THE EFFECT OF DEER ON SUBALPINE FOREST AND SCRUB

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During the last few years there has been a great deal of controversy about deer. The debate centres on the following three questions:

Do deer cause any damage of consequence to the forests and mountain vegetation?

Is any damage offset by the benefits which deer confer as game animals?

If control of deer numbers is necessary, how is this to be achieved?

A team from the New Zealand Forest Service has been studying these questions in the field, and during the past three years my part has been to study the vegetation near the tree line.

First, I shall compare conditions in three mountainous localities which all receive very heavy rainfalls, probably far exceeding 100 in. per annum. Red deer are the main browsing animals in all three localities.

In the northern part of the Tararua Range the subalpine vegetation is mainly scrub dominated by *Olearia colensoi*. On slopes steeper than 30°-35° this scrub is healthy and has been scarcely damaged by deer, but on more gentle and accessible slopes, which include broad ridges and cirque-like valley heads, the scrub has been nearly exterminated. *Olearia colensoi* has been the first to go, and in many places only bleached sticks remain. Most of the remaining species of shrubs are also heavily browsed, often to the point of elimination. At best, snow-tussock has replaced the scrub, more often a browse resisting turf has developed. But all too frequently the bared ground has eroded down to the rocky subsoil, and recovery of the vegetation is likely to be very slow.

Silver beech forest is the main subalpine vegetation in the southern part of the Tararua Range. In contrast to the scrub to the north, much of this forest is outwardly intact, but despite the fact that seedlings appear in profusion after seed years, effective regeneration of silver beech is generally lacking. Other parts of the subalpine silver beech forest are very open as a result of damage by gales. Normally, wind-throw gaps are quickly filled by thickets of young beech. However, in the Tararua Range nearly all the beech seedlings have been killed by browsing, and the plants of the shrub storey, *Nothopanax*, *Coprosma*, and *Olearia colensoi*, have also been killed. It seems likely that most of this wind-damaged forest is destined to be replaced by grassland or parkland, in which the dominant species will be *Danthonia cunninghamii*.

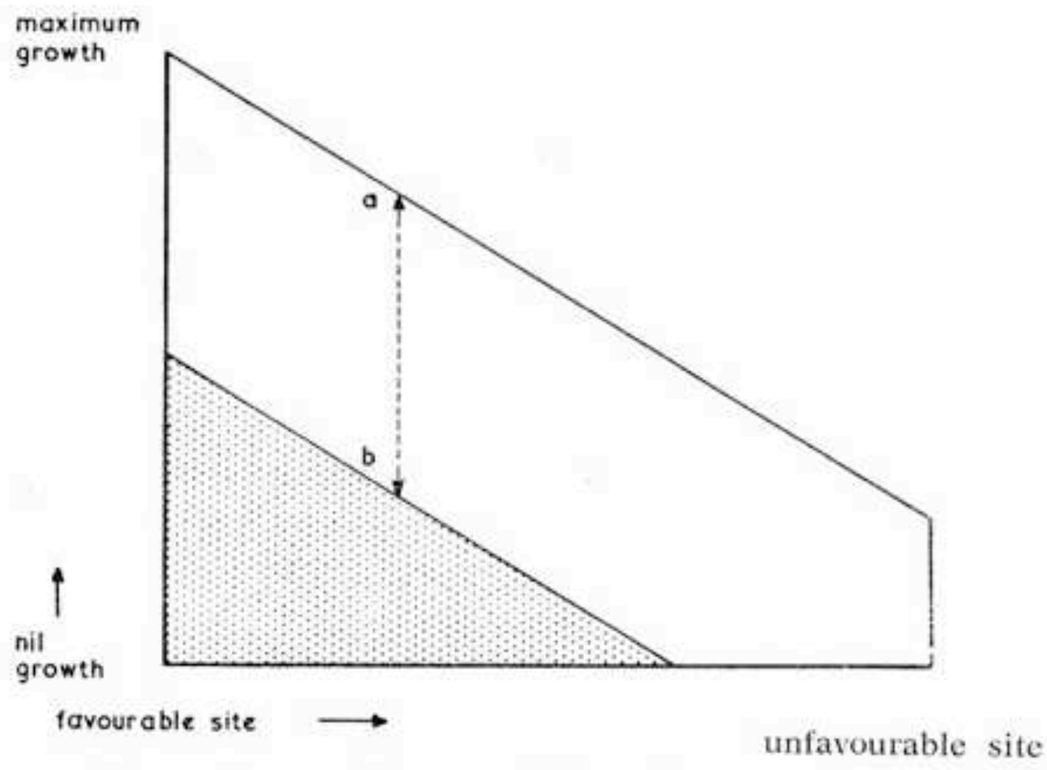
The subalpine vegetation in the catchment of the Hokitika River is again mainly subalpine scrub dominated by *Olearia colensoi*. However, slopes are generally much steeper than they are in the Tararua Range, which is probably the explanation of the virgin condition of most of the scrub. Red deer and chamois have formed tracks which lead through the scrub from the forest to the alpine grasslands, but highly palatable species such as *Nothopanax colensoi* survive a few yards from these tracks. Nevertheless the subalpine scrub is probably a significant component of the deer habitat, because it acts as a barrier which protects animals frequenting the uppermost forest from shooters who operate on the grassy tops. This uppermost forest is heavily damaged. In places its floor is churned up like a sheep yard.

Slips in the Hokitika catchment are another habitat favoured by deer, and have suffered accordingly. In the subalpine zone slips were once colonised by communities of the fast growing *Hoheria glabrata*. But its palatable seedlings can no longer become established on fresh slips, which are now colonised by open vegetation. Under the Hokitika conditions of rainfall and erosion this open vegetation does not check further slipping.

The inland part of the Haast region in South Westland resembles the southern part of the Tararua Range in that the subalpine vegetation is mainly silver beech forest. But this seems to be in quite good order, even though the Haast area supports large numbers of deer at times. On the other hand the lower-altitude mixed forest has been denuded of nearly all its palatable seedlings and shrubs. The upper Haast area differs from the Hokitika catchment and the Tararua Range in that it contains wide, grassy valley flats. Thus, a possible explanation for the different pattern of damage to the vegetation is that the presence of these flats induces the deer to frequent lower altitudes, at least during the winter when the alpine grasslands are under snow. Speaking generally, there is scope for the animal ecologist to explain regional differences like the ones I have mentioned in terms of animal behaviour.

Next, I shall discuss the complexities of the relationships between red deer and individual plant species. For example, I have mentioned the extent of dead *Olearia colensoi* in the Tararua Range. There is no doubt that deer must bear the ultimate blame. This is proved by the concentration of the damage on more accessible terrain, and by the occurrence of obvious browse lines on taller shrubs. Yet we had only limited success when we searched during the summer of 1958-59 for direct evidence of browsing by deer. By far the greatest amount of damage was caused by a caterpillar (identified by Mr. George Gibbs as *Agriophara coricopa* Meyr.) which destroys the buds of *Olearia colensoi*. The total evidence indicates that stands of *Olearia colensoi* are normally in equilibrium with a number of destructive factors, and that the introduction of deer into the habitat is sufficient to cause the system to overbalance. It may be that deer kill the seedlings, and attack the older bushes more frequently during severe winters. Deer have not yet reached Secretary Island in Fiordland, and though there is much dead or dying *Olearia colensoi* on the island, there is also free regeneration.

Mountain beech can be used to illustrate another sort of interaction. At the head of Broken River in Canterbury, pure forest of this species covers the mountain sides from 3000 ft. to the tree line at 4500 ft. The deer population has been maintained at a low level, at least during the past decade. On the lowest slopes young mountain beech forms a dense and nearly continuous lower storey. However, towards dry spurs and higher elevations, the density and vigour of the regeneration decreases, until there are no healthy seedlings and saplings. The few battered survivors are suppressed plants which are probably over 50 years old. This situation is not due to a poor supply of seed, or to a failure of the seedlings to establish. Following the seed crop of autumn 1957, a carpet of seedlings appeared, and from 15-50 per cent of these are still surviving. It seems that they will persist until they are tall enough to attract the attention of deer. The explanation, as I see it, can be illustrated by the diagram. The horizontal axis represents a



gradient from favourable (foot of slope) to less favourable (tree line) sites for mountain beech. The vertical axis represents the corresponding decline in the growth rates of young beech. The upper sloping line indicates that there will be survival and nett growth of the young beech on all sites. Now,

suppose that deer are introduced into the system, and that they remove equal quantities of browse, represented as *a-b* on the diagram, from all the sites. The lower line now indicates that, though regeneration will continue on the more favourable sites, it will fail on the less favourable sites.

Polystichum vestitum resembles *Olearia colensoi* in that the degree of browse damage which it suffers in the forest is related to the topography. It is often browsed to the point of extinction on flat valley bottoms; yet on the adjacent slopes it may remain rank and healthy, even where well trodden animal tracks pass among it. *Polystichum vestitum* also suffers much less apparent damage from browsing when it is growing in the open. Is this because it is more vigorous in the open, or are the fronds harsher and less palatable?

The last facet of the relationship between deer and native vegetation which I shall mention is the different susceptibility to browsing damage of related species of plants. For instance most of the *Coprosma* species which grow in the forest interior are palatable, and are liable to be eaten out. But *Coprosma colensoi* is only lightly browsed, although it is so closely related to the highly palatable *Coprosma foetidissima* that it hybridises with the latter. The small-leaved densely divaricating *Coprosma* species of open habitats are also strongly resistant to browsing. Within the generally unpalatable genus *Dracophyllum, D. uniflorum* and allied forms are browsed and often killed by deer. With *Aristotelia fruticosa,* there seem to be differences in palatability between the races of different localities.

Finally, let us consider research methods. Different methods must be used, according to whether we are assessing past or future effects of deer. It is difficult to give a valid quantitative basis to studies of past effects. The only published attempt of which I know concerning subalpine forest and scrub is the recent bulletin on the Lake Monk expedition (Riney *et al.* 1959). In this bulletin several lines of quantitative data are claimed to support the authors' contention that deer are not a threat to the protection forest. In my opinion, these data are of questionable validity. I give one example. Measurements were made of the proportion of annual shoot growth which had been removed by browsing and it was concluded that browsing exceeded annual growth in only four per cent of the plants. However, I do not accept that the authors could tell what constituted annual growth. I have been studying annual growth of subalpine woody plants for two summers, and only now am I convinced that I can distinguish annual growth of mountain beech by external characters. Annual growth of the subalpine *Coprosma* species can be distinguished only by microscopic examination of transverse sections of shoots.

So, I believe that we are thrown back to assessing past deer damage by intelligent guesswork, based on a wide knowledge of vegetation in both virgin and modified conditions. This, incidentally, illustrates the practical desirability of maintaining reference areas of virgin vegetation, such as the wilderness area of Secretary Island.

We can make a quantitative approach to assessing future effects of deer, by measuring samples of vegetation and remeasuring them after certain periods. I have been doing this type of work during the past three years and I have been in a quandary all the time. To yield valid, unequivocal and useful results, the measurements must be carried out carefully and, I think, in considerable detail. But this is a difficult task, because the vegetation which we are considering is distributed through the larger part of the New Zealand mountain system, and the physical difficulties of making detailed measurements are very great, especially in subalpine scrub. There is a case for confining detailed measurements to selected study areas, but it is not certain that these will yield results of general validity.

This paper has taken the form of an enumeration of difficulties and complexities; yet it is essential that the problem be studied, for not only the ecologist, but also a much larger public are anxious to be given accurate information about the effects of deer on the mountain vegetation.

REFERENCE

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