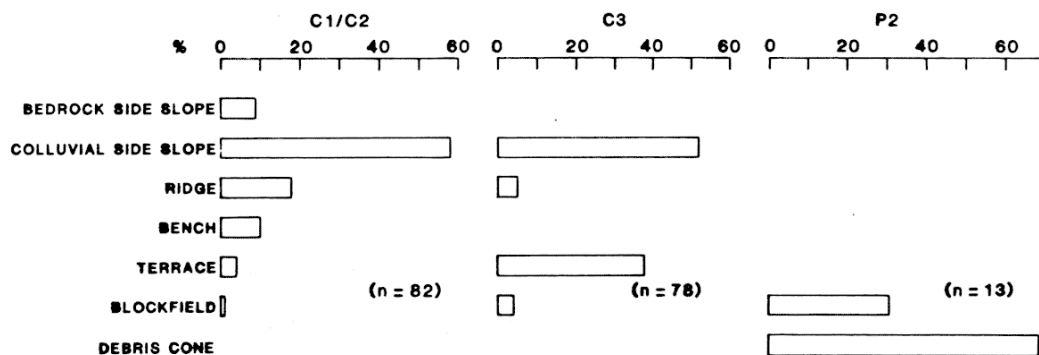


Figure 3: Percentages of different landforms under different forest types in the Glaisnock catchment, northern Fiordland. n = number of variable area plots sampled.

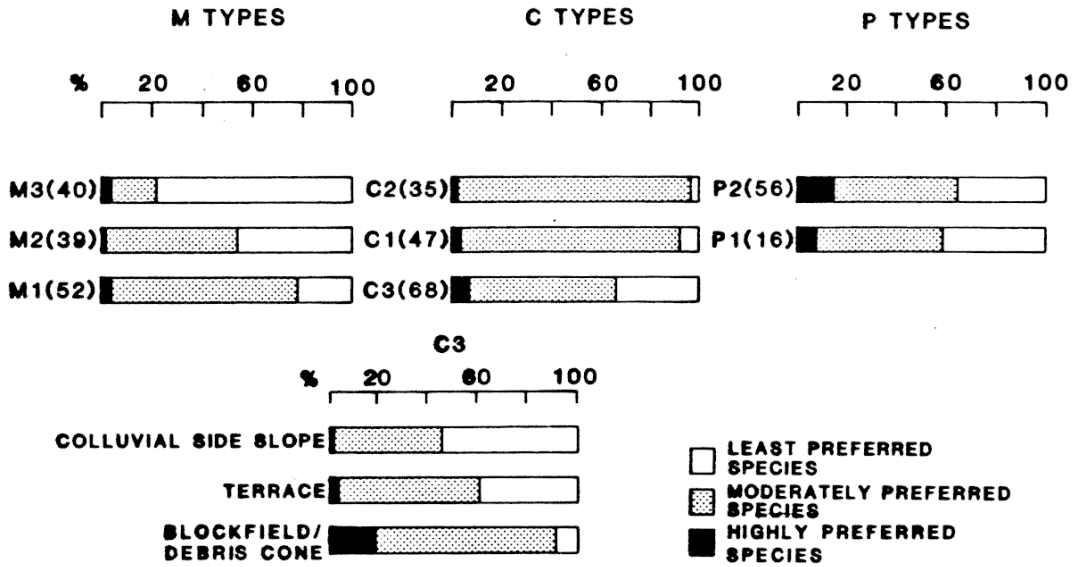


Figure 4: Percentages of differently preferred species groups in forest types and on different landforms (C3 forest) in the Wapiti/Doon catchments, northern Fiordland. Numbers in parentheses are the number of variable area plots sampled.

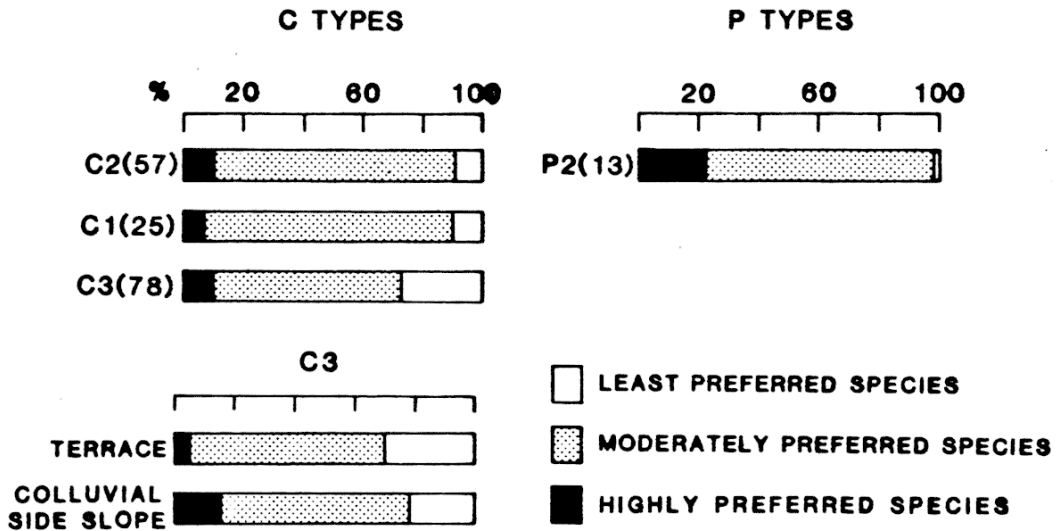


Figure 5: Percentages of differently preferred species groups in forest types and on different landforms (C3 forest) in the Glaisnock catchment, northern Fiordland. Numbers in parentheses are the number of variable area plots sampled.

except C3. The highest proportion of stems in all types were moderately preferred species (Fig. 5).

Understorey variation within a forest type

Although highly preferred species were restricted to a few landforms or soil types in some forest types (e.g., M2 and M3) they occurred on a range of soils and landforms in others. Silver beech-pepperwood-*Blechnum* forest occurred on all landforms described except bedrock sideslopes and benches (Figs. 2 and 4). In the Wapiti/Doon C3 forests, highly preferred species comprised a larger proportion of total stems on block fields and debris cones 18% than on colluvial sideslopes or terraces (< 1, 3%, Fig. 4). Least preferred species were proportionally the most common on colluvial sideslopes. In contrast, in the Glaisnock catchment highly preferred species in C3 forest had their largest proportional representation (15%) on colluvial sideslopes (Fig. 5). Least preferred species were uncommon on terraces and colluvial sideslopes.

Distribution of species and forest types

Axis 1 of the DCA ordination of 1053 recce plots reflected an elevational gradient (Spearman rank correlation = 0.86, $p < 0.001$; Fig. 6). Changes in species composition and the distribution of forest types along this gradient have also been related to declining rainfall from west to east (J. Wardle, 1984).

The relationship of soil types, landforms and forest types in the Wapiti/Doon and Glaisnock catchments suggests that Axis 2 of the DECORANA ordination reflects a complex soils gradient (Fig. 6). Additionally, Axis 2 was correlated with the broad survey physiography classes; plots with high scores generally occurred on terraces or gullies, and those with low scores, on faces or ridges (Spearman rank correlation = 0.32, $p < 0.001$). Because soil fertility generally declines with soil development and organic/peaty soils are also generally infertile (see Introduction) inferences may be made about the distribution of forest types and species in relation to soil nutrient status.

The 16 forest and scrubland types established in the 1969/70 survey occupied different positions in relation to altitude (Axis 1) and soils (Axis 2). The E types formed an altitudinal sequence. Simple mountain beech forest (E3) tended to be lower on Axis 2, perhaps indicating more well developed soils than either E1 or E2 (Fig. 00; Wardle *et al.*, 1971). The subalpine scrub types occurred over similar ranges of altitude but short *Hebe-Dracophyllum* scrub (S1) was located at the high end of Axis 2, perhaps

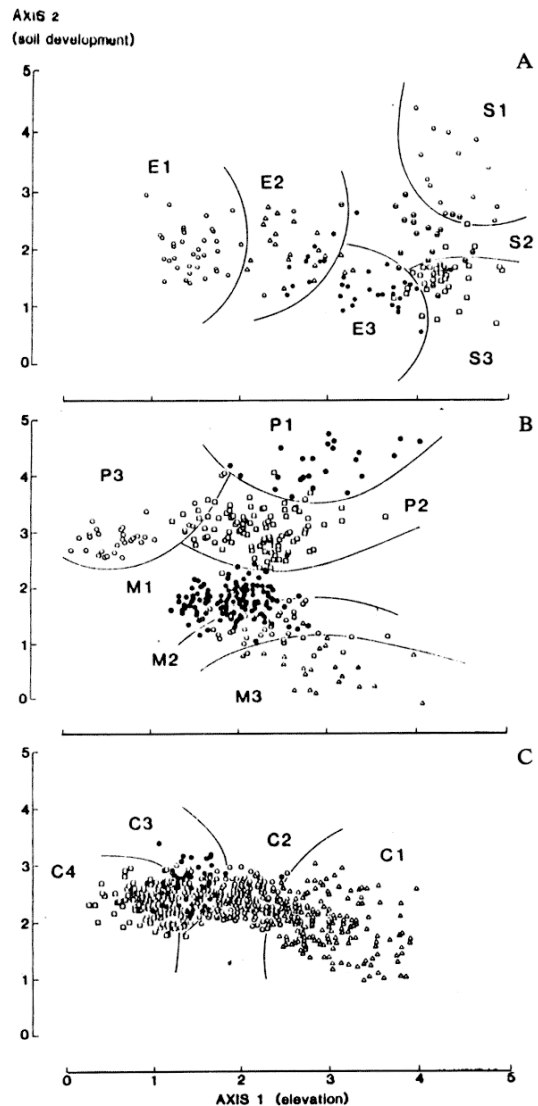


Figure 6: Scatter figures from DCA ordination of 1053 samples from northern Fiordland. Symbols represent in (a) E and S forest types; (b) P and M types; and (c) C types. Axis lengths are scaled in SD units of DCA ordination. Eigenvalues for Axis 1 and 2 are .545 and .343, respectively. N.B. Although the data are portrayed in three diagrams all 1053 samples were ordinated simultaneously.

indicating soils of high nutrient status (Fig. 6a).

The P and M types occupied opposite ends of the soils gradient (Axis 2, Fig. 6b). Mountain beech-manuka-*Dacrydium* forest (M3) occupied well-developed and poorly-drained shallow soils and taller stunted forest (M1) a greater range of well-developed soils. P types occupied disturbed recent or compound soils. P3 occurred at lower elevations; P2 and P1 at higher elevations, especially in glacial cirques.

Silver beech types (C1-4) were differentiated by altitude, C4, at the lowest in the west, C1 at the highest (Fig. 6c). There was little separation of the types along the soils axis.

The M, P and S types showed distinct separation along both axes of the ordination but there was considerable overlap with C and E types (Fig. 6). The simple E types dominated by mountain and/or silver beech are more prevalent along the eastern boundary of northern Fiordland (Wardle *et al.*, 1971) and showed similar altitudinal differentiation to the more complex silver beech (C) types located further to the west. Thus, although they overlap on the ordination they are separated by differences in canopy dominance.

Species at the low end of the soils gradient were therefore characteristic of well developed and/or poorly drained infertile soils on infrequently disturbed landforms (e.g., *Gahnia procera*, *Leptospermum scoparium*, and *Dacrydium bifforme*; cf., Holloway, 1951). At the high end of the gradient, species characteristic of recently (frequently) disturbed, well drained, fertile soils were *Hoheria glabrata*, *Fuchsia excorticata*, *Cardamine debilis* and *Hebe salicifolia* (cf., Mark *et al.*, 1964; P. Wardle, 1960, 1977, 1985; J. Wardle, 1984; Stewart and Harrison, in press). Scrubland type SI contained species that characterise soils of high nutrient status (e.g., *Anisotome haastii*, *Oxalis lactea* and *Bulbinella gibbsii*; Rose and Platt, 1987).

Although different forest types often occupied opposite ends of the soils gradient, they were not necessarily successional related, e.g., it is unlikely that P2 forest would develop over time into M3 forest or that M3 forest occurred on soils that were once like those beneath P2 forest. Because P2 forest occupies landforms subjected to frequent soil disturbance it is likely that it will be perpetuated by further physical disturbances. If sufficient time elapsed between disturbances, however, P2 forest may develop into C3 forest since they often occur on similar landforms (Table 2; Wardle *et al.*, 1971). In contrast to P2, M3 forest occurred on stable landforms and well-

developed soils.

Discussion

The proportion of preferred deer habitat within an area can be related to the distribution and stability of component landforms. Thus, in the Wapiti/Doon catchments preferred habitat was limited by the large areas of stable bedrock sideslopes, benches and ridges that supported mountain beech types containing few highly preferred plants. In contrast, extensive areas of debris cones and colluvial sideslopes in the Glaisnock supported seral and C3 forest containing many highly preferred species. This larger proportion of preferred habitat in the Glaisnock supported many more deer in 1969/70 than the Wapiti/Doon (Nugent, Parkes and Tustin, 1987).

The distribution of highly preferred plants in different forest types reflects the effects of physical disturbances on soils. The proportion of woody species highly preferred by deer was low in the browse tier of mountain beech types (M2, M3), moderate in complex mountain beech forests (M1) and high altitude silver beech types (C1, C2), slightly greater in complex lower altitude silver beech forests (C3), and highest in seral forest (P1, P2). This increase in preferred species across forest types parallels the landform stability gradient and thus the soils gradient.

Therefore seral types are among the most preferred habitat due to high nutrient status, while mountain beech types are least preferred (cf., Rose and Burrows, 1985). A similar pattern was found in the unmodified forests of Milford/Bligh Sound area (Stewart *et al.*, 1987).

If preferred deer and wapiti habitat can be predicted from landforms and soils, deer distribution should be closely related to forest type. Deer pellet group densities by forest type for northern Fiordland in 1984, in order of declining density were P1/2, C3, M1, C1/2 and M3 (Nugent *et al.*, 1987). Thus, utilization of forest types by deer closely approximated the landform/soils gradient.

Accessibility of terrain will affect the degree of modification of a forest type containing species preferred by deer, e.g., C3 forest understoreys on blockfields were minimally modified but on terraces they were preferentially browsed. Conversely, other habitats that do not contain as many species preferred by deer may be favoured for other reasons, e.g., benches in M1 forest are used by deer for lying up or for moving between areas. Even in easily accessible and heavily used areas, however, the degree of modification depends on forest structure, e.g., in all-

aged C3 forests on terraces many highly preferred species occurred on logs or in tree crowns, sites that were inaccessible to deer (Stewart, 1986).

Other disturbances also influence the distribution of preferred food species and thus deer habitat. For example, all-aged C3 forest contained many deer-preferred small trees and shrubs in treefall gaps (Stewart, 1986). In contrast, dense silver beech canopies in even-aged C3 forest resulted in sparse understoreys and thus, poor deer habitat.

The interpretation of the original survey data was improved by ordination and by site factor information collected in 1984. The elevational gradient that influences the distribution of forest types had been documented in other areas of northern Fiordland (Mark and Sanderson, 1962; Mark, 1963; Scott, Mark and Sanderson, 1964; Wardle *et al.*, 1971). However, the distribution of forest types on different landforms, observed by Poole *et al.* (1951) and Wardle *et al.* (1971) was related to patterns of landform stability and soil type. Stratification by landform in combination with forest type may therefore improve interpretation of catchment surveys aimed at determining the effects of animal browsing on forest. Sites that are heavily used by deer could be identified and periodic remeasurement of them would be an efficient method for monitoring the effects of animal browsing on the status of deer habitat.

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