

# FOREST PATTERNS AND POSSUM DENSITIES WITHIN PODOCARP / MIXED HARDWOOD FORESTS ON MT BRYAN O'LYNN, WESTLAND

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**SUMMARY:** The podocarp/mixed hardwood forests on Mt Bryan O'Lynn, Central Westland, are described from 304 plots surveyed during 1975-77. Eight major plant associations are identified, using patterns of forest structure, physiognomic dominance, diversity and distribution. Each association possesses distinct physiographic requirements, which ultimately results in a broad altitudinal stratification of the forest. Thus, the forests on low-altitude cutover terrace lands are dominated by *Weinmannia racemosa* and *Cyathea smithii* on partially cleared areas and by scrub hardwood species on clear-felled sites; the unmilled mid-altitudinal slopes are dominated by *W. racemosa* and *Quintinia acutifolia*; the ridges by *Metrosideros umbellata* and *W. racemosa*; the high altitude forests by *Griselinia littoralis* and *Libocedrus bidwillii*; and the alpine scrublands by scrub hardwoods, e.g., *Olearia* spp. and *Dracophyllum* spp.

Forest mortality is altitudinally stratified also. Few dead stems occur in the low-altitude and alpine scrub forests. Conversely, in mid and high-altitude forests 9.6-15.5% of all standing stems are dead. The latter forests are structurally simple, are highly palatable to browsing animals, particularly possums, and appear to have been extensively modified by this marsupial.

Possum densities throughout the forest profile are derived from a comprehensive extinction-trapping programme and verified by faecal pellet surveys. Mean density is 10.7/ha, ranging from 25.4/ha to 1.9/ha in the low and high-altitude forests respectively. Current densities correlate with a gross palatability index calculated for each association, but do not reflect present patterns of forest mortality as possum densities within the highly modified mid-altitude forests are moderate to low.

## INTRODUCTION

The mixed hardwood protection forests of central Westland play a vital role in maintaining the stability of the steep hillsides characteristic of the region. Over the last 40 years many of Westland's forests have shown a widespread and progressive canopy mortality and a consequent acceleration in erosion, especially in land mass movements. The reasons for forest death are many, but have been argued to result principally from the browsing habits and dietary preferences of introduced animals, especially the brush-tailed possum (*Trichosurus vulpecula*) (Wardle, 1974). A considerable depth of literature, both published and unpublished, exists on the mortality of Westland's mixed hardwood forests (e.g., James, Jane and Barr, 1973; Wardle, *op. cit.*), and an even more impressive quantity on the browsing and dietary habits of the possum in New Zealand's native forests (e.g., Kean and Pracy, 1949; Mason, 1958; Gilmore, 1967; Fitzgerald, 1976; Meads, 1976). However, little attempt has been made to relate possum densities in specific habitats to the structure and composition of the living and dead forests present.

The present paper arose out of a broader study of possum movements, dispersion and feeding patterns over a complete altitudinal profile from forest/pasture margin to alpine scrub. To elucidate and understand the interactions between the possum population and the various forest habitats, comprehensive surveys were made of both the local forest, its living and dead components and of the density of possums within. This paper first identifies the broad forest associations or "types" in the study area and describes them in terms of their structure, composition, stocking rates, local distribution, mortality, and site characteristics. Then, within-forest possum densities are tabulated, their selective browsing patterns identified, and the inter-relationship of the forest and possum population discussed.

The study area comprises a belt 1.5 km wide on the north-facing forested slopes of Mt Bryan O'Lynn and extending from farmland at 250 m altitude to alpine grasslands at 1200 m (see NZMS 1, 852, 190690). The area lies astride the main alpine fault, revealed through the sharp truncation of all major ridges; at the bottom lie terrace lands up to 700 m

in width and of 5-80 mean slope; at the top are moderately steep faces and ridges of 350 mean slope: The terrace lands comprise moraine and outwash morainic debris from the Otira glaciation covered by poorly drained, easily erodible, sandy loams of low nutritional status. The steeper slopes comprise garnet and biotite schists. These are overlain by upland podzolised yellow-brown earths and podzols-typically very shallow, heavily leached and prone to sheet and gully erosion (NZ Soil Bureau, 1968).

The climate is dominated by high rainfall and high humidity. Summers are warm and winters cool with frequent heavy frosts and occasional high level snow. Winds are generally light, although strong gusting south-easterlies blow occasionally.

## METHODS

### *Vegetation studies*

The composition and structure of the vegetation on the northern slopes of Mt Bryan O'Lynn near Lake Haupiri (see Fig. 1), was assessed over the summers of 1975/76 and 1976/77. Prior to this study, there had been no comprehensive botanical survey of the Mt Bryan O'Lynn area, although Wardle (1974) included the Haupiri catchment in an extensive reconnaissance survey of the Grey valley headwaters. The vegetation description was derived from a total of 304 separate sociological descriptions of plots located within the study area (Fig. 1). Plots on the lower slopes were located at 100 m intervals on transects that ran uphill on identical compass bearings, 100 m apart. On the steep middle to upper slopes this design was modified, and only those transects meeting with major spurs were extended through to the alpine grasslands. Transects between spurs were terminated at the bottom of the steep slopes and replaced by horizontal transects and plots originating from even-numbered plots on the major spurs. Thus, the vegetation plots were set out on a 100 m grid over the lower slopes, but were less regularly spaced at higher altitudes.

Complete plot descriptions using the botanical nomenclature of Allan (1961) and Moore and Edgar (1970), were developed from the integration of three discrete but commonly employed field techniques (Wardle, Hayward and Herbert, 1971; James, *et al.*, 1973) and included:

1. A "recce survey" or listing of all vascular plant species including lianes, epiphytes and ferns growing adjacent to the plot centre, and an accompanying estimate of the physiognomic dominant species present. Listings were subsequently sorted on similarity and physiognomic dominance, and using

multilinkage techniques (Wardle, 1970) plots of greatest similarity were progressively clustered into eight major forest associations. At each plot the altitude, aspect, drainage, slope and site physiography were recorded.

2. A "variable-radius constant-count plot" in which a minimum of 30 living stems (including tree ferns) nearest to the plot centre and over 50 cm in height were identified and measured to provide quantitative estimates of species stem frequencies and stem basal areas. Where the plot did not include ten living stems of half canopy height or greater, the technique was modified to include additional canopy stems by adding an annulus of known radius (total radius = plot centre to point between the  $n$  and  $n + 1$  trees) to the existing plot. In addition, all standing dead stems over 50 cm in height and within the prescribed plot radius were measured and, where possible, identified to provide estimates of species and association-specific forest mortality.

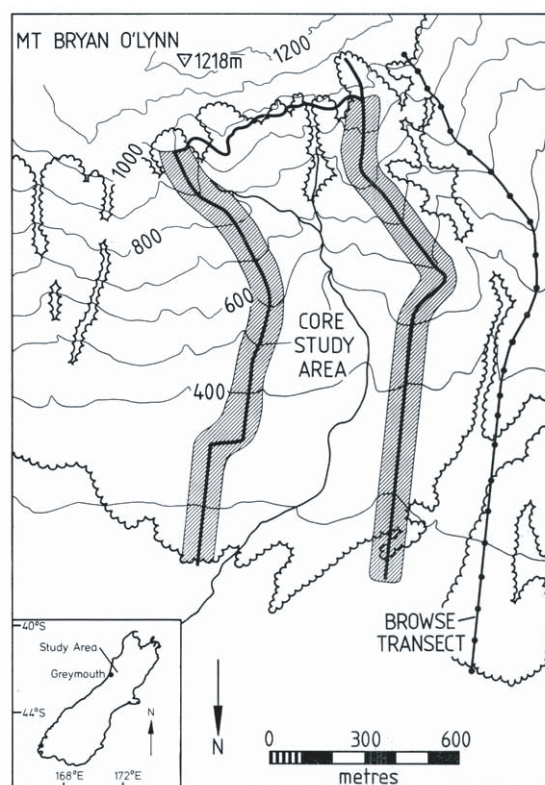


FIGURE 1. Location and topography of the Mt Bryan O'Lynn study area, Westland. (Cross-hatched areas indicate buffer zones).

3. "Ground counts" of the forest floor provided estimates of the ground covered by cryptogamic and vascular vegetation, as well as that occupied by leaf litter, bare soil and rock. At each plot, 20 counts each of 13 cm in diameter were made on a crucifix pattern—five counts being made 50 cm apart along each axis.

#### *Possum browse studies*

Possam browsing patterns were determined from observations on forest vegetation in an area immediately adjacent to the core study site (see Fig. 1). Observations were made at 26 plots spaced at 100 m intervals along a transect 2 600 m in length which extended from the forest/pasture margin to the alpine scrublands. In each plot four trees considered to be representative of the surrounding forest and climbable by field observers were marked with aluminium tree tags. Four canopy twigs within each tree and possessing approximately 100 leaves, were selected and identified for monthly examination. In all, 104 trees/shrubs were labelled in a ratio roughly equal to their local abundance. Each month between November 1975 and November 1976, an "in hand" examination was made of all marked twigs, and notes taken on:

- (a) the number of entire leaves present;
- (b) the number of leaves browsed by possums;
- (c) the amount of possum browse on other plant tissues; and
- (d) the current phenology of the plant.

At the completion of the browse survey, the cross-sectional areas of stems of species found to be browsed by possums were summed ( $m^2/ha$ ) for each association, and the total palatability (= foliate acceptability) estimated for forest associations on Mt Bryan O'Lynn.

Variability in forest diversity, mortality and palatability to possums was analysed by parametric single classification analysis of variance techniques. Where overall significance occurred, Duncan's multiple range test was employed (Sokal and Rohlf, 1969, Ch. 9), to test differences amongst forest association means. Duncan's test ranked group means in increasing magnitude, such that means not covered by two lines (see text below) and enclosed by the range of anyone line were significantly different. Where the basic assumptions for analysis of variance techniques could not be met (*viz.*, homogeneity of variance and normality), even through data transformation, Kruskal-Wallis's non-parametric ranking test (statistic H) was employed (Siegel, 1956). In all tests, statistical significance was set at the 0.05 per cent probability level.

#### *Possum densities*

Absolute possum densities within the forest were determined through a comprehensive and intensive kill-trapping programme. The core study area (see Fig. 1) was trapped continuously over 6 weeks in the winter of 1978, using 450 gin and 250 box traps. All traps were set out along contoured marked lines located at 50 m intervals up the hill. Lines contained about 30 traps each (1 trap/20 m), and all traps were shifted about and between lines to facilitate an even and simultaneous trapping effort within altitudinal strata. When catches fell to low levels, traps were placed wherever fresh possum dung or "tracking" existed, until no further animals were recovered.

Possum densities were calculated from the summation of all animals removed from the core study site, plus one half of those taken within 100 m wide buffers which bestrode the site's lateral boundaries; previous studies on Mt Bryan O'Lynn (unpubl. data) had indicated that lateral movements within the forest were well within such a distance. Areas within altitudinal zones were determined with the aid of a map of Mt Bryan O'Lynn produced by the New Zealand Lands and Survey Department (Scale 1:5 000). Planar areas were transformed into slope areas using the mean of all slopes recorded on relevant vegetation plots (see above).

At the completion of the kill-trapping project a check was made for surviving trap-shy animals through the use of Potassium cyanide paste lines randomly located throughout the forest, by nocturnal spotlight searches along the adjacent forest/pasture margin, and through faecal pellet surveys within the forest. For the latter, point-distance sampling techniques (see Batcheler and Bell, 1970) were employed and 920 plots, each 114 cm in radius, and regularly located along six pellet lines up the hill were searched for pellets. In all, about 0.05 % of the study area was surveyed twice for the estimate obtained. Contrasting pre-kill estimates of possum density were similarly determined, but because of the higher pellet densities involved, only 600 plots were searched.

## RESULTS

### *Description of extant vegetation*

The forests on Mt Bryan O'Lynn fall into eight major plant associations (see below), based on their floristic composition and structure. Some minor associations exist which are recognisable in the field, but these have been lumped into broader associations and discussed in context. A few plots (< 20), located on stream beds or bluff systems and unrelated to any major association, have been ignored.

TABLE 1. Forest diversity on Mt Bryan O'Lynn. Associations are ranked from lowest to highest diversity and significance indicated by lines below (see Duncan's test in Methods).

Plant Association	A. Understorey—ferns and higher plants							
	4	1	7	6	5	2	8	3
Mean no. of species per plot	11.3	12.0	12.0	12.5	13.4	13.9	15.0	16.3
Plant Association	B. All forest tiers—woody species only							
	6	4	1	3	2	7	5	8
Mean no. of species per plot	6.5	6.6	6.9	6.9	7.2	7.5	8.1	8.5

Association key:

1—Kamahi	5—Southern Rata / Kamahi
2—Tree-Fern	6—Broadleaf
3—Pepperwood Scrub	7—Cedar
4— <i>Quintinia</i> / Kamahi	8—High-Altitude Scrub

### 1. Lowland Cutover Kamahi Forest—(91 plots)

The most abundant association identified, which in conjunction with Lowland Cutover Tree-Fern Forest (see 2 below), encompasses all of the lower slopes on Mt Bryan O'Lynn. Kamahi Forest is a moderately stocked association (Fig. 3B) located on well-drained lower faces and terraces (Fig. 2A) of medium gradient (Fig. 2B) and high basal area (142.3 m<sup>2</sup>/ha, see Fig. 3A). The understorey and total woody species component is, compared with most other associations, floristically simple (Table 1).

The canopy of Kamahi Forest is irregular and has been lowered to 8-10 m through past selective logging. It is now dominated by kamahi (*Weinmannia racemosa*) with 66% of the total basal area and by occasional emergents such as rimu (*Dacrydium cupressinum*), southern rata (*Metrosideros umbellata*), miro (*Podocarpus ferrugineus*) and kahikatea (*Dacrycarpus dacrydioides*). The sub-canopy is more complex and in decreasing order of abundance comprises kamahi, *Quintinia acutifolia*, *Cyathea smithii* and *Dicksonia squarrosa*, with mahoe (*Melicytus ramiflorus*), broadleaf (*Grisebinia littoralis*) and putaputaweta (*Carpodetus serratus*) as less frequent local components. The shrub tier principally comprises pepperwood (*Pseudowintera colorata*), *Coprosma parviflora*, *C. colensoi*, *C. rhamnoides* and weeping matipo (*Myrsine divaricata*); all of which are locally abundant but contribute little in basal area.

Cryptogamic vegetation, particularly the Pteridophyta, dominate the ground storey, with hard fern (*Blechnum discolor*), hen and chicken fern (*Asplenium bulbiferum*) and *B. fluviatile* particularly

common. Vascular vegetation is less common but includes rata vine (*Metrosideros perforata*) as the most abundant single species present, hook grass (*Uncinia uncinata*), pepperwood, *Nertera dichondraefolia* and bush rice grass (*Microlaena avenacea*). Litter and bare soil together constitute less than 20% of the ground storey. Throughout all tiers, lianes and epiphytes abound. Rata vines are ubiquitous together with bush lawyer (*Rubus* spp.) and very occasionally, supplejack (*Rhipogonum scandens*).

### 2. Lowland Cutover Tree-Fern Forest—(74 plots)

A common association occurring on terraces and faces of low slope, low mean altitude and poor drainage, from the bush edge up to 675 m. Tree-Fern Forest characteristically occupies sites severely depleted by previous milling. Consequently, the basal area of the standing forest (107 m<sup>2</sup>/ha) is lower than Kamahi Forest and of this, 62 % is tree fern (*Cyathea smithii* and *Dicksonia squarrosa*). However, although few woody stems remain, stocking rates are high (13 934 stems/ha, see Fig. 3B).

The canopy of Tree-Fern Forest is broken, impoverished, and drastically lowered to 3-5 m. It is dominated by *Cyathea smithii*, with lesser components in order including *Dicksonia squarrosa*, kamahi, mahoe, putaputaweta, pepperwood, wineberry (*Aristotelia serrata*), broadleaf and *Coprosma parviflora*. Emergents are limited to the occasional kamahi. The shrub tier is dominated by the species listed immediately above, but commonly includes the following-nettle (*Urtica ferox*), kaikomako (*Pennantia corymbosa*), *Coprosma rhamnoides*, *C. rotundifolia* and kahikatea.

The ground storey is similar in species composition to that of Kamahi Forest, although the cryptogams constitute 75% by area and are clearly dominant. Bare soil and litter occur infrequently. Rata vine is generally replaced by hard fern, especially in sites of low incident light.

Cutover Tree-Fern Forest is a less homogeneous association than Kamahi Forest. It includes a sub-association dominated by mahoe which occurs commonly as discrete enclaves on old, well-drained, outwash sites along the edge of the lower slopes.

3. Pepperwood Scrub-(37 plots)

Pepperwood Scrub is a distinct and diverse forest occurring as two altitudinally separate sub-associations. However, because of similar species composition, they are treated as one below despite the markedly different site characteristics shown such as altitude ( $252 \pm 31.8$  m;  $762 \pm 36.8$  m), slope

( $4.8 \pm 1.37^\circ$ ;  $36.5 \pm 8.03^\circ$ ) physiography (terrace; upper face), and drainage (medium-poor; good). The lower sub-association has a pioneering role on sites recently clearfelled, the upper association grows on stabilising screes of past "natural disturbance" areas such as broad slip sites or washed out/undercut gully heads.

Pepperwood Scrub is characterised by its extremely low basal area ( $32.4$  m<sup>2</sup>/ha, see Fig. A3), its contrasting extremely high stem density ( $24\ 885$  stems/ha, see Fig. 3B) and, at 2-4 m, its irregular and very low canopy. Further, it contains the most diverse understorey of any association measured, and is significantly different from *Quintinia/Kamahi*, Kamahi, or Cedar (*Libocedrus bidwillii*) Forests ( $F_s = 3.8770$ ,  $P < 0.01$ ) (Table 1).

The canopy / shrub tier of Pepperwood Scrub includes dense assemblages of pepperwood, wineberry (locally dominant on previously scarified sites), *Coprosma rotundifolia*, *C. parviflora*, putaputaweta and *Cyathea smithii*. Emergents exist but are limited to scattered miro, kahikatea and kamahi. Other

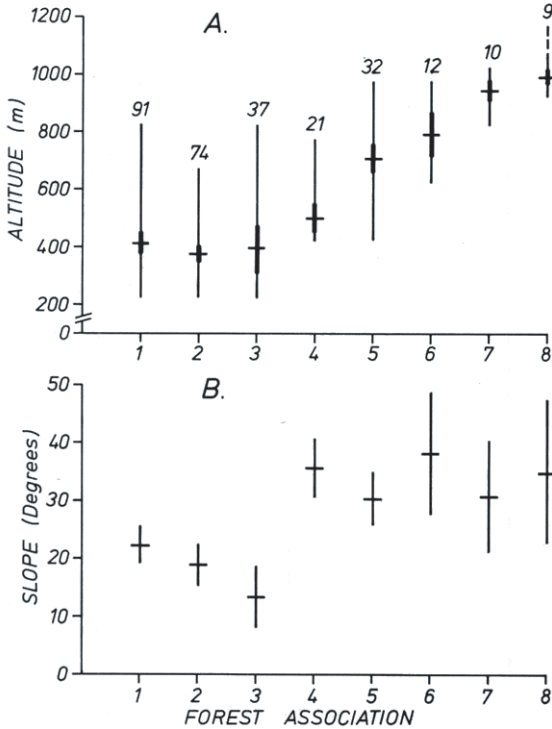


FIGURE 2. Forest association variables: topographical parameters.  
 A. Altitudinal stratification (mean  $\pm$  95% confidence limit (CL), range, and the number of plots sampled). Note: broken line indicates extension of range above area sampled.  
 B. Slope (mean  $\pm$  95% CL).

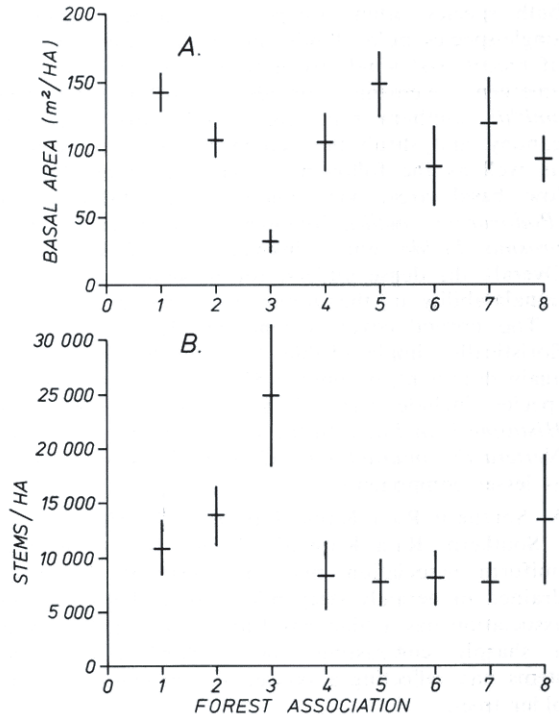


FIGURE 3. Forest association variables: biomass parameters.  
 A. Total stem basal areas (mean  $\pm$  95% CL).  
 B. Stacking rates (mean  $\pm$  95% CL).

species which show high stocking rates but insignificant basal areas include nettle, kaikomako, *Neomyrtus pedunculata*, *Dicksonia squarrosa* and *Coprosma rhamnoides*. In addition, *Olearia ilicifolia* and broadleaf occur in the upper sub-association but are replaced by *C. rotundifolia* and miro at lower altitudes.

The ground storey has an equal proportion of cryptogamic and vascular components (35 % each) and an unusually high litter/soil component (30%). The major species present include hook grass, bush rice grass, *C. parviflora*, kaikomako, rata vine and *Blechnum fluviatile*.

#### 4. Quintinia/Kamahahi Forest—(21 plots)

*Quintinia/Kamahahi* Forest is a medium altitude, lightly stocked association (8340 stems/ha) with a basal area of 105.2 m<sup>2</sup>/ha, and occurs exclusively on low to mid faces of steep slope and good drainage.

The canopy, at 10-12 m, is broken and is considerably less complex than that of lower associations. It is characterised by the co-dominance of *Quintinia* and kamahahi (79% of the association), both species often occurring as densely growing single-species pole stands on locally extensive sites of recent past wind thrown forest. Lesser canopy or emergent elements include broadleaf, *Cyathea smithii*, southern rata, cedar and miro. The sub-canopy and shrub tiers comprise the same species as well as the following in large numbers but of low basal area, viz., pepperwood, Hall's totara (*Podocarpus hallii*), *Neomyrtus pedunculata*, *Coprosma lucida* and stinkwood (*C. foetidissima*). Overall, the dense understorey probably reflects the unpalatability of the dominant species present.

The ground cover is generally dense (80 %) but floristically simple (Table 1), with the cryptogams again dominant, occupying 58 %. The most common species include hard fern, *Cyathea smithii* and *Histiopteris incisa*, with the vascular plants rata vine, *Nertera dichondraefolia* and bush rice grass present as lesser components.

#### 5. Southern Rata/Kamahahi Forest—(32 plots)

Southern Rata/Kamahahi Forest is a common uniform association mantling most of the well-drained moderately steep mid-altitudinal ridges. The association has a high basal area (147.8 m<sup>2</sup>/ha), and a sharply contrasting low stocking rate (7720 stems/ha), reflecting a skewed age structure towards older trees.

The canopy at 10-12 m is simple in structure and somewhat open. Southern rata is dominant, and on the ridge crests particularly, forms even-sized single-species juvenile stands. Conversely, senescent

trees occur as isolated individuals on ridge and face sites. Together, both age groups provide 48% of the association's basal area, the remainder consisting principally of *Quintinia*, kamahahi and cedar. The sub-canopy where present, is dominated by broadleaf and *Quintinia*, the shrub tier by *Quintinia* but with the following minor species, viz., broadleaf, pepperwood, *Coprosma colensoi*, *C. parviflora*, mountain heath (*Archeria traversii*), *Cyathea smithii*, and *Neomyrtus pedunculata*, with southern rata noteworthy by its absence.

The ground cover is predominantly cryptogamic (57%), with vascular vegetation (32%) and litter (7%) comprising most of the remainder. The ferns *Blechnum minor*, *Grammitis billardieri*, *Hymenophyllum* spp. and hard fern are common while other vegetation such as bush rice grass, pepperwood, kamahahi, *Quintinia* and broadleaf are of lesser consequence.

#### 6. Broadleaf Forest—(12 plots)

A minor, remarkably uniform, mid-altitude association (Fig. 2A) which together with Cedar Forest (association 7) forms the timberline on Mt Bryan O'Lynn. Broadleaf Forest is sited on well-drained steep ridges or upper faces (38.1 ± 10.72°), has an average basal area of 87.7 m<sup>2</sup>/ha, and a low but uniform stocking rate of 8 116 stems/ha.

The 5 m high canopy is generally intact. It is dominated by broad leaf (56 % of the basal area), with kamahahi also important. Minor species include *Cyathea smithii*, putaputaweta, pepperwood, southern rata, weeping matipo and cedar.

The shrub tier is dominated by pepperwood, but includes such minor species as *Cyathea smithii*, weeping matipo, *Pittosporum crassicaule*, *Pseudopanax linare*, broad leaf, *Coprosma rhamnoides* and *C. parviflora*.

The ground tier differs from most other associations in its high proportion (28%) of bare soil—perhaps a result of local heavy use by red deer (*Cervus elaphus*). Vascular vegetation occurs infrequently (19%) and is dominated by bush rice grass with *Uncinia filiforme*, *Histiopteris incisa*, hard fern, and *Leptopteris superba* of lesser importance.

#### 7. High-Altitude Cedar Forest—(1 plots)

A minor association which includes many of the uppermost plots on Mt Bryan O'Lynn. Cedar Forest is found on high altitude ridges and upper faces (945 ± 34.8 m), of average to steep slope, and good drainage. The basal area of the forest is medium-high at 118.8 m<sup>2</sup>/ha with cedar constituting 41% of this. Conversely, the density of the standing crop is quite low (7 705 stems/ha).

The canopy (3-4 m) is irregular, and is dominated

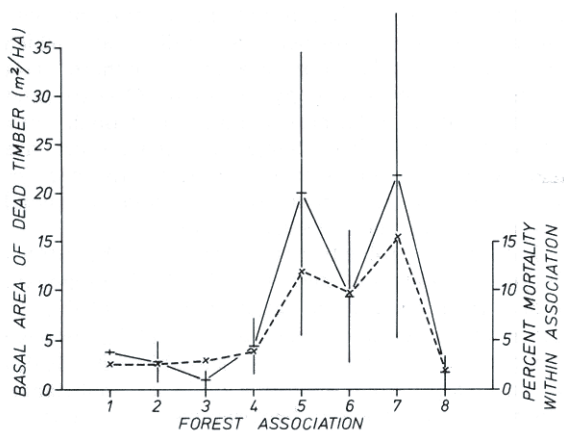


FIGURE 4. Forest mortality within associations. Real (solid line; mean  $\pm$  95 % CL) and proportional estimates shown.



FIGURE 5. Altitudinal stratification of forest canopy mortality on the north-facing slopes of Mt Bryan O'Lynn.

by emergent cedars along with the occasional southern rata and pink pine (*Dacrydium biforme*). Minor canopy species include mountain heath and broadleaf. The shrub tier includes stinkwood, *Coprosma ciliata*, mountain toatoa (*Phyllocladus alpinus*), *Pseudopanax lineare*, *P. colensoi* and pepperwood.

The ground tier, as in Broadleaf Forest, possesses a high bare soil/rock component (40%). Cryptogams (30%) and vascular vegetation (20%) are of less than usual dominance, but include *Gahnia procera*, mountain flax (*Phormium cookianum*), bush rice grass, *Uncinia filiforme* and *Histeriopteris incisa*.

8. High-Altitude Scrub (9 plots)

A common, lightly sampled association differing sharply in species composition from all lower forests. High-Altitude Scrub occurs above the high forest timberline ( $990 \pm 26.8$  m) on steeply sloping, well drained ridges and faces ( $34.8 \pm 12.88^\circ$ ). The basal area is medium ( $92.3$  m<sup>2</sup>/ha), and is much higher than that of the early seral Pepperwood Scrub association described (see 3). Stocking rates are also medium ( $13449$  stems/ha) but variable, and are influenced by the intrusion of high altitude screens,

The low, diverse and irregular canopy (2-5 m) is dominated by pink pine and *Dracophyllum traversii*, with mountain toatoa, southern rata, broadleaf and *Olearia colensoi* lesser elements. The shrub layer is dense enough to be largely impenetrable to humans and consists principally of pepperwood, *Pseudopanax lineare*, weeping matipo, turpentine shrub (*Dracophyllum longifolium*), stinkwood and *C. pseudocuneata*.

The diverse ground layer is dominated by the cryptogams (63 %), with vascular vegetation (23 %) and particularly the litter/soil combination (16 %) similar to levels encountered in the low-altitude forests. The dominant species present include *Gahnia procera*, mountain flax, *Uncinia filiforme* and *Lycopodium volubile*.

Overall, the diversity of woody species from all tiers is highest in this association, with differences approaching significance ( $F_s = 1.9583$ ,  $F_{0.05} (7,276) = 2.14$ ,  $p > 0.05$ ) (see Table 1).

Forest mortality

The standing dead component of each association monitored on Mt Bryan O'Lynn varies both in absolute quantity (Fig. 4) and in the species involved (Table 2). In brief, few dead stems exist in the low altitude associations, especially in Pepperwood Scrub. A significant 2 to 5-fold increase in dead stem area occurs in the mid to high forest ( $H = 39.3008$ ,  $P < 0.01$ ), with levels in Southern Rata/

Kamahi, Broadleaf, and Cedar Forests reaching 20.0, 9.3 and 21.7 m<sup>2</sup>/ha respectively. By contrast, the High-Altitude Scrub possesses little dead timber (see also Fig. 5).

A comparison of the absolute basal area/ha of dead stems exaggerates inter-associational comparisons because of size differences between the species characteristics of different associations. This effect is overcome by examining the proportion of dead timber per association expressed as the percentage of live stems present. As expected, this reduces the difference between associations while reflecting the same overall pattern of forest mortality (Fig. 4). The proportion of dead stems in associations 1 to 4 is very similar (2.6-4.0%) with the dead stems in Pepperwood Scrub (3) now better represented. The proportion of dead timber in the mid to high-altitude associations (5 to 7) rises dramatically (9.6-15.5%), which clearly defines this as the area of highest mortality. The dead component within High-Altitude Scrub remains at a low level (1.9%).

A more detailed interpretation of the dead forest



FIGURE 6. Recent slipping and forest death on 35° mid-altitudinal slopes within the zone of highest canopy mortality on Mt Bryan O'Lynn.

component on Mt Bryan O'Lynn is fraught with difficulty as dead stems decay and fall at rates which are species-specific. For example, southern rata stems remain in the canopy for about 30 years after death (K. Platt, FRI, pers. comm.) but kamahi only about half this time. Subjective impressions are that dead cedar stems may well stand for decades and thus give an erroneous impression of actual mortality rates and causative factors.

The above problem notwithstanding, the contribution by individual species to the dead component within each association varies markedly (Table 2). In the major terrace associations (1 and 2), the dead component is dominated by kamahi, with Hall's totara and *Quintinia acutifolia* of lesser importance. Differences are marked between these two associations at the minor dead "species" level. In addition, Kamahi Forest contains a considerable dead input from two species abundant in high forests—southern rata and cedar, but both are largely replaced in Tree Fern Forest by rimu and wineberry; the latter is confined largely to old scarified sites where it is now being rapidly superseded by other species.

The seral Pepperwood Scrub association (3) contains few dead stems, but of those present southern rata and cedar are the most common with kamahi kaikomako and pink pine lesser contributors. With the exception of kaikomako, all the other dead "species" occur quite infrequently within the association as remnants of previous vegetation.

Few dead stems exist in *Quintinia*/Kamahi Forest (association 4), where the dominant species, *Quintinia acutifolia*, contributes only 0.4% of the dead stems; the bulk being kamahi. Once again, southern rata, cedar and Hall's totara are important contributors to the dead forest.

Within the higher associations the dead component of Southern Rata/Kamahi Forest (5) is dominated by dead rata, Broadleaf Forest (6) by dead kamahi, and Cedar Forest (7) by dead cedar. Minor dead elements, other than the dominant species, include Hall's totara, southern rata, broadleaf and cedar.

Mortality in High-Altitude Scrub (8) is limited to four species, with pink pine dominant, while Hall's totara, cedar and turpentine scrub constitute lesser elements.

Intra-association mortalities of the four species contributing most to the dead forest throughout the study site differs sharply. Kamahi, the most common canopy species in the study area, provides an important dead component in most associations and the most important in some, viz., Kamahi (1), Tree-Fern (2), *Quintinia*/Kamahi (4) and Broadleaf Forests (6) (Table 2). Proportionately however, kamahi contributes relatively few dead stems to the



TABLE 2. *Per cent Basal area of dead standing forest within plant associations.*

Species recorded	Association							
	1	2	3	4	5	6	7	8
<i>Weinmannia racemosa</i>	47.3	64.7	19.5	70.9	8.4	42.3		
<i>Metrosideros umbellata</i>	21.7		36.4	15.7	57.7		14.6	
<i>Podocarpus hallii</i>	14.6	9.0		3.3	15.9	30.4	2.5	20.8
<i>Griselinia littoralis</i>	0.5			0.5			11.3	
<i>Libocedrus bidwillii</i>	8.6		32.5	8.6	16.5	24.2	69.6	20.8
<i>Podocarpus ferrugineus</i>	0.2			0.7	0.2	1.0		
<i>Quintinia acutifolia</i>	6.5	7.5		0.4	0.3			
<i>Cyathea smithii</i>	0.7							
<i>Pseudowintera colorata</i>	0.1							
<i>Aristotelia serrata</i>		5.6						
<i>Dicksonia squarrosa</i>		0.4						
<i>Meliccytus ramiflorus</i>		1.4						
<i>Dacrydium cupressinum</i>		9.1						
<i>Carpodetus serratus</i>		2.4						
<i>Dacrydium biforme</i>			5.6		1.0		2.1	49.2
<i>Pennantia corymbosa</i>			6.1					
<i>Myrsine divaricata</i>						2.1		
<i>Coprosma robusta</i>					0.1			
<i>Dracophyllum longifolium</i>								9.2

TABLE 3. *Intra-association mortality of kamahi, southern rata, Hall's totara and cedar.*

Association	Per cent of species dead			
	Kamahi	Southern rata	Hall's totara	Cedar
1. Kamahi	1.6*	21.1	99.7	100.0
2. Tree-Fern	13.1	-	93.5	-
3. Pepperwood	12.3	100.0	0.0	100.0
4. <i>Quintinia</i> / Kamahi	13.2*	23.4	40.2	18.6
5. Southern Rata/Kamahi	4.0*	12.2*	79.1	34.6
6. Broadleaf	29.5	0.0	100.0	52.9
7. Cedar	0.0	17.0	19.7*	20.1*
8. High-Altitude Scrub	-	0.0	97.9	44.2

- species not measured in association  
\* "home" association for each species (see text)

associations in which it is most abundant, viz., in Kamahi and Southern Rata/Kamahi Forests (Table 3).

Similar patterns of intra-association mortality exist for southern rata, Hall's totara and cedar, with the proportional mortality of each species again low in its "home" association (Table 3). The small numbers of dead stems present in most associations, and the non-normality of the data, precluded any robust analyses.

The diameter distribution of the dead trees within the mid to high-altitude forests provides some insight into forest mortality. An analysis based on

all trees alive or dead over 20 cm in diameter of the four main contributing species, viz., southern rata, kamahi, cedar and Hall's totara, indicate that, for each species, dead and living trees are of similar size (see Table 4). If tree death follows solely from old age, then it is likely to be confined to the larger classes of each species. This is not so however, and both natural competition and possum browsing (see section below) are acting fatally on trees of the above species within all measured canopy size classes. However, as Harper (1977) has pointed out, tree size is not necessarily a good correlate with age and thus a more meaningful and useful interpre-

tation of mortality patterns must necessarily depend on direct ageing techniques.

#### Forest regeneration

The short term future of the Mt Bryan O'Lynn forests is dependent upon some balance being reached between the high forest mortality discussed above and forest regeneration. Of the 10 canopy species dominant in the Mt Bryan O'Lynn forests (see Fig. 7), kamahi, *Quintinia*, southern rata and broadleaf show good numbers of stems in all size classes. Within the Gymnospermae, regeneration patterns are variable, but almost all common canopy species show deviation from a balanced size class distribution. Hall's totara, rimu and kahikatea show moderate to high stem numbers in the understorey, although all are rare as mature trees. Conversely, miro, pink pine and cedar possess very few understorey stems but remain common canopy elements.

Regenerative patterns amongst the dominant sub-canopy and shrub tiers, though not portrayed, show similar variability. Thus, the tree ferns *Dicksonia squarrosa* and *Cyathea smithii*, wineberry and pepperwood were well represented and possessed 470, 1327, 717 and 2659 stems/ha respectively throughout the study area. Conversely, such species as kaikomako and mahoe, although common in the shrub tiers, possess few canopy stems, while pate (*Schefflera digitata*) is now very rare in all size classes. Other seral species such as *Fuchsia excorticata* and *Hoheria glabrata* formerly constituted extensive colonising stands on mid/high-altitude slip sites but now remain largely only as dead stems; both species have largely been replaced by pepperwood and nettle.

#### Possum densities

Just as the living (Fig. 2A) and dead forests (Fig. 4) of Mt Bryan O'Lynn are altitudinally stratified, so too the local possum population density tends to vary inversely with altitude (Fig. 8). Possum kill-trapping within the core study area and contiguous buffers (see Fig. 1) realised 1 284 animals in

42 days before the traps ceased to catch. In addition, a further three, presumably totally trap-shy possums, were obtained subsequently using Potassium cyanide paste. No possums were observed during post-trapping spotlight searches along forest/pasture margin routes where previously 10-50 animals were commonly observed. Concurrent faecal pellet surveys suggest equally dramatic population changes, with a post-trapping occurrence of dung on faecal plots of only 0.7% compared with 20-30% prior to trapping (unpubl. data). While neither the post-kill

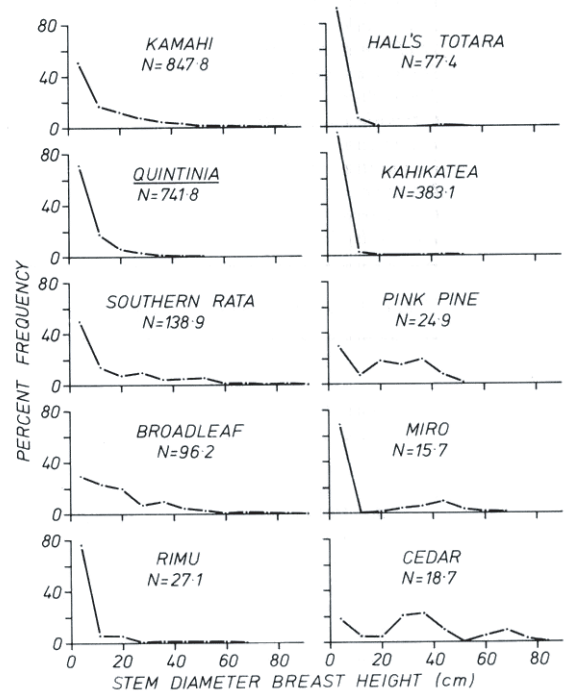


FIGURE 7. Stem frequency distributions of dominant canopy species on Mt Bryan O'Lynn ( $N$  = mean number of stems/ ha).

TABLE 4. Species-specific mortalities on Mt Bryan O'Lynn.

Species	Mean stem diameter (cm)		Degrees of		Significance
	Dead	Alive	Freedom	Fs	
Kamahi	43.6	42.6	1,168	0.04	ns
Southern rata	53.6	48.5	1,86	0.78	ns
Cedar	49.6	55.6	1,43	0.96	ns
*Hall's totara	33.7	33.6	1,16	Ö	Ö

\* Hall's totara not treated statistically, data limited.

spotlight search nor faecal pellet data are robust enough for detailed statistical treatment, both techniques attest to the completeness of the trapping regime.

In total, 1287 possums were removed from the core area plus buffers, a figure which we believe was very close to the absolute number present. Of these, 1045 were included in subsequent density determinations (see methods). Thus, the density within

the core area (estimated to be 98.0 ha) averaged 10.7 possums/ha and varied from 25.4/ha along the bush edge to 1.9/ ha within the 800-900 m altitudinal zone (Fig. 8A).

While the complexity of the vegetation present does not permit the generation of possum densities for specific vegetation associations, some animal density patterns emerge. For instance, highest densities of possums are recorded from altitudinal strata dominated by the two low-altitude cutover terrace associations (1 and 2). Densities are lowest on the mid/high altitude slopes-particularly on the steeper sites occupied by *Quintinia* / Kamahi Forest (4) and within the damper gully-head sites occupied by Broadleaf Forest (6) and Pepperwood Scrub (3). Moderate densities of possums are recorded on the dry ridge sites vegetated by Southern Rata/Kamaha (5) and Cedar Forests (7), and about the high altitude forest/High-Altitude Scrub interface.

Altitudinal variations in possum density revealed through kill-trapping are corroborated through a faecal pellet survey of the core study area made immediately prior to the kill-trapping programme (Fig. 8B). In summary, the number of faecal pellets recruited onto the forest floor per ha per day, as an indication of the numbers of possums present, falls steadily from  $292 \pm 60$  for the low-altitude forest adjacent to the forest/pasture margin, to  $55 \pm 35$  for the highest forested levels.

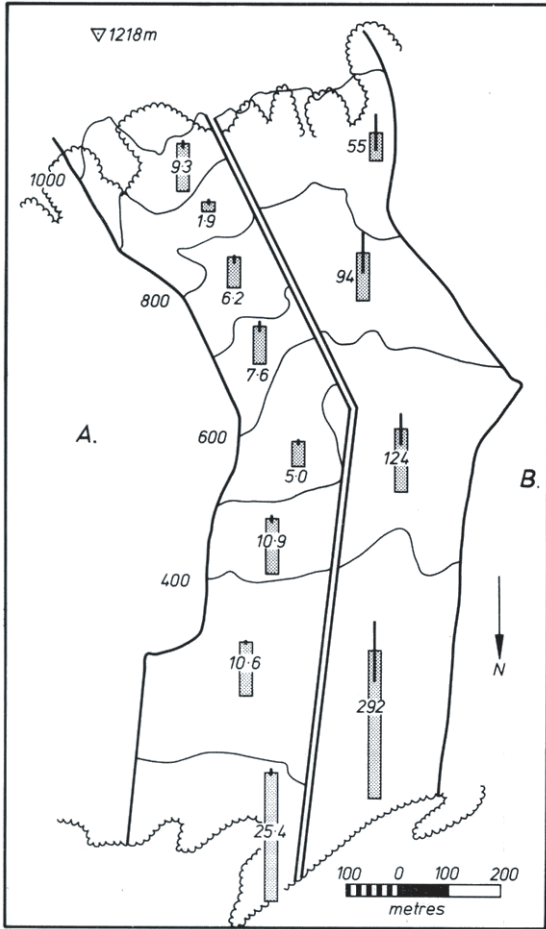


FIGURE 8. Possum densities on Mt Bryan O'Lynn. A. Absolute densities (possums/ ha) within successive 100 m altitudinal strata, as determined by kill-trapping. Densities calculated from derived planar areas  $\pm 95\%$  CL of area.

B. Relative densities within successive 200 m altitudinal strata as indicated by the number of faecal pellets recruited onto the forest floor / ha / day (mean  $\pm 95\%$  CL).

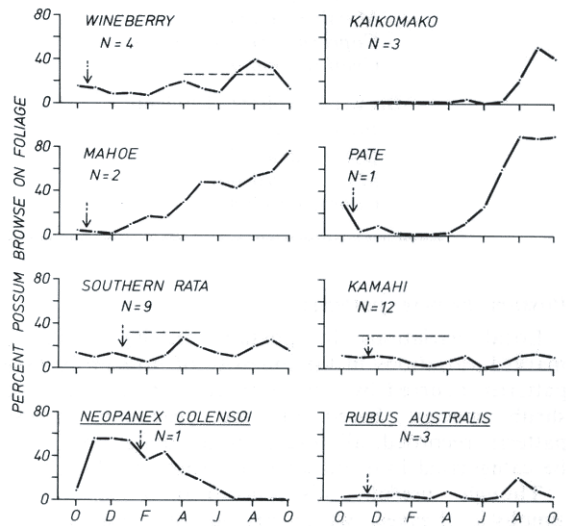


FIGURE 9. Monthly patterns of browse on forest species heavily damaged by possums. The period of species-specific leaf fall is indicated by a broken line, and that of leaf burst by an arrow (N = number of trees / shrubs sampled).

TABLE 5. *Possum browse patterns on Mt Bryan O'Lynn.*

	No. of Trees Monitored	Species position in canopy		
		Understorey	Subcanopy	Canopy
<b>Heavily Browsed Species</b>				
<i>Melicytus ramiflorus</i>	2			2
<i>Metrosideros umbellata</i>	9			7
<i>Aristotelia serrata</i>	8		4	4
<i>Rubus australis</i>	3	2	1	
<i>Pennantia corymbosa</i>	3			3
<i>Schefflera digitata</i>	1		1	
<i>Pseudopanax colensoi</i>	1			1
<i>Weinmannia racemosa</i>	20			20
<b>Lightly Browsed Species</b>				
<i>Podocarpus hallii</i>	2		2	
<i>P. ferrugineus</i>	1			1
<i>Carpodetus serratus</i>	5			5
<i>Griselinia littoralis</i>	11		3	8
<i>Coprosma rotundifolia</i>	2			2
<i>C. foetidissima</i>	2	2		
<b>Not browsed</b>				
<i>Libocedrus bidwillii</i>	1			1
<i>Dacrydium cupressinum</i>	1	1		
<i>Fuchsia excorticata</i>	1			1
<i>Metrosideros perforata</i>	1	1		
<i>Elaeocarpus hookerianus</i>	1	1		
<i>Plagianthus betulinus</i>	1		1	
<i>Pseudopanax edgerleyi</i>	1		1	
<i>P. crassifolium</i>	2			2
<i>Myrsine divaricata</i>	2			2
<i>Coprosma parviflora</i>	1		1	
<i>Cyathea smithii</i>	4		4	
<b>Browsed, Animal, Unidentified</b>				
<i>Pseudowintera colorata</i>	2	2		
<i>Quintinia acutifolia</i>	5			5
<i>Myrsine australis</i>	4		4	
<i>Coprosma ciliata</i>	1		1	

*Possum browse patterns*

Local variations in possum density result in marked variations in the intensity of possum browse patterns incurred by a wide range of forest tree and shrub species. Based on the year-long browse patterns recorded, all forest species under study can be categorised into one of four groups (Table 5).

Though useful, this classification is clearly simplistic. Leaves, which provide the bulk of the possum's diet (Kean and Pracy, 1949), are also browsed by insects and, where browse patterns coexist, interpretative problems arise. Such problems in classification are clarified by reference to other local possum activity, viz., the presence of dung, the

scratching or biting of bark, or through broken branches. Additional problems arise through the seasonal loss and replacement of foliage, but are in turn overcome for each tree by reference to the preceding month's leaf counts.

Eight forest-shrub species under study are heavily browsed by possums and together appear to provide the bulk of the species foliate ingesta (Table 5). Browsing on individual species is generally seasonal and, apart from the few exceptions discussed below, is confined to canopy foliage (see Fig. 9; only heavily browsed species shown).

The most dramatic browse was recorded on mahoe and pate-both low-altitude, early seral,

sub-canopy elements that are often totally defoliated. For mahoe, possums browse most commonly on mature foliage in late summer and autumn and to a lesser extent on new leaf buds in spring. In sharp contrast, browse attacks on pate are confined to the mid-late winter period and then to the stipules of mature foliage only. The leaf lamina is characteristically discarded onto the forest floor below.

Less dramatic damage occurs on two other low-altitude seral species-wineberry and kaikomako. For wineberry, browse damage is limited largely to mature exposed canopy foliage in the autumn and late winter periods, although leaf and flower buds are occasionally consumed in spring. In contrast, kaikomako is browsed most heavily in early to mid-spring when only the canopy foliage is taken. Coincidentally, the stripping of bark from many canopy branches and twigs occurs, a feeding habit we found only on this species.

The two dominant canopy elements, southern rata and kamahi, are also browsed extensively by possums. In both, some damage occurs throughout the year, but is most obvious on the mature canopy foliage in autumn and spring and on new foliage in spring. Heavy damage leads to the "dieback" typical of many of Westland's mixed hardwood forests. However, a substantial autumnal leaf fall in both species (James, FRI, unpubl. data), rules out any robust numerical analysis of recorded browse patterns.

Data on *Pseudopanax colensoi* from a single study specimen indicates a heavy pattern of browse confined to spring on all foliage. The liane, *Rubus australis*, is heavily browsed in spring and to a lesser extent in autumn when mature leaves are freely taken, although leaf buds and new leaves are invariably ignored.

Six forest species studied are infrequently and irregularly browsed by possums. Of these, the most obvious damage occurs on two podocarps-Hall's totara and miro. Both species show light winter browse on mature foliage, but seasonal patterns are confused by winter leaf fall (James, FRI, unpubl. data). Browse damage on *Coprosma rotundifolia* and stinkwood is, for the same reason, equally difficult to categorise. However, both species are browsed by possums over autumn and winter. *Coprosma rotundifolia* is also browsed by wood pigeons (*Hemiphaga novaeseelandiae*) (pers. obs.). Browse damage on putaputaweta and broad leaf is irregular and somewhat unexpected.

Four species exhibit some foliage damage not readily identifiable as possum browse. Browse on all four species is irregular and aseasonal, occurs on sites beyond the reach of possums, and is unaccompanied by all of the customary "sign" (see

above) associated with possum feeding sites. In each instance, it appears likely that the browse patterns observed result either from the activities of lepidopteran (pers. obs.) or phasmatid insects (Meads, 1976).

Eleven plant species under study appeared to be free of browsing by possums or any other animal (see Table 5).

*Forest palatability*

Palatability indices are derived from a summation of stem basal areas of palatable species within each association. Heavily browsed species (from Table 5) are given a multiplier of 1.0; lightly browsed species a multiplier of 0.5; unbrowsed species are omitted. The resulting indices are plotted against altitude using the 95% confidence limits of the altitudinal stratification for each association (Fig. 10). These indices assume that stem basal areas usefully reflect the biomass of leaves and fruits that are available as food and that 0.5 is an appropriate multiplier for lightly browsed species. Both points may be disputed and more sensitive calculations are clearly desirable.

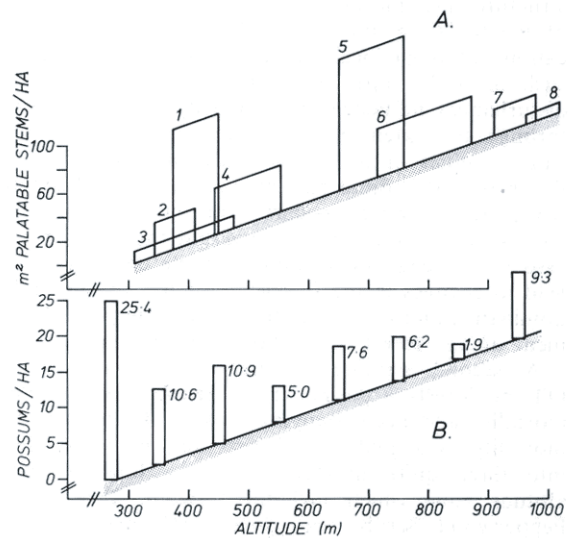


FIGURE 10. Palatability profile and possum densities on Mt Bryan O'Lynn. A. Index of palatability by forest association. Altitudinal range of each association is derived from figure 2A.

B. Possum density for 100m altitudinal zones derived from kill-trapping data (see Fig. 6A). The left-hand density value (25.4 / ha) is for forest / pasture margin animals.

Nonetheless, the results suggest that forest associations vary significantly in their gross palatability ( $H = 170.5$ ,  $P < 0.01$ ) and in directions we expect from estimates of possum densities (Fig. 10). Kamahi and Southern Rata/Kamahi Forests are clearly the most palatable associations. Pepperwood Scmb contains very few palatable stems and ranks similarly to High-Altitude Scrub. One important food component which cannot be included in this type of index is the contribution made by pasture species and herbs to possum diets. Since possum density is highest where bush meets pasture such species are clearly an important component of diet for low-altitude possums. Grasses and herbs may also contribute significantly to possum diet in the high-altitude associations (7 and 8) which have a low palatability ranking despite moderate possum densities.

#### DISCUSSION

The forests of Mt Bryan O'Lynn fall into eight well-defined associations or forest types (see above). Each association possesses characteristic patterns of species frequency and diversity, as well as forest structure and mortality. The most striking feature of the forest in toto is its broad altitudinal stratification, although local changes in site characteristics such as soil, slope or drainage, or local natural disturbances influence the simplicity of this pattern through the extension of associations up or down ridges, gullies or hill faces. Only one exception to this broad altitudinal pattern exists, namely Pepperwood Scrub, which occurs both on induced and natural disturbance sites throughout the area. In all associations changes in influential site characteristics lead to changes in the frequency of the physiognomic dominants, and eventually to the merging or replacement of one forest association with another.

A second striking feature of the Mt Bryan O'Lynn forests is the pattern of recent overt canopy mortality and accompanying erosion. Using canopy mortality as a guide, the forests may be reclassified into three quite uniform strata: a low to mid-altitude zone which includes Kamahi, Tree Fern, Pepperwood Scrub, and *Quintinia* / Kamahi Forest with a dead stem component of about 3%; a mid to high-altitude zone which includes Southern Rata/Kamahi, Broadleaf, and Cedar Forests with a dead stem component of 9.6 to 15.5%; and a High-Altitude Scrub with a dead stem component of about 2%.

Canopy death in the low altitude terrace associations, though infrequent, results largely from past logging operations. In addition to their dead stem component, the mid to high forest slopes, while too

steep and unstable for exploitation, contain many natural disturbance areas of slip and gully bounded by dead forest; such sites originate largely from the collapse of large canopy stems sited on superficial rock shear planes (Fig. 6).

Canopy mortality in most of Westland's mixed hardwood forests has long been considered to result in large part from the browsing patterns and dietary preferences of possums (see introduction). On Mt Bryan O'Lynn possums appear to obtain most of their forest food from a rather limited number of forest species, amongst which kamahi and southern rata stand supreme. The dietary importance to possums of both species throughout the year arises largely from their palatability and widespread dominance over much of the canopy of the study site with individual trees in all of the larger size classes being browsed. On the mid to high-altitude slopes kamahi and southern rata occur alongside two other lesser palatables namely cedar and Hall's totara and together they constitute a dominant, highly palatable canopy, as well as a significant fraction of the dead stems. Cedar and Hall's totara occur as decadent stands in several areas of

New Zealand (Wardle, 1978), often quite unrelated to possum browsing, and in the absence of long-term data the primary cause of death within the study area of either species must remain in doubt.

Lesser local food species such as pate, mahoe, kaikomako, wineberry and *Neopanax colensoi* are all quite limited in distribution, show sharply seasonal patterns of browse, and appear to constitute the "cream" in the possum's forest diet. A restricted intake of the foliage of many of New Zealand's forest species by introduced browsing animals has clearly been a wise precaution. Possums fed exclusively on mahoe died after a short interval (Fitzgerald, DSIR, unpubl. data), while many other indigenous plant species ingested by possums possess plant toxins (see Connor, 1951), e.g., tutu (*Coriaria* spp.) ngaio (*Myoporum laetum*), nettle, rangiora (*Brachyglottis repanda*) and kowhai (*Sophora* spp.).

Dietary selectivity by possums also shows in browse patterns within individual trees. For most species, damage is confined to the outermost canopy foliage. Sub-canopy leaves generally differ in gross form and colour from canopy leaves, and clearly differ in acceptability to possums as well. Age-related foliage acceptability gradients also exist.

Thus, in species such as kamahi and southern rata, new leaves are at least as acceptable as older foliage, while for most other palatable species the reverse is true.

Species present on Mt Bryan O'Lynn but not browsed by possums included raukawa, lancewood,

pokaka, *Plagianthus betulinus* and *Fuchsia excorticata*, all of which have been recorded as common possum foods from one or more areas of New Zealand (Kean and Pracy, 1949). All these species were represented by 1-2 sub-canopy specimens in the browse survey, and their rarity within the study site (together they constituted 0.2 per cent by number of all stems surveyed), coupled with their position within a stratified canopy, probably accounts for their lack of use on Mt Bryan O'Lynn. A low level of browse by possums on rare forest species formerly thought to be of high palatability has been recorded elsewhere, e.g., *Fuchsia excorticata* and *Plagianthus* spp. in Southland (Pracy, pers. comm., in Gilmore, 1967), although Fitzgerald (1976) argued that highly palatable species were browsed by possums to extinction in the Orongorongo Valley, Wellington. Of the remaining species surveyed, weeping matipo and *Coprosma parviflora* have not been recorded as food species anywhere in New Zealand, rimu and cedar have been recorded infrequently in other dietary studies of possums and were clearly of low palatability (Kean and Pracy, 19~9) while one species—*Cyathea smithii*—was a common spring food of possums elsewhere in the study area.

Possum numbers on Mt Bryan O'Lynn, though still moderate to high, show distinct altitudinal variation. Numbers are greatest in the low-altitude forests although both major associations there show very limited canopy death. The reasons for this are largely two-fold. First, the adjacent pasture is a highly preferred feeding zone and relieves the browsing pressure on the forest. Second, the two low-altitude associations possess a multi-tiered diverse canopy system which provides a wide range of food sources and feeding niches, thus easing the browse pressure on anyone species. Possums on Mt Bryan O'Lynn move considerable distances to forage (Green and Coleman, in press), and it might be argued that the frequent movements to farmland by animals dwelling in medium to low-altitude forest zones may have artificially raised the density estimate determined by kill-trapping for the lower zones. This can be discounted for two reasons. First, the high density of traps across the whole study area severely curtailed possum movements and their subsequent trapping outside their home altitudinal zone was unlikely. High-altitude possums are more sedentary (op. cit.) and are even more likely to be caught in their home zone. Second, the density gradients as revealed by kill-trapping and the pre-kill pellet survey are similar. Both show a 5 to 6-fold decrease in density from bush-edge to high-altitude forest.

Possum densities in mid and high-altitude Southern Rata/Kamahahi and Broadleaf associations are at low levels, yet these forests exhibit a high level of damage. Animals in this lowest density strata (700-900 m) no longer utilise the pasture as do mid-forest animals (see Green and Coleman, op. cit.) and are also in a forest association of low species diversity and simple canopy structure. Both the living and dead canopy components of these associations are dominated by only three species (southern rata, kamahi, Hall's totara) and all are palatable. The low possum density despite the presence of palatable canopy trees suggests that resident possums lack the diversity of diet, and hence the necessary nutritional balance they would obtain elsewhere.

Finally, the rise in possum density at the High-Altitude Scrub and Cedar Forest interface probably results from the great species diversity of this zone. Here possums have access to the high altitude forest associations, to the Pepperwood Scrub, to the very dense and diverse High-Altitude Scrub, and to the adjacent tussock and herb covered slip sites.

Overall, the forest mortality on Mt Bryan O'Lynn is sufficient to place the short-term future of the present forest structure in some doubt. Changes are occurring at sites of high canopy mortality (or high animal use), but need be of future consequence only if there is an accompanying lack of regeneration of the canopy species or a change in the present stability of the hillside. Much may depend on the future levels of the possum and red deer populations which are both under pressure of commercial exploitation at present. It has been suggested (J. Wardle, pers. comm.), that the regeneration of many of Westland's mixed hardwoods is at best intermittent, and the lack of regeneration of some major canopy species on Mt Bryan O'Lynn, revealed through stem size frequency patterns (Fig. 7), indicates that short-term changes in forest structure are inevitable.

To sum up, the altitudinally stratified forests of Mt Bryan O'Lynn appear, through preferential browsing, to have undergone quite substantial changes both in canopy and understorey elements over the last two decades. Such changes continue even though the numbers of browsing animals, particularly possums, are probably now at lower densities than before and closer to the carrying capacity of the modified habitat. The current vegetation trend within all forest tiers appears to be towards less palatable and more browse-resistant species such as

*Quintinia*, pepperwood and small-leaved *Coprosma* spp. in place of such highly palatable species as southern rata, pate, *Fuchsia* spp. and *Neopanax*

spp. Unfortunately, some species heavily browsed by possums possess very low stem frequencies amongst most age classes, and as has been recorded elsewhere (Fitzgerald, 1976) may well be in danger of local extinction. Kamahi is apparently the exception to this trend, as it is highly palatable and yet regenerating freely throughout the study area. The rate of vegetation change is specific to each association, but for the Mt Bryan O'Lynn forests in toto, is likely to be as dramatic as anywhere in the Grey River catchment.

#### ACKNOWLEDGEMENTS

The authors wish to thank FRI colleagues for assistance in the vegetation and possum surveys, especially M. D. Thomas, J. G. Polson and B. Warburton. In addition, M. McLennan and C. L. Batcheler of FRI provided specific advice on sampling procedures, while J. Leathwick (FRI) took the photographs. Dr E. B. Spurr critically read the manuscript.

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