

MAMMALS AND BEECH (*NOTHOFAGUS*) FORESTS

I.L. JAMES

*Protection Forestry Division, Forest Research Institute,
Rangiora*

At some time in the past almost of all of our beech (*Nothofagus*) forests have contained higher numbers of red deer (*Cervus elaphus*) than could be supported by the annual growth of palatable plants within browse range. During this period the natural balance of the forest understorey composition was upset by losses of seedlings and saplings of palatable plants, including the beeches. As long as seed sources of the palatable species are present the understorey composition tends to revert to the original situation whenever deer numbers are reduced. Additional growth of unpalatable or browse tolerant plants partly compensates for the losses, but the understorey still shows no real stability in composition even though deer have been present for over 50 years. Prediction of the future composition of the understorey while deer numbers continue to fluctuate is therefore difficult. It is easier to determine whether the present densities of deer are hindering the rate of forest regeneration.

This work is one of the main tasks of the Watershed (condition and trend) Surveys made annually by the Forest Research Institute in important high country catchments. Over the past 17 years, 20 initial surveys have been completed, of which 11 have been resurveyed—some three times. The area of beech forest covered is approximately 900,000 ha. The results of individual surveys are available in several publications (Holloway 1963, Wardle 1967, 1970, 1971 a & b, Wallis and James 1972), and in unpublished Forest Service reports.

One of the major aspects of survey work is relating the population levels of mammals to the mortality and recruitment rates of understorey plants, particularly the advance growth of canopy trees. The interpretation of these data relies either on comparisons between similar forest areas with different densities of mammals, or between successive assessments of the same area. There are so few areas left now which have

not suffered from the effects of mammals that a knowledge of the autecology of the major tree species is the only way to distinguish between normal and abnormal conditions of forest regeneration. For beech forest the autecological information is especially important because the life cycles of the beech species have peculiarities which could be confused with the results of deer browsing.

A good deal of this confusion arises from the assumption, based on the silvicultural requirements for sustained yield forestry, that the numbers of stems of a tree species from seedlings through to large trees should follow a negative exponential distribution, commonly referred to as the "J" curve. This assumption is only true for beech forest when a reasonably large area is measured. On a small scale the multi-storeyed forest cannot be appreciated because of the widespread occurrence of size-class stratifications in beech stands. Wardle (1970) noted that most of the monotypic forests are composed of one, two, or three aged stands; truly mixed-age stands seldom occur. Similar even-aged stands commonly occur in mixed beech forests (see Wardle 1974, p.23). Such size stratifications appear to be the result of three factors, occurring either singly or in combination.

First, the flowering and seed production of the beech species is irregular. Records indicate that the average interval between good mast years of *Nothofagus solandri* var *cliffortioides* (mountain beech) is 10 years (Wardle 1970). *Nothofagus fusca* (red beech) and *Nothofagus menziesii* (silver beech) may be more regular seeders, although current information is scanty (Wardle 1965). Once the seed has fallen, most germination occurs during the following spring, producing the characteristic size stratifications of beech seedlings (see Franklin 1974, p.18; Wardle 1974, p. 24; Manson 1974, p.27).

These stratifications are further accentuated by intra-specific competition. Suppression of seedlings by adult trees becomes so intense that seedling growth is severely limited above an apparent threshold of overstorey basal area. This level is about 45-60 m²/ha for mountain beech and near 75 m²/ha for silver beech; these figures also constitute the predominant stocking of stands found in both the North and South Islands. Wardle (1970) states that "... when the basal area drops below 45 m²/ha, ingrowth from seedlings rapidly makes up the difference. Conversely, if growth in the adult tree is capable of replacing the loss due to mortality and maintaining the basal area in the region of 50, the advance growth is held in check ..." It is therefore evident that absences of saplings within closed stands of beech cannot be equated simply with high deer numbers. Nor can any sudden upsurge in seedling or sapling growth be attributed to a reduction in deer numbers without also considering the status of the overstorey (see also Wardle 1974, p.23).

Finally, natural catastrophes form a major cause of even-aged stands of beech. Mass movements, extreme snowfalls, extensive windthrows (e.g. the 1936 Tararua blowdown), severe insect attack or fire may all result in either complete openings within the forest or sufficient reduction of canopy cover to release suppressed advance growth. Mass movements commonly produce an intricate mosaic of even-aged stands, while snowfalls and windthrows may affect whole valleys and ranges. After snow damage the response of advance growth can be so extensive that seedling and sapling growth rates are unimpeded by browsing unless the deer are present in very high numbers.

From what has been discussed so far it should be obvious that interpreting the influences of mammals is not easy. In most field situations we have to deal with the many different beech communities that result from various permutations and combinations of beech and associated tree species. Depending on climatic, altitudinal and physiographical gradients, upwards of a dozen broad forest communities may be recognised within a typical survey area. Each community has its own peculiarities

according to the autecology of the constituent species and their interactions. It cannot be assumed that all will react similarly to browsing by mammals. On the animal side, it must be known which mammals are present, for how long, and in what numbers.

Survey work has shown that none of the beech species are highly preferred browse for deer or opossums. (*Trichosurus vulpecula*). Broadly speaking, silver and mountain beech are browsed more frequently than red and hard beech, but browse preferences are not particularly uniform amongst different forest communities. However, the growth of beech seedlings may be seriously inhibited by deer browsing as was well demonstrated during the periods of high deer numbers in the past. Since the decline of deer numbers browsing is more localised, especially on north or west aspects. While these favoured areas may suffer sufficient browsing to inhibit forest regeneration the remainder of the forest suffers only light or intermittent use. Small clearings are also favoured by deer, and when these clearings are the result of mass movements, or stream channel erosion, browsing becomes important in terms of catchment stability. Deer hinder the recovery of the forest cover — first by trampling which retards the achievement of the site stability necessary for the establishment of tree seedlings and then by browsing, which limits the survival and growth of the seedlings. Conditions tend to favour the dominance of indigenous grasses and unpalatable shrubs, and any established beech seedlings may suffer abnormally high browsing. Even normally unpalatable species are browsed on open areas. Nonetheless, it has become noticeable over the past few years that the numbers of deer are no longer sufficient to totally halt the re-establishment of beech species on clearings. The rate of succession, however, is not the same as when mammals were absent.

The impact of deer within closed forest depends very much on the composition of the particular community. Within a monotypic beech forest deer have little effect on advance growth until the canopy opens. In the mixed broadleaf/podocarp/beech stands, which commonly occur near the ecological range of the

beech species, selective browsing of palatable species may initiate many long-term changes in composition. The first and obvious changes occur within the forest understorey and are well described in the literature. Less is known of the subsequent influence of deer on the overstorey composition. Many of the tree species associated with beech (e.g., *Weinmannia racemosa*, *Griselinia littoralis*, *Fuchsia excorticata*, and *Pseudopanax simplex*) are very sensitive to deer browsing in the sapling and seedling stages, and to opossum browsing in the adult stage. The long-term result of persistent deer browsing must be to reduce the importance of the broadleaf-hardwood component. If seed is available, and light and soil conditions are suitable, beech species may regenerate as a response to the broadleaf losses, and the forest will tend to become a more monotypic community. Otherwise the unpalatable understorey species (principally *Pseudowintera colorata*, *Dicksonia*, *Cyathea*, and *Blechnum* ferns) are likely to rapidly increase, and this leads to senescent stands characterised by a dense ground cover without any tree seedlings and an incomplete overstorey of large beech trees.

The situation is further complicated by the fact that similar senescent stands have developed naturally before the advent of mammals in regions where beech is competing with podocarp or broadleaf/hardwood species for forest dominance (Cockayne 1926, Holloway 1950, type B5, p. 131). It is difficult either to distinguish natural from mammal-induced senescent communities or to predict their future.

Opossums have never been considered a pest of beech forests, mainly because they rarely browse any beech species. However, the majority of beech forests contain seral vegetation along stream channels and on mass movement sites. This component is highly susceptible to opossum browsing. Stream channels appear more susceptible to lateral erosion following the loss of seral species such as *Fuchsia excorticata* and *Schefflera digitata* trees lining the banks. Mass movement sites may be reactivated by the loss of *Aristotelia serrata* and *Hoheria sextylosa* trees. It is because seral communities form a small part of the total forest, and are heavily utilised by deer as

well, that the influences of opossums are easily overlooked. There are few other seral species which are resistant to deer and opossums and able to take the place of the susceptible species.

The advent of helicopter shooting has much reduced the influence of deer in the upper forest/scrubland zone. Animals that once grazed the alpine grasslands took shelter within the lower scrubland and severely depleted the vegetation. Opossums compounded the problem by browsing *Senecio* and *Olearia* species beyond the reach of deer. Since helicopter shooting has reduced the deer numbers the upper forest/scrubland vegetation has made a remarkably swift recovery. In some areas, such as the Haast/Arawata, foot-shooting also has reduced numbers on the lower valley slopes, so that the main impact of deer is not confined to the central forested slopes (Wardle 1971, Challies 1974, p.47).

All the watershed surveys made over the past five years have concluded that deer in their current numbers are a lesser threat to the monotypic beech forest than was once considered. There is little doubt that this situation has resulted from the substantial reduction of deer numbers since the 1960s by increased recreational and commercial hunting. With the greater knowledge of the autecology of beech species we are also able to differentiate between normal and abnormal patterns of forest replacement. It is in the mixed broadleaf/podocarp/beech forests that both deer and opossums still appear a danger to the continuation of a forest cover.

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