

SELECTIVE FORCES INFLUENCING THE EVOLUTION OF DIVARICATING PLANTS

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SUMMARY: Diels (1897) first put forward a climatic hypothesis for the origin of divaricating plants. This hypothesis has been elaborated by subsequent authors and is further extended herein. In contrast, Greenwood and Atkinson (1977) proposed that the divaricating shrub form evolved as a protection against moa-browsing. These two hypotheses are critically compared and it is concluded that the climatic hypothesis better explains the ecology, distribution and morphology of divaricating plants.

Divaricating plants are adapted to existing non-forest and forest margin habitats and it is suggested that they arose during the harsh, near-treeless glacial periods of the Pleistocene. The main function of the divaricating form is to protect growing points and leaves from wind abrasion, desiccation and frost damage. Also, a favourable microclimate is maintained inside the shrub and this may permit higher rates of photosynthesis during periods of adverse weather. Distribution and ecology of divaricating plants are related to these factors. We consider divaricating plants evolved in New Zealand as one of the responses of a sub-tropical flora, isolated from sources of arctic-, alpine-, and desert-adapted plants, to the onset of harsh glacial climates.

INTRODUCTION

Aim

Greenwood and Atkinson (1977) in a detailed and stimulating paper put forward the hypothesis that moa-browsing has been responsible for the evolution of the divaricating plant form in New Zealand. Since that time we believe that the 'moa-browsing' hypothesis has been widely accepted (e.g. Smalley, 1979). In this paper we restate the 'climatic' hypothesis for the origin of divaricating plants, first proposed by Diels (1897), and since elaborated and extended by other authors. We then critically examine the two hypotheses in relation to how well they explain aspects of the ecology, distribution and morphology of divaricating plants.

Divaricating plants

Divaricating plants are small-leaved shrubs or tree juveniles which characteristically have a wide branching angle, as a result of which the branches form an interlaced, three-dimensional structure with a relatively leafless exterior. Greenwood and Atkinson (1977) list 54 species of plants native to New Zealand which they consider (using divergent branch angle as the critical criterion) to be divaricating.

While we accept Greenwood and Atkinson's list, we think that a strict definition of divaricating plants based on branching angle is misleading. As Tomlinson (1978) has demonstrated, divaricating shrubs have a variety of architectures, and similar physiognomies are achieved in very different ways.

Tomlinson also points out that a wide angle of branching is also a feature of tropical lianes, and that the chief factor controlling the development of divaricating plants is a change from the usual methods of organisational control in the shoot system.

As Greenwood and Atkinson (1977) and Tomlinson (1978) have stated, New Zealand has an unusually high concentration of divaricating plants, and nowhere else do they play such an important ecological role in the vegetation. Any hypothesis as to the origin and evolution of divaricating plants must therefore explain the adaptive significance of their structure and show why this life form is rare in other parts of the world.

THE CLIMATIC HYPOTHESIS FOR THE ORIGIN OF DIVARICATING PLANTS

Structure of divaricating plants in relation to climate

The structure of divaricating plants has been interpreted as being an adaptation to windy, xeric climates (Diels, 1897; Cockayne, 1912). The densely branched structure acts as a wind break that reduces transpiration of the leaves by providing a relatively moist interior to the bush. This adaptation enables divaricating plants to thrive in areas marginal for forest. Wardle (1963) pointed out that most divaricating species occur in forest and scrub, and suggested that such species were adapted to dryish forest environments. Rattenbury (1962) stressed the xeromorphic nature of divaricating plants and

suggested that low soil temperatures, resulting in poor absorption to water through the roots, was one cause of this xeromorphy.

Wind, as well as increasing the transpiration of the leaves, can also cause direct damage. In a large-leaved shrub, leaves are generally close to, or touch, other leaves, twigs and branches. In windy conditions, repeated collisions of leaves against other leaves or twigs can lead to damage that ranges from tearing of leaves to microscopic abrasion of leaf surfaces (Grace, 1977, p. 80; Wilson, 1980). Such damage, besides destroying photosynthetic tissue, greatly increases transpiration losses (Grace, 1977, p. 68). Wind-borne particles enhance the destructive capabilities of the wind, and Savile (1972) commented in relation to the arctic flora, that a single exposure to such wind abrasion may reduce the vigour of some plants for several years, or may even prove fatal. The small, well-separated leaves of divaricating plants are much less exposed to abrasion by neighbouring leaves and stems. Further, more, the springy network of interlaced branches and twigs tends to move as a whole, thus minimising contact of individual leaves.

Frost is a further climatic factor that has not been discussed in the literature in relation to divaricating plants. Observations that we have made on a variety of divaricating shrubs at Botany Division, Lincoln, and Cass, inland Canterbury, have shown that even in severe frosts in which exposed leaves are frozen the interior leaves of the shrubs are unaffected. Even a relatively slight network of branches and twigs seems to be effective in preventing frosting of leaves. We suggest, therefore, that the divaricating form provides its own frost-screen with the relatively leafless exterior branches protecting the interior leaves from damage. The significance of this frost-shielding effect does not reside solely in the prevention of frost damage to the leaves; in conifers, the rate of photosynthesis drops markedly in undamaged leaves that have been frozen, but subsequently thawed, and this check in photosynthesis is directly related to the severity and frequency of frosts (Tranquillini, 1979).

Besides possibly acting as a frost-screen, the protective network of branches may, on cold, but sunny days, act as a heat trap, raising the temperature of the air mass inside the shrub, and this may permit higher rates of photosynthesis. Effects similar to those suggested here have been recorded inside tundra plants on cold sunny days in the high arctic (Billings, 1974).

The divaricating habit involves a high degree of self-shading and therefore the cost to the plant is great. For that reason, the more extreme forms of

divarication should only be found in habitats in which there is a high risk.

Habitat of divaricating plants in relation to climate

As a consequence of its position in the mid-latitudes and its isolation in a large area of ocean, New Zealand has a mild, generally humid, windy climate. However, it is also a very variable climate and the continental pattern of a cold winter and a consistently warm summer does not apply here. Winters are relatively mild, but the frost-free season in many areas is probably shorter than that at equivalent altitudes overseas (Morris, 1965). Damaging frosts can occur in any season of the year in many forest areas of New Zealand, whereas in continental areas they are generally confined to the period from late autumn to early spring (Warrington and Rook, 1980). Further, in continental areas frost conditions may last for weeks or months, but in New Zealand frost generally occurs only at night, and then lasts only a few hours. It is not uncommon on a winter afternoon after a frost for air temperatures to rise as high as 15°C (Warrington and Rook, 1980). Because of its high relief and its orientation to the predominant westerly airflow, much of New Zealand is subjected to foehn winds. When these occur in early spring, temperatures may rise to high enough levels to encourage an early start to spring growth. These foehn wind episodes are often followed in montane areas by periods of cold, frosty weather which can therefore have disproportionately adverse effects on new growth (Morris, 1965).

We suggest that the majority of divaricating plants and heteroblastic juveniles in the New Zealand flora have evolved in response to lowland and montane environments which are unsuitable for normal tree growth because of the high and unpredictable incidence of frost, wind and drought. Whereas most plants that grow in alpine areas are adapted for year round cool temperatures and those of continental areas for a cold winter and a warm, reliable summer, the kinds of climates and habitats in which divaricating plants have specialised are very different. Therefore, divaricating plant adaptations do not involve great modifications of the leaf and bud anatomy, as do those of alpine regions, nor do they, for the most part, possess winter deciduousness, as do many shrubs and trees of continental areas. Instead, in keeping with the highly variable climates, the main adaptation is an alteration of the plant form which will function in any season of the year. Divaricating plants can therefore take advantage of warm winter days and also be protected against frost and unusually cold days in spring and summer. At any time of the year they

are protected against most of the deleterious effects of high winds.

Divaricating plants are most commonly found in forest margin and successional habitats. When exposed at the forest edge, or in the open, most divaricating shrubs develop a dense, protective palisade of twigs; the same species just within the forest margin is more lax and some species become more leafy. Although most divaricating plants exhibit this behaviour to some degree, there is marked variation between species in their ability to alter their degree of divarication under shaded or sheltered conditions, and it is likely that different species are exploiting different parts of the light-shade continuum. For instance, exposed and shade forms of *Hymenanthera alpina* at first sight appear to belong to different species, but there is very little apparent difference between the exposed and shade forms of *Myrsine divaricata*.

Almost as important as the fact of divarication, is this ability of form that enables a single species to successfully exploit a great range of habitats without, presumably, the necessity of major physiological or structural alteration of the leaves.

Only a few studies relate the distribution of divaricating shrubs specifically to climate. Wardle (1977) in his study of the plant communities of Westland National Park mentions a phase dominated by small-leaved, divaricating shrubs in the succession that occurs on lowland river terraces. These terraces are often subjected to frost, and there are some hardy species of *Coprosma*, (*C. parviflora*, *C. wallii*, *C. rigida* and *C. rugosa*) that can withstand severe frost. This divaricating shrub stage of the succession also includes the seedlings of the succeeding forest phase, and it is significant that some of the most common of these (*Paratrophis microphylla*, *Pennantia corymbosa* and *Plagianthus betulinus*) are divaricating. In the same region, at a much later stage of the succession on alluvial flats, two divaricating species (*Myrsine divaricata* and *Coprosma parviflora*) are among a group of subalpine species that persist around wet 'frost hollows' within the hardwood forest (Wardle, 1980).

Esler (1967) makes specific mention of the behaviour of the divaricating shrub *Pseudopanax anomalus* on Kapiti Island. There, *P. anomalus* is invading open grassland at the top of a wind-swept valley after having been kept in check until recently by grazing sheep and goats. *P. anomalus* acts in this situation as a pioneer, moving by saltation out into the exposed ungrazed turf. However, in the same area *P. anomalus* can survive and reproduce under a canopy of trees and shrubs.

EVOLUTION OF DIVARICATING SHRUBS IN RELATION TO CLIMATIC CHANGE

Climate and vegetation of the Last Glaciation

During the Quaternary, that is approximately the last two million years, New Zealand was subjected to numerous glaciations. Although the evidence as to the number of these glaciations is limited and fragmentary in New Zealand, evidence from other countries suggests that globally there were at least 17 during this period (Bowen, 1978). For most of the last two million years, therefore, the New Zealand climate was very different from that of the present.

There is now enough information to reconstruct a reasonably accurate picture of climate and vegetation during the peak of the Last Glaciation, which ended about 14000 years ago, and it may be assumed that this is fairly representative of older glacial cycles as well. Although the climate was colder than present, and ice occupied larger areas of the Southern Alps than now, temperatures in most lowland areas should have remained high enough to permit tree growth. The standard estimate for depression of the annual temperature is 6°C (Gage, 1965), although recently it has been suggested that in some areas it may have been less than 5°C (Soons, 1979).

Despite this, palaeobotanical evidence indicates that most of the New Zealand landscape was covered with scrub or grassland. From the Waikato Basin (McGlone, Nelson and Hume, 1978) through Wellington (Brodie, 1957) to the far south of the South Island (Moar, 1971; 1980; McIntyre and McKellar, 1970) almost treeless landscapes prevailed. We also know that this type of vegetation was widespread even during milder episodes of the Last Glaciation (Moar and Suggate, 1979). Why forest was so rare during the glaciation has not been totally explained, but it has been suggested that a generally more variable climate with stronger winds, and more frequent drought and frost may have been involved (McGlone *et al.*, 1978). New Zealand trees are, in general, frost-sensitive (Sakai, Paton and Wardle, in press) and this may have been a crucial factor.

Although forest was uncommon, there can be no doubt that forest survival was widespread. The present distribution of *Nothofagus* requires that these trees survived even in the far south close to the ice front (Wardle and McKellar, 1978; Johnson, 1978). The absence of any discernible migration pattern of podocarp species after the end of the Last Glaciation suggests that most, if not all, of the podocarp forest species common today in a given area were present there throughout the peak of the glaciation. Forest survival seems to have been most

marked in the more hilly, dissected regions of both islands. Here, the warm, north-facing valley slope habitats may have permitted the survival of species not capable of tolerating the exposed, frost- and drought-prone plains and rolling country.

Under these circumstances there would have been large areas of the landscape which approximated to present day habitats of divaricating plants. Forest areas were small and dispersed, and each one would have had its edging stand of divaricating shrubs. The more exposed regions, though unsuitable for forest, would have been able to support a low scrub, and there also divaricating shrubs may have been prominent. In general, potential soil fertility was high during the glaciation, as much freshly eroded rock was distributed across the landscape. Loess was deposited in many regions, especially the east, and there would have been few areas that did not receive at least a light coating. In other areas, erosion of the tops of the ranges and the action of glaciers in inland valleys led to deposition of outwash terraces and plains which created fertile, open and constantly changing habitats.

Quaternary climate change and evolution of divaricating plants

New Zealand enjoyed a mainly sub-tropical to warm temperate climate during the Tertiary (Mildenhall, 1980). Most Tertiary floras are broad-leaf assemblages and, although the climate was never tropical, many tropical elements occurred in the flora. Throughout much of the Tertiary New Zealand was characterised by an oceanic environment and relatively stable climatic regimes, and was a land of low relief. It was not until the late Miocene that the climate started cooling and reduced some forested areas to scrubland / grassland on occasions (Mildenhall, 1980). By the beginning of the Pleistocene the climate had cooled substantially, and the succession of glacials and interglacials that characterise this period had begun.

The New Zealand flora is derived mainly from sub-tropical and warm-temperate stock (Dawson, 1962), although Wardle (1963; 1978) has put forward the hypothesis that some cool-temperate adapted groups arose here during the Tertiary. New Zealand lacks many of the plant groups that are adapted to harsh climates in the Northern Hemisphere, such as firs, pines and birches. One exception is *Carmichaelia*, which with its leafless, photosynthetic branches is adapted to exposed, dry habitats, as are shrubby legumes such as *Cytisus* and *Spartium* in the Northern Hemisphere.

With the onset of cooler conditions during the Miocene-Pleistocene period, this largely sub-tropical

flora was forced to adapt not only to cool, drier climates, but also to rapidly varying, unstable environments. Unlike most regions of the world, New Zealand, being an isolated archipelago, had no links with either a cold arctic, dry steppe, or desert region. Also, for most of the Tertiary New Zealand lacked high mountains and, therefore, had no plant groups specifically adapted to cold, wet, alpine climates. We can assume that there were only a few species that could have occupied the new habitats opened up by the changing climate, and that migration of better-suited plant groups from other botanical regions was almost negligible. We believe that the divaricating plant habit was one of the responses of this essentially sub-tropical flora to the onset of glacial climates.

One other constraint makes New Zealand unique. Although for long periods cool, harsh climates prevailed during which forest was rare and scrub and grassland dominant, these were broken by sharp transitions to interglacial climates during which nearly all of New Zealand was forested except for alpine areas. All other parts of the world were subjected to these changing climates during the Quaternary, but even during the peak of the warm interglacials, refugia for species adapted to glacial climates existed in the steppes, deserts and the arctic regions. During glacial periods these species spread while tropical and temperate elements of the flora contracted in range (Henley, 1979).

During the interglacials, there were very few habitats available in New Zealand to species adapted to the open, treeless, cool and windswept landscape of the glaciations. Aside from the cold, wet, and markedly seasonal habitats of the alpine regions, there were almost no large, stable areas of treeless vegetation. Instead, there were small, scattered, unstable areas of forest margin habitats, such as riverbeds, dunes, and wind-induced scrub, and it is these that probably acted as refugia for a great proportion of the species that were dominant during the glaciations.

THE MOA-BROWSING HYPOTHESIS FOR THE ORIGIN OF DIVARICATING PLANTS

Several authors, in particular Carlquist (1974) and Taylor (1975), have mentioned the possibility that moa-browsing pressure was a factor in the evolution of the divaricating plant form. However, it was Greenwood and Atkinson (1977) that fully developed this hypothesis. Their argument is based on the feeding mode of moas, and the consequences of this type of browsing in an area that possessed no indigenous mammalian herbivores. As they state: 'What is unique about New Zealand is that here

we had ratites in the absence of browsing mammals' (p. 23).

As we understand it, the Greenwood-Atkinson hypothesis can be stated as follows:

Moas, having horny beaks but no teeth or prehensile tongues, did not browse in the same manner as mammals, especially ungulates. Clamping, pulling and breaking were important, but chewing was impossible. Sight, not smell, was important in the selection of food, so appearance of foliage was significant. The height of the taller moas was an adaptation to reaching up to shrub and tree foliage.

The divaricating shrubs are seen by Greenwood and Atkinson as presenting an effective deterrent to moa-browsing. The leaves are small, and mainly in the interior of the bush. Tough, springy branches and twigs form a protective cocoon around them. Individual twigs and branches are difficult to detach from the bush. Vulnerable spring growth often appears little different from mature growth, or even appears dead, and was, therefore, avoided. As a result of these features, feeding on divaricating plants involved a great deal of energy when compared with the nutrition obtained so the focus of moa-browsing shifted to other, more palatable species.

COMPARISON OF THE TWO HYPOTHESES

Both hypotheses view the divaricating habit primarily as a defence against environmental damage. Physiologically important parts of the divaricating plant, namely the leaves and the growing points, are protected to some extent by less vulnerable twigs and branches, and growing points are many and scattered. In this way damage, whether by browsing or adverse weather, is minimised and, when it does occur, the ability of the plant to recover is not destroyed. In contrast, many non-divaricating shrubs have growing points and leaves which are concentrated on the exterior of the plant, and thus far more exposed and liable to damage. Therefore, the habit itself does not allow us to discriminate between the two hypotheses.

Discrimination between the hypotheses involves two main questions. Did in fact moas browse in the manner outlined by Greenwood and Atkinson (1977) and, if not, did their method of browsing differ significantly from that of mammals, and especially ungulates, in its effect? Second, is the ecology and distribution of divaricating plants at present consistent with a climatic explanation, or does it have features that can be only explained by reference to moa-browsing?

The first question has been answered by recent work of Burrows (1980a; 1980b) which has shown

that most of the plant material contained in fossilised moa (*Dinornis*) gizzards consisted of twigs, commonly 1.5-6.0 mm thick and 10-30 mm long. Some of these twigs are of *Olearia virgata* and *Plagianthus betulinus* (both divaricating species), and much material appears to have come from *Coprosma*, a genus which contains a large number of divaricating species. Most of the twigs were cleanly cut, probably by a shearing action of the moa beak, rather than broken. Burrows concludes that moas did not browse in the manner outlined by Greenwood and Atkinson. This is an important result. If, as is suggested by Burrows, the moas had no difficulty in detaching and digesting the twigs and branches of divaricating shrubs, the features stressed by Greenwood and Atkinson (1977), such as tough, flexible, interlaced branches, small leaves, and the mature appearance of new growth would not have deterred the moas to any greater extent than mammalian herbivores. There is, therefore, no reason to suggest that moa-browsing would be any different from that of other browsing animals in its ultimate effect on the plant.

The second question cannot be as decisively answered, but climate-based explanations for the ecology of divaricating plants seem to be more convincing than those based on moa distributions and feeding behaviour.

Greenwood and Atkinson (1977) claimed that the preference of divaricating plants for open, forest margin habitats and fertile soils reflect the assumed preference of moa for such sites because of the high production of foliage of superior nutrient status. The propensity of divaricating plants to become laxer and more leafy when under shade seems at odds with this explanation, while being entirely consistent with the climatic hypothesis. Even if it is given that moas preferred open bush edge habitats, it is difficult to believe that browsing would not have been just as intense *within* the shaded forest margin.

Forest margin habitats in New Zealand are often associated with fresh soils, as natural forest margins occurred along river edges, slips and debris fans, and other areas where erosion was taking place, or the products of erosion being deposited. These soils are usually relatively high in phosphorus and potassium and therefore potentially fertile. One can easily argue that open habitats, favoured by divaricating plants for climatic reasons, also tended to have higher fertility.

Greenwood and Atkinson (1977) stated that on these fertile soils 'one expects to find mainly fast-growing broad-leaved plants' (p. 25). From the arrival of man, approximately 1000 years ago,

populations of moas underwent a sharp population decline leading to the virtual extinction of most species by about 400 years ago (McCulloch and Trotter, 1975; Cracraft, 1980). If it is true that divaricating shrubs evolved in response to browsing pressure, cessation of browsing should have led to their replacement within a few generations at most sites by less browse-resistant shrubs. This seems not to have happened, as divaricating plants were common, even before the introduction of browsing mammals into New Zealand. At the present time, divaricating plants are often abundant in regions that suffer little or no browsing.

Greenwood and Atkinson (1977) noted that areas where moas were either absent, such as offshore islands, or found difficult to browse, such as cliffs, have no, or very few, divaricating shrub species. However, offshore islands are renowned for the mildness of their climates (Carlquist, 1974), and although they are often windy, variation in temperature and rainfall is usually only moderate, and the difference between summer and winter climates nowhere near as great as on larger landmasses. It is entirely consistent with the hypothesis that divaricating shrubs are adapted to changeable, and relatively harsh conditions, that divaricating shrubs are scarce on islands.

Greenwood and Atkinson (1977) also pointed out that there are several divaricating plant species which are often, or always, divaricating on the mainland, but which have non-divaricating populations on offshore islands which lacked moas. One of their examples of this phenomenon, *Sophora microphylla*, varies greatly throughout the mainland as to the presence or absence of a divaricate form, but as Godley (1979) points out, the juvenile divaricate form reaches its strongest expression in the south-east and south of the South Island. This pattern, rather than indicating the pre-historic distribution of moas, would be better explained by the relative harshness of the climate in that region of the South Island.

The transition of divaricating juveniles to non-divaricating adult plants often occurs in the height range of three to four metres. Greenwood and Atkinson (1977) commented that this is about the level that would have been necessary to carry foliage above the reach of the tallest moa. The transition from the juvenile form at this height can be equally well explained by the climatic hypothesis, as it ensures that plants have a deep, well-established root system and that their foliage is well above the height of damaging ground frosts. The divaricating juvenile form may thus enable forest trees to act as colonisers in forest margin habitats.

The fossil record is silent as to the time of origin of divaricating shrubs. Greenwood and Atkinson (1977) believed that the divaricating plant form is of recent origin. As moas are presumed to have been present in New Zealand from at least the Cretaceous this recent origin is surprising, and not explained by the moa-browsing hypothesis. As we have stated above, we believe that the onset of harsh climatic conditions and treeless landscapes in the early Quaternary led to the development of divaricating plants.

THE POSSIBLE EFFECTS OF MOA-BROWSING ON THE
FLORA AS A WHOLE

The 'Survival' hypothesis for the origin of divaricating plants

Until now we have dealt solely with the hypothesis of Greenwood and Atkinson (1977) in which the distinction between the way moas and mammals browsed was of crucial importance. Divaricating plants were seen as providing a unique defence against moa browsing.

Lowry (1980) suggested that, rather than providing a defence against browsing, the divaricating habit, by dispersing the growing tips into a large number of small and spatially separated units, makes browsing less rewarding energetically and also minimises the effect of that browsing on the plants.

Atkinson and Greenwood (1980) in reply to Lowry's suggestion stated that they did not argue in 1977 for the divaricating plant habit being an effective defence against moa browsing. Instead they claimed that '... such features [of divaricating plants] must have had some effect in increasing the reproductive success of divaricating plants, perhaps by increasing survival, but this does not mean that browsing of these plants was either prevented or even greatly reduced.' This statement seems to be a contradiction of a reasonable interpretation of their 1977 suggestion that '... the combined effect of these three major trends [divergent lateral branches; reduced leaf size and number on the exterior of the plant; toughness of the stems] developing in one plant species would have been to make it less profitable, in terms of energy expenditure, for a moa to continue its primary feeding on such plants. Thus the focus of feeding would have gradually shifted towards other plants where palatable foliage was easier to obtain.' (p. 24-25). And again '... it seems clear that however effective the divaricate habit may have been in protecting a plant against browsing by moas, there were major limitations on the extent to which plants could exploit the strategy; ...' (p. 27).

There are thus two separate hypotheses, each with quite different implications. If, as Lowry (1980) and

Atkinson and Greenwood (1980) suggested, the divaricating form enables the browsed plant to survive, but does not prevent browsing, it is no longer clear why this adaptation is not more common elsewhere. In particular, there is no reason to suggest that the effects of mammal browsing on divaricating plants would be any different to those of moas, as in both cases growing points would be destroyed. In fact it is clear that at least some divaricating plant species have a great deal of resistance to repeated browsing by introduced mammals. For this reason one might expect both the divaricate form and other anti-browsing features to be more common in other countries.

We doubt that floras that have evolved in the presence of ungulate browsing mammals do have many species with anti-browsing features, or particularly high levels of browsing resistance. Shelford (1963) commented on the large number of forest dominants and understorey shrubs that are highly palatable to deer in temperate deciduous forest in North America. Many trees will not establish in regions heavily used by deer, and regeneration depends upon fluctuations in deer abundance. Shelford (1963, p. 33) states 'Thus the forest stands are what the deer and associated animals permit to grow from what they miss in their feeding on the seed crop'.

The only way in which the moa-browsing hypothesis can offer a credible explanation of the evolution of divaricating plants in New Zealand is if it is also postulated that the browsing pressure exerted by moas in New Zealand was uniquely intense and pervasive. It is in the light of this that suggestions made by Greenwood and Atkinson (1977) regarding other anti-moa browsing adaptations in the flora become significant. We deal with these putative anti-browsing adaptations below.

Spiniferous plants (Aciphylla spp.)

Greenwood and Atkinson (1977) suggested that the spinescent rosette form of aciphyllas would have prevented moas from pulling the leaves firmly. They also noted that spines are absent or only weakly developed in the two Chatham Island species of *Aciphylla*. However, it is highly probable that the shearing capabilities of the moa beak as revealed by Burrows (1980a) would have permitted moas to eat *Aciphylla*. Introduced mammals eat both seedlings and adult plants.

We believe that the spinescent habit in *Aciphylla* is correlated with exposure to damaging and drying winds. Oliver (1956) suggested that their spinescence was a xeromorphic adaptation, but Dawson (1971) regarded this as being unlikely - except in the case of *A. aurea* which has the undoubted xeromorphic

adaptation of sunken stomata - as most aciphyllas grow in moist, or even saturated soils. Several mainland species have relatively soft, weakly spinescent leaves and these species are either low-growing in exposed situations (e.g., *A. divisa*, *A. polita*) or taller and in sheltered situations (e.g., *A. anomala*).

Seedlings of all species that we have examined are relatively soft and would not be resistant to browsing. As plants grow larger, and so become more exposed, the typical rigid, spinescent leaves are developed. *Aciphylla hookeri* has two distinct leaf forms previously treated as distinct species (Le Comte and Webb, 1981). Juvenile foliage is 1-pinnate, soft and only weakly spinescent, and may persist through to flowering and fruiting when plants are in sheltered situations. In contrast, the adult foliage is 2-pinnate with stout, rigid, pungent segments and characterises plants in exposed situations.

Mimicry

Greenwood and Atkinson (1977) suggested that the aciphylla-like appearance of *Celmisia lyallii* may be an example of a palatable plant mimicking a species avoided by moas. *Celmisia* exhibits a wide range of adaptations to exposure: leathery leaves, dense tomentum, low-growing mat-forming habit. We suggest that the narrow, coriaceous leaves of *C. lyallii* are simply part of this range of adaptations. The fact that most species of *Aciphylla* are hardly less palatable than *C. lyallii* (particularly seedlings of *Aciphylla*, which *C. lyallii* most closely resembles), and also the frequency and wide distribution of *C. lyallii*, all argue against its candidacy as a mimic.

Tough leaves

Phormium and *Cordyline* have tough leaves which are difficult to detach, and Greenwood and Atkinson (1977) suggested that this is an adaptation to the pulling and breaking feeding mode of moas. Burrows (1980b) reported the occurrence of several cut leaves of *Phormium* in moa gizzard contents, and this is consistent with the shearing action he postulates for the beak of the moa. Furthermore, as Agavaceae with leaves similar to those of *Phormium* and *Cordyline* occur in many other places, it is unlikely that the New Zealand members of the family evolved their leaf structure as a response to moa-browsing.

Large-leaved plants

Meryta sinclairii and *Stilbocarpa polaris* are large-leaved palatable plants restricted to outlying islands. Greenwood and Atkinson (1977) claimed that these species could not have originated in the presence of moas.

A close and equally palatable relative of *Stilbocarpa polaris*. *S. lyallii* (Philipson, 1965), occurs on Stewart Island which had a population of moas. During the Last Glaciation one of the two islands on which *Meryta* now occurs was connected to the mainland, and was presumably accessible to moas.

Toxic compounds

As Greenwood and Atkinson (1977) pointed out, several New Zealand plants have distasteful or toxic secondary compounds, and we agree with them that these may have also been toxic or repellent to moas. But as they note, these may have evolved in response to phytophagous insects. Furthermore, at least one of the species they mention, *Pseudowintera colorata*, has close relatives in other countries that are equally distasteful, and is unlikely to have developed this feature as a response to moas. Connor (1977, p. 18) pointed out that all the indigenous flowering plants that are toxic to domestic livestock in this country have close, toxic relatives elsewhere.

CONCLUSIONS

We believe that the moa-browsing hypothesis regarding the origin of divaricating plants in New Zealand, as put forward by Greenwood and Atkinson (1977), fails to explain the concentration of this life form in New Zealand, nor does it give a credible method by which it may have arisen. The work of Burrows (1980a; 1980b) has conclusively demonstrated that moas did not browse in the manner suggested by Greenwood and Atkinson, and therefore the basis for the hypothesis is seriously weakened.

The newly modified hypothesis which states that divaricating plants, rather than providing an effective defence against moa-browsing, are capable of surviving heavy browsing because of the dispersion of the vulnerable growing points (Lowry, 1980; Atkinson and Greenwood, 1980) cannot be so easily dismissed. However, even if the divaricating habit was effective in permitting survival of browsed plants, there is still no explanation as to why this adaptation is so common in New Zealand and so rare elsewhere. There is no good evidence for other browsing adaptations in the New Zealand flora as a whole; rather the opposite is true, as many of our trees and shrubs are extremely vulnerable to browsing. We therefore regard the modified hypothesis as unsubstantiated as an explanation for the origin and evolution of divarication, even though its central thesis that many divaricating plants were resistant to moa-browsing seems highly plausible.

We believe that the divaricating habit is an adaptation which enables the plant to resist damage

from wind, frost and desiccation, while retaining enough flexibility to exploit a wide range of habitats. Because of this, many divaricating plants can take part in the early stages of a vegetation succession, and persist when forest is established.

The high incidence of divaricating shrubs in New Zealand is explained by three factors:

- (i) the highly variable nature of the New Zealand climate, and the lack of a consistently cold, harsh winter;
- (ii) the effects of the Quaternary glaciations on a Tertiary flora largely adapted to sub-tropical and warm-temperate climates;
- (iii) the lack of refugia for glacial climate adapted species during interglacial periods.

ACKNOWLEDGEMENTS

We thank Dr P. Wardle, Dr N. T. Moar, Dr P. A. Williams, Dr D. Lloyd and several anonymous referees for comment on, and criticism of the manuscript. We are grateful to Mr A. P. Druce, Dr I. A. E. Atkinson, Dr C. J. Burrows, and many others for enlightening discussions on the vexed problem of the origin of divaricating plants.

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