EVOLUTION OF DIVARICATING PLANTS IN NEW ZEALAND IN RELATION TO MOA BROWSING

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SUMMARY: New Zealand appears to be the only country where spineless, small-leaved divaricating plants make up nearly 10% of the woody flora. Climatic explanations have been advanced to account for the origin of these divaricating plants. We suggest that the divergent and interlaced branching, the woody exterior and the tough stems of these plants are adaptations evolved in response to browsing by moas. Together with a few species of much smaller birds, moas were the only browsing vertebrates in New Zealand prior to the arrival of man. The divaricate habit is probably only one of several strategies evolved by plants in response to moa browsing. However, because moas fed in a different way from mammals there is little to support the idea that introduced browsing mammals have merely replaced moas as an ecological factor in New Zealand.

MORPHOLOGICAL FEATURES OF NEW ZEALAND DIVARICATING PLANTS

The term "divaricating", indicating branching at a wide angle, is used in New Zealand to describe the many species of small-leaved woody shrubs that have closely interlaced branches. Some are the juvenile stages of trees that lose the divaricate habit as they grow taller. The interlacing arises from reduced apical growth associated with a continued growth of lateral branches, either straight ones produced at widely divergent angles (often 90° or more) or recurved ones bending downwards or sideways in directions away from the main stems (Fig. 1). In some species sympodial branching occurs in which a branch apex ceases growth and lateral buds produce new branches from just behind the apex. The interlaced branch system may vary from stiff with frequent branching, to flexible with thinner branches and less frequent branching. A cut branch is usually difficult to disentangle.

Another common feature of New Zealand divaricating plants is that the outer branches often have longer internodes with fewer and smaller leaves than the inner branches, a trend which becomes more marked with increase in the degree of divarication.

Often the stems of New Zealand divaricating plants are very difficult to break being tougher than those of their non-divaricating relatives.

The similarity in leaf and stem morphology among divaricating plants belonging to taxonomically unrelated families sometimes makes identification difficult. The most helpful keys are those of Bulmer (1958) and Taylor (1961), which deal specifically with these plants. New Zealand species found in this investigation to be capable of divaricating are listed in Table 1. In cases where there was difficulty in deciding whether a species should be included in the table the criteria used for inclusion were (i) 10% or more of the branches of at least some individual plants of the taxon should diverge to angles equalling or exceeding 90° and (ii) the interlacing of branches should be three-dimensional, rather than two-dimensional as in some prostrate plants. On the basis of the limited number of individual plants examined, some species listed by earlier authors as divaricating, have been excluded. Thus Table 1 should be considered as a minimum list of New Zealand divaricating plants. Many species show considerable within-population and between-population variation in the degree of divarication, and there may be further species which, unknown to us, include divaricating populations.

INCIDENCE OF DIVARICATING PLANTS IN THE NEW ZEALAND FLORA AND ELSEWHERE

A remarkable feature of the New Zealand flora is its high incidence of divaricating plants. The 54 species listed in Table 1 belong to 20 genera and represent 16 families of angiosperms and one family of gymnosperms. This number is nearly 10% of the woody flora.* There are in addition at least 9 species from 6 genera representing 4 additional families of angiosperms that can be described as semi-divaricat-

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* Percentage based on an unpublished estimate by Mr A. P. Druce of 540 species of woody plants, excluding lianes, in the flora.
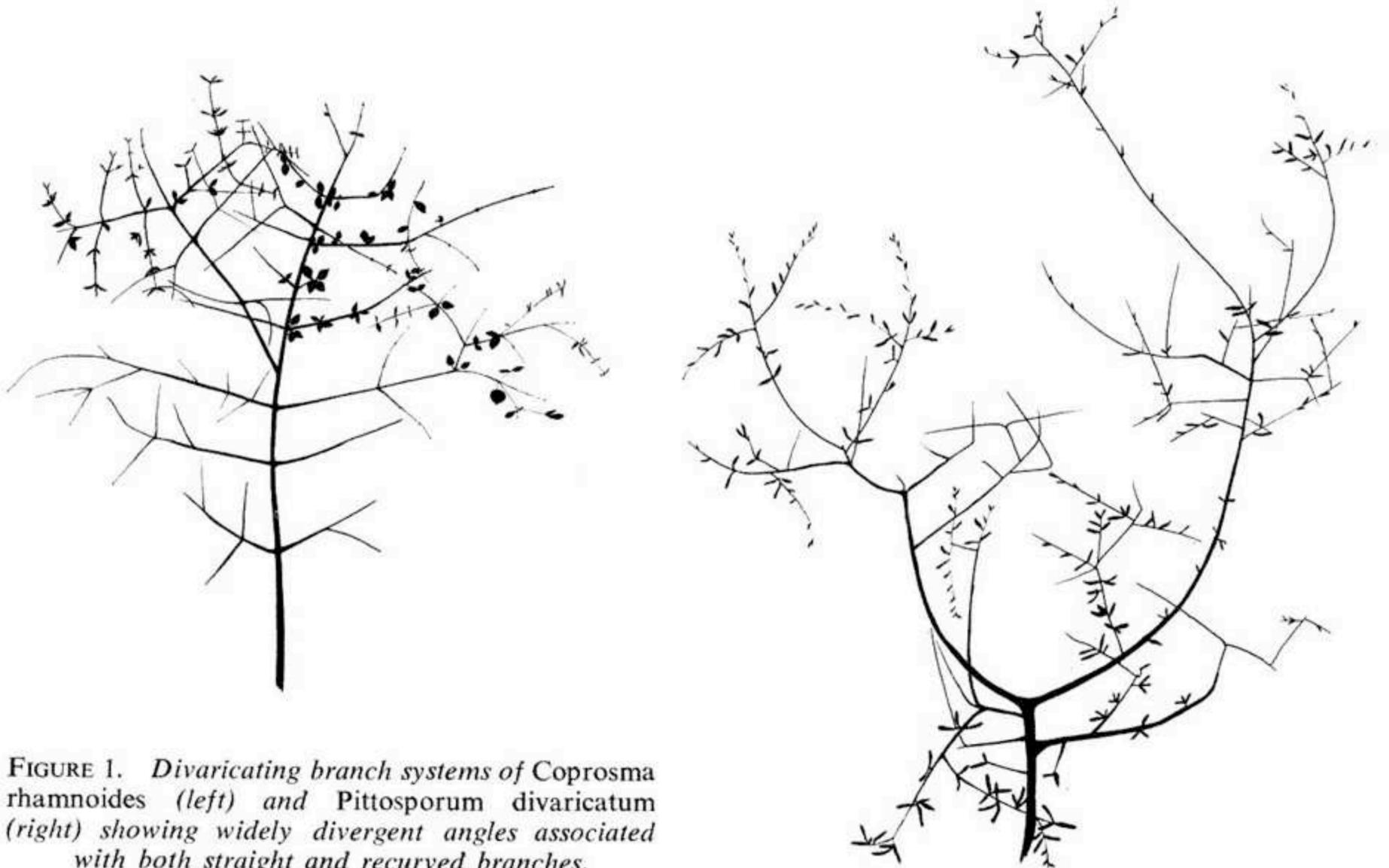
FIGURE 1. *Divaricating branch systems of* Coprosma rhamnoides *(left) and* Pittosporum divaricatum *(right) showing widely divergent angles associated with both straight and recurved branches.*

ing, e.g. juvenile *Nothofagus solandri, Neomyrtus pedunculata, Teucridium parvifolium* and juvenile *Rubus squarrosus.*

Divaricating plants are apparently absent from other Pacific islands but whether this is true of New Guinea, Australia and Tasmania is not known to the writers. *Coprosma quadrifida* from Tasmania and eastern Australia has numerous short spiny branchlets with reduced leaf size and number on the outer branches. However, representative specimens examined, though frequently branched, lacked the stiff habit and widely divergent branch angles of a typical New Zealand divaricating plant.

Judged from photographs and descriptions in floras, divaricating plants do occur in some other countries, particularly in xeric environments. Examples are *Decaryia madagascariensis* (Didiereaceae) from Madagascar with zig-zag thorny branches (Carlquist, 1965) and *Condalia microphylla* (Rhamnaceae), a thorny divaricating shrub from Patagonia (Bartlett and Bartlett, 1976). Whether such plants have the combination found in New Zealand divaricating species of interlaced branching, small leaf size, stem toughness and difference in leaf size

between outer and inner branches is not known. Tucker (1974) gives a list of 53 species he considers as divaricating from the desert and chaparral communities of California and Arizona. Study of individual species descriptions shows that at least 44 of these species have spiny branches or leaves and that their average leaf size (ca. 1.5 cm) is much larger than that of most New Zealand divaricating species. On present evidence there appears to be no country apart from New Zealand where spineless, small-leaved divaricating shrubs constitute anything approaching a tenth of the woody flora.

HYPOTHESES CONCERNING DIVARICATING PLANTS

That so many unrelated plant families show the same parallel trend towards divarication indicates environmental conditions peculiar to New Zealand. Cockayne (1912) considered that the divaricate habit was a xerophytic growth form resulting from adaptation to an earlier "steppe-climate period" when conditions were more windy and drier than at present. In discussing *Sophora microphylla* he suggested that the divaricating juvenile "arose during a probable period of drought on the east of

the Southern Alps at the time of the glacial period". Rattenbury (1962) considered that the divaricate habit was an adaptation to drier or cooler conditions in the Pleistocene and suggested that the compacted nature of the growth form, with leaves confined mostly to the inner shoots, acts as an effective windbreak. Wardle (1963) pointed out that there was scarcely any development of a distinctive xeric flora adapted to areas of New Zealand which experience dry climates at present. He suggested that the divaricate growth form was an adaptation to still-existing conditions such as occur in drier forests or shrub communities .

Several difficulties are apparent with climatic explanations for divaricating plants. As pointed out by Dawson (1963a), the conditions described are not peculiar to New Zealand but can be found in other parts of the world where divaricating plants are unimportant or lacking. If wind is emphasised, then in some of the windiest parts of the country such as the Cook Strait coast, the Rangipo desert east of Ruapehu and outlying islands such as the Chatham group, divaricating plants are a very minor component of the vegetation. Furthermore, in an archipelago such as New Zealand, wind is frequently associated with wind-carried salt. Divaricating plants apparently have no particular adaptations to withstand salt such as waxy leaf cuticles or tomentose leaf surfaces, although the woody exteriors of the more extreme forms might reduce salt entry to leaves. If on the other hand drought is emphasized, then some simple experiments comparing water loss between divaricating plants and their large-leaved non-divaricate relatives have failed to demonstrate that the small-leaved species are more drought-resistant (Keen, unpub. 1970). Furthermore, divaricating plants occur in a wide range of habitats (Fig. 2) and some, *Pennantia corymbosa* for example, are typical of moist sheltered lowland forest. Finally, the climatic explanations altogether fail to explain why wide branching angles would be an adaptive advantage.

A non-adaptive explanation was proposed by Went (1971) who suggested that a particular chromosome segment carrying the genes controlling divarication was transferred asexually between families in some way. There is little to support the idea. Tucker (1974) pointed out the difficulty of assuming that any given taxon would carry all the genes controlling the divaricate habit on one segment of one chromosome. Our own examination of these plants shows that the interlaced branch system has evolved in more than one way. Thus assuming Went was correct, one would have to invoke the transfer of several different chromosome segments between unrelated families.

It was however a reading of Went's (1971) statement: "One might e.g. have assumed that the extreme degree of branching, combined with microphylly, would be an adaptation against browsing animals, but New Zealand is the only extensive geographical area without larger native herbivores .." that lead one of us in 1974 to consider a possible connection between moas and divaricating plants. Further enquiry showed that such a connection had been considered at least ten years earlier. Denny (1964) had concluded that the divaricate habit was an adaptation to present-day climate, but she suggested as a "remote possibility" that "grazing" by moas had had some effect on the shape of divaricating shrubs (p. 30). Livingstone (1974) speculated that some of the leaf changes occurring between young and adult forms of some trees were an adaptation to browsing by moas. Carlquist (1974: p. 242) suggested that the tough tangled microphyllous branches of many divaricating shrubs were functioning as "armor" devices with virtually the same effect as thorny branches, and Taylor (1975) raised the question of whether the "dry, unpalatable twigs" of divaricating shrubs gave them an advantage during "grazing pressure" from "flocks of herbivorous moas". Apparently none of these authors have explored the matter further.

The superorder Ratites, to which moas belong, are not restricted to New Zealand. There are the emus, cassowaries and extinct dromornithids of Australia and New Guinea, the rheas of South America, the ostriches of Africa and the extinct elephant-birds of Madagasca. What is unique about New Zealand is that here we had ratites in the absence of browsing mammals.

SOME RELEVANT FEATURES OF MOAS

Ratite birds have possibly been present in New Zealand since the Cretaceous (Fleming, 1975). During the Tertiary period, the long intervals of warm temperate climate experienced by New Zealand (Devereux, 1967, Fleming, 1975) imply that for much of that time the country was forested. Thus moas are likely to have evolved mainly in a forest environment, as argued by Simmons (1968), although it need not have been exclusively so. Postglacial deposits of subfossil moa bones, for example those in the Awakino-Mahoenui caves, Martinborough caves and Pyramid Valley swamp, are consistently associated with forest birds (Oliver, 1949, Yaldwyn, 1958, Medway, 1967, 1971). There is no reason to think that such places were deforested during the post-glacial period until after the arrival of man (cf.

Moar, 1970 for Pyramid Valley). Most genera of moas, *Dinornis, Emeus, Pachyornis, Euryapteryx* and *Anomalopteryx,* have been recorded from these localities. The height of the taller species appears as an evolutionary anachronism if not interpreted as an adaptation for reaching up to shrub and tree foliage. A primarily herbivorous diet including several woody species is indicated by the very few gizzard samples examined from Pyramid Valley (Mason in Oliver, 1949). Thus woody plants must have suffered varying degrees of browsing stress from moas during the 65 million years of the Tertiary and Pleistocene. Moas are likely to have bred slowly and there is no evidence at present to show that they occurred in flocks (Falla, 1974). Nevertheless, in places where food supply was abundant it could be expected that moa numbers would have been relatively high. This is borne out by the carbon-dates from archaeological sites in the eastern South Island (Scarlett, 1974) which show that moa numbers were sufficient to have been a significant food source for the early Polynesian settlers for several centuries, although by no means the only food source. In short, moas should be considered as having been a potent selective force acting on plants, particularly those woody species which they frequently browsed.

It is possible to infer certain features of the feeding behaviour of moas that contrast with those of mammals. The lack of teeth and presumed lack of a prehensile tongue is likely to have made clamping, pulling and breaking action important, whereas chewing afer the manner of an ungulate would have been impossible. Typical moa bills are rather blunt in shape but, as the horny covering of the mandibles has only once been found, we cannot assume that cutting actions in the manner of a takahe were not possible.

In contrast to browsing or grazing mammals, most birds depend more on sight than smell in selecting food. Here again we should be cautious for a few bird groups do have a well-developed sense of smell (Welty, 1975). Nevertheless, assuming moa vision was well developed as in the great majority of birds, a plant's appearance, including its colour, may have been important to moas during food selection.

A third point concerning feeding behaviour is that mammals such as deer and goats reach into plants with an unprotected soft nose as the leading point of contact: spines are at least partially effective against this sort of browsing. In contrast, a moa's head was well protected by a heavy horny covering up to almost the full depth of the bite. This we suggest is the reason why there are few spiny plants in the flora, a marked contrast to other temperate floras such as those of Europe and California where browsing mammals have been present.

EVOLUTION OF DIVARICATING PLANTS

The morphological features of divaricating plants described above suggest these plants have undergone at least three associated evolutionary trends. The first and most fundamental is development of an increasing proportion of widely divergent lateral branches: straight branches produced at wide angles, recurved branches bending to wide angles, and branches at wide angles resulting from the death of the original apex (sympodial branching). In some species, zig-zag branching has resulted from the apical dominance of a lateral branch on one side being lost to a lateral branch produced from it on the opposite side, e.g. *Corokia cotoneaster.* In other species, such as some races of *Coprosma acerosa,* recurved branches have resulted from the sequential development of lateral buds on one side only of what would otherwise have been a zig-zag branch system. Varying degrees of tertiary and quaternary branching can be associated with any of these growth forms. Continued growth of divergent branches results in some growing towards the centre of the plant to produce the characteristic interlacing. The adaptive significance of these inner branches appears to be that they can carry both leaves and growing points in positions relatively protected from browsing. The great majority of species with divaricate branch systems show a genetically controlled loss of apical dominance which in some respects simulates the loss of apical dominance that occurs when normally-branched plants are browsed.

The second trend is towards reduced leaf size, and sometimes leaf number, on the outer, uppermost or most exposed branches, a trend frequently accompanied by increased internode length. This results in increase in the wood/leaf ratio with the plant's "exterior" becoming more woody than its relatively leafy "interior." The trend reaches an extreme in a minority of divaricating plants, such as *Hymenanthera alpina* and *Aristotelia fruticosa,* in which the tips of the outer branches appear spine-like, though not sharply pointed. These rigid interlocking outer branches would have made it very difficult for a moa to reach the more leafy interior of the plant.

The third trend, towards increasing toughness in the stems of divaricating plants compared to their non-divaricating relatives, would make browsing by tugging and breaking branches more difficult. In some species springiness has developed as well, which again would make it more difficult to remove portions of the plant.

We suggest that the combined effect of these

three major trends 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.

A fourth trend seen in some divaricating species is that soft new spring growth sometimes looks little different in colour and structure from the old growth. In other cases the reduction in leaf size and number on the developing branches is so marked that the soft new growth appears dead, e.g. in some populations of *Pennantia corymbosa* and *Coprosma rhamnoides*. Assuming the appearance of a plant influenced moa browsing this may be an adaptation that protected the new spring growth during its most vulnerable period.

From the foregoing we suggest that the divaricate growth form evolved in plants primarily as a response to moa browsing. To test this supposition, further facts can be sought or inferred about the behaviour of divaricating plants and moas and these examined for consistency with the evolutionary pathway proposed.

SOME ECOLOGICAL FEATURES OF DIVARICATING PLANTS

The distribution of divaricating species in relation to the soil fertility of their habitats, as indicated by base-leaching, is shown in Fig. 3. In comparison with a random sample of non-divaricating woody plants,
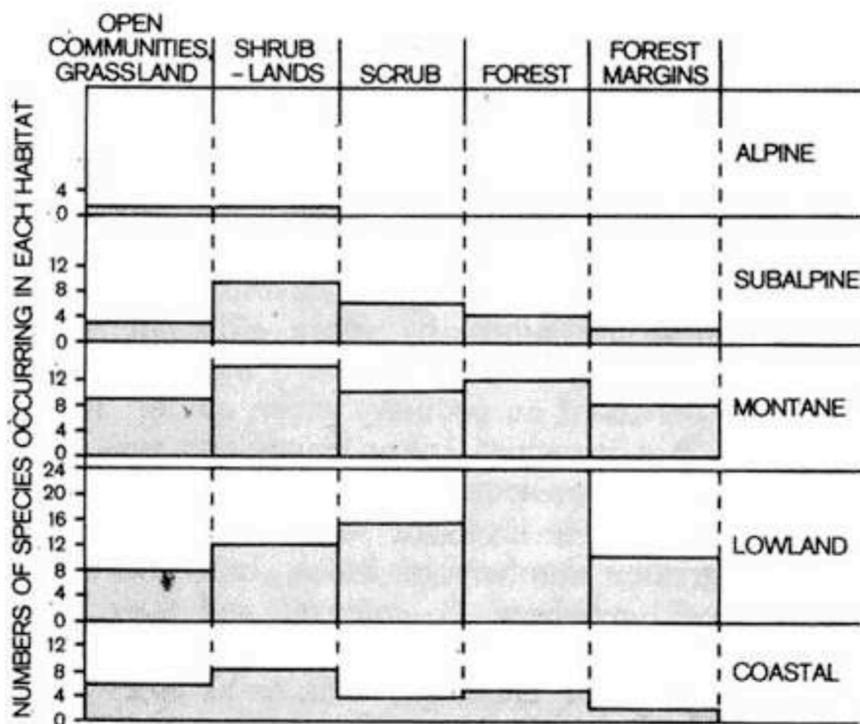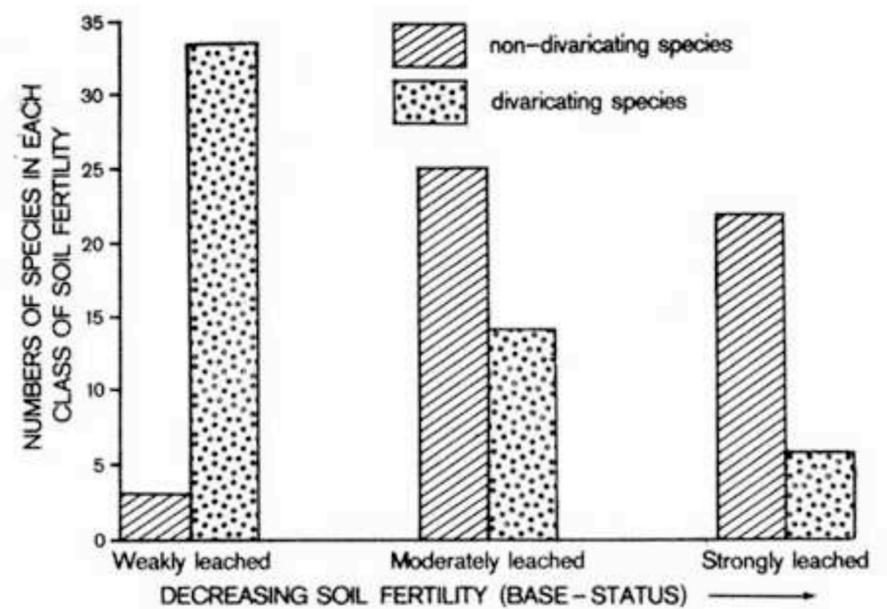

FIGURE 3. *Soil-fertility tolerance (judged by the base status of the soils where each species occurs) of 50 divaricating species compared with a random sample of 50 non-divaricate species.*

the divaricating species show a marked bias towards habitats where soil fertility is relatively high. This reflects the rather strong association between these species and young soils derived from river alluvium, talus or volcanic ash (Table 1). All divaricating species we have observed grow more slowly in height than their non-divaricating relatives.. On young high-fertility soils one expects to find mainly fast-growing, broad-leaved plants. Yet many of these soils in New Zealand support relatively slow-growing, small-leaved divaricating plants. This is explicable if one postulates that the young soils of river flats and swamps, because of their enhanced productivity, supported the largest numbers of moas. Thus the plants of these soils were more frequently browsed.

The rather frequent association of divaricating species with soils that are only weakly leached can account for their common occurrence in the drier eastern parts of the North and South Islands (Table 1) commented on by earlier observers. An example is Carter's Bush in lowland Wairarapa which is an open kahikatea-matai forest on both weakly leached and recent gley soils from alluvium. Of the 62 woody species listed from this reserve by Mr A. P. Druce (pers. comm.) 19 are divaricating and many of them abundant in the understorey. The only broad-leaved plants of importance are *Melicytus ramiflorus* and *Alectryon excelsus*.

As can be seen from Fig. 2 there is no reason for associating divaricating species with either mountain or coastal habitats as has sometimes been done. The greatest number of species occurs in lowland

FIGURE 2. *Distribution of 52 species of New Zealand divaricating plants in relation to altitude and vegetation type (data from Table 1).*

habitats, consistent with the lowland character of New Zealand during the Tertiary (Fleming, 1975) when much of moa evolution and that of woody plants must have occurred. Again, the incidence of divaricating plants on offshore and outlying islands, never reached by moas, is significantly lower than on comparable parts of the mainland (Table 2) suggesting that evolution of the growth form may have been confined to the mainland. One or two species of plants, often or always divaricating on the mainland, have related non-divaricating populations on islands. These include a non-divaricating relative of *Myrsine divaricata* on the Poor Knights, the non-divaricating juvenile forms of *Plagianthus betulinus* and *Sophora microphylla* on the Chatham Islands and a non-divaricating form (var. *martinii*) of *Coprosma propinqua* also on the Chatham Islands. Comparable non-divaricating populations are not represented on the subantarctic islands but this presumably is related to their more recent colonisation from the mainland following decimation of their woody floras during the last glacial period.

Divaricating species are not characteristic of cliffs nor are divaricating epiphytes known. Moas would have experienced difficulty in browsing either on cliffs or up trees!

The nine species of trees with divaricating juveniles are of special interest (Table 1): Philipson (1963) has pointed out that such trees are virtually confined to New Zealand. The transition from divaricating juvenile to non-divaricating adult often occurs in the height range of three to four metres, about the height that would have been necessary to carry foliage above the reach of the taller moas. However *Sophora microphylla* can make the transition as low as 1.4 m (Cockayne, 1912), and this species has races on the mainland without a juvenile form. This could be explained if *S. microphylla* originated relatively recently from hybridisation between *S. prostrata* and *S. tetraptera* (Godley, 1975a) and has not been subjected to the same selection pressure as the other tree species with juvenile forms.

If divaricating species were palatable to moas, it would not be surprising to find that many were palatable to mammals. All of the 27 species checked are eaten by browsing mammals. Some divaricating species are from plant families the New Zealand members of which are generally highly palatable to mammals, e.g. Araliaceae, Cornaceae and Rubiaceae. Members of the family Podocarpaceae are generally rather unpalatable, but foliage of the single divaricating member in New Zealand, *Podocarpus spicatus*, together with that of another divaricating plant, *Myrsine divaricata*, was eaten by moas (Mason in Oliver, 1949).

Godley (1961 p. 11) suggested that divaricating shrubs could be said to have been pre-adapted to attack by introduced mammals. And indeed, if they could withstand moa-browsing some degree of resistance to browsing by mammals would be expected, even allowing for differences in feeding habits of moas and mammals. Such species as *Coprosma rhamnoides*, *C. rigida*, *Myrsine divaricata* and *Pseudopanax anomalus* can withstand browsing to a remarkable degree.

EVOLUTION OF OTHER STRATEGIES IN RELATION TO MOA BROWSING

If the divaricate growth form evolved in response to moa-browsing, have other strategies evolved in response to the same selective pressure? Several New Zealand plants have toxic or distasteful secondary compounds, e.g. *Hedycarya arborea*, *Brachyglottis repanda*, *Melicytus ramiflorus*, but it is not known whether such compounds were evolved in response to moa-browsing, phytophagous insects or some other cause.

There is a strong indication that at least one species, *Pseudowintera colorata*, was as distasteful to moas as it is to ungulates. This species is mimicked in colour and leaf form to a remarkable degree by *Alseuosmia pusilla* which is a very palatable shrub readily killed by browsing mammals. Such convergent evolution is difficult to explain unless there was a selective advantage for *A. pusilla* to mimic the more widespread *P. colorata*.

Another response appears to have been the development of tough fibrous leaves of great tensile strength as found in the genera *Phormium* and *Cordyline*. In addition juvenile leaves of *C. australis* are more difficult to pull off the stem than adult leaves.

The lancewoods (*Pseudopanax* spp.) may illustrate a diversity of strategies within a single genus. Juvenile *P. crassifolius* is well known for its narrow-linear very stiff dark-coloured leaves, often deflexed, replaced in the adult by more elliptical greener leaves. By contrast *P. chathamicus* has non-deflexed broader leaves of an ordinary green colour. Juvenile *P. ferox* has brownish spiny leaves and this species is commonly present in limestone areas where, because of higher levels of soil fertility, one would expect greater numbers of moas. Individuals of *P. lessonii*, *P. arboreus*, *P. colensoi* and *P. edgerleyi* presumably evaded moa-browsing through their capacity to grow either on cliffs or as epiphytes. *P. anomalus* is the only member of the genus to have evolved the divaricate habit.

Although spines are not important in the flora they are relevant to this discussion. The most spiny

species is *Discaria toumatou*. The genus *Discaria* is centred in South America with one species in Australia closely related to the New Zealand species. The development of spines almost certainly did not take place in New Zealand.

In the genus *Aciphylla*, however, which may have originated in Antarctica (Dawson, 1963b), the leaflets form long sharp spines. These are not effective against browsing by hares, which eat the leaves from one side (Dr J. E. C. Flux, pers. comm.), or deer. However, the spiny rosettes of these leaflets may have prevented moas from gripping and pulling the leaves firmly (without endangering their eyes). The high sugar status of some aspects of *Aciphylla* (Dr J. Mills, pers. comm.) also suggests that some adaptations against browsing could be expected. Spines are either absent or weakly developed in the two species of the genus found on the Chatham Islands. The aciphylla-like appearance of *Celmisia lyallii* may be a further example of a palatable plant mimicking a species avoided by moas.

Finally it may be noted that large-leaved plants such as *Meryta sinclairii, Myosotidium hortensia, Stilbocarpa polaris* and *Pleurophyllum* spp. are restricted to outlying islands (Godley, 1975b). All are highly palatable to ungulates. It seems unlikely that species with such large palatable leaves could have originated in the presence of moas.

DISCUSSION

The fossil record of divaricating plants is almost completely unknown apart from the fact that some families now containing divaricating species have been present since at least the Oligocene (Couper, 1960). Identification of pollen and seeds of what are now divaricating species from Tertiary strata would not prove that these species were divaricating at that time. The lack of any genus consisting only of divaricating species and the facility with which several divaricating species hybridize with non-divaricating relatives (Table 1) may suggest a relatively recent origin for the growth form. More information concerning rates of species evolution in New Zealand is needed to answer this question.

The association of divaricating plants with soils of high fertility is attributed here to increased browsing stress related to locally greater numbers of moas. An additional possibility, however, is that moas were able to select plants of higher nitrogen, phosphorus or calcium levels during their feeding in a similar manner to that demonstrated for deer (Knott, 1956, Thomas *et al.*, 1964), red grouse (Miller, 1968, Moss, 1972), while-fronted geese (Owen, 1975) and takahe (Mills and Mark, *in press*). If so the browsing stress on such plants would have been considerable.

It seems likely that many divaricating species were restricted in range by competition from broader leaved plants, particularly in areas of higher rainfall where it is well known there are fewer divaricating species.

The extinction of the moas during the Polynesian period must have set in train major changes in the vegetation. With the disappearance of all large browsing animals, the relatively slow growth rates of divaricating species would have placed them at a disadvantage relative to faster growing non-divaricating species. Thus the range and numbers of some divaricating species may have diminished during this time, independently of any direct effects of the Polynesians through forest destruction.

From the time of Cockayne (1912) onwards, observers have noticed how within a single species population, markedly divaricating individuals growing in open habitats give way to semi-divaricating individuals within the forest, e.g. *Pittosporum divaricatum*. An increasing degree of divarication leads to increased shading of the leafy interior by the woody periphery of the plant so that in the shade of forest there may be a limit on the degree of divarication beyond which the plant cannot manufacture sufficient carbohydrates to survive. Physiological investigations would probably clarify this point.

From the foregoing 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; one of these limitations is apparently the inability of many divaricating species to grow on soils of low fertility.

The thesis advanced here is that adaptations to browsing are likely to be more widespread in the flora than hitherto believed. At first sight this might seem to support the view that the introduction of large browsing mammals to New Zealand has merely replaced moas as an ecological factor and that therefore there is too much concern about the damage these mammals cause. This viewpoint is not supportable for at least two reasons. In the first place, as discussed earlier, there appear to be major differences between moas and mammals in their modes of feeding. This point is illustrated by the fact that flax (*Phormium tenax*) can be readily killed out through the chewing action of cattle or goats, yet the genus *Phormium* evolved in New Zealand in the presence of moas. Secondly, the greatest impact of browsing mammals such as deer, chamois, and thar is on steep slopes at higher altitudes where, excepting limestone areas, the present evidence suggests that moas were much less important than they were in the lowlands. Thus the browsing

of mammals is a new influence so far as our mountain lands are concerned.

ACKNOWLEDGEMENTS

REFERENCES

ALLAN, H. H. 1961. *Flora of New Zealand*. Vol. 1. Government Printer, Wellington, 1085 pp.

BARTLETT, D.; BARTLETT, J. 1976. Where two worlds meet. *National Geographic* 149(3): 298-320.

BAYLIS, G. T. S. 1958. A botanical survey of the small islands of the Three Kings group. *Records of the Auckland Institute and Museum* 5: 1-12.

BEUZENBERG, E. J. 1961. Observation on sex differentiation and cytotaxonomy of the New Zealand species of the Hymenantherinae (Violaceae). *New Zealand Journal of Science* 4: 337-349.

BULMER, G. MARIE. 1958. A key to the divaricating shrubs of New Zealand. *Tuatara* 7: 48-61.

CARLQUIST, Sherwin, 1965. *Island Life*. Natural History Press, New York.

CARLQUIST, Sherwin, 1974. *Island Biology*. Columbia University, New York.

CHEESEMAN, T. F. 1909. On the systematic botany of the islands to the south of New Zealand. *In* CHILTON, Chas. (Ed.) *The Subantarctic Islands of New Zealand*. Vol. II, pp. 389-471. Government Printer, Wellington.

CHEESEMAN, T. F. 1925. *Manual of the New Zealand Flora*. 2nd ed. Government Printer, Wellington. 1163 pp.

COCKAYNE, L. 1909. *Report on a botanical survey of Stewart Island*. Department of Lands. Government Printer, Wellington.

COCKAYNE L. 1912. Observations concerning evolution derived from ecological studies in New Zealand. *Transactions of the New Zealand Institute* 44: 1-50.

COOPER, R. C. 1956. The Australian and New Zealand species of *Pittosporum*. *Annals of the Missouri Botanical Garden* 43: 87-188.

COUPER, R. A. 1960. New Zealand Mesozoic and Cainozoic plant microfossils. *Paleontological Bulletin of the N.Z. Geological Survey* 32. 87 pp.

DAWSON, J. W. 1963a. A comment on divaricating shrubs *Tuatara* 11: 193-4.

DAWSON, J. W. 1963b. Origins of the New Zealand alpine flora. *Proceedings of the New Zealand Ecological Society*. 10: 12-15.

DENNY, G. 1964. Habit heteroblastism of *Sophora microphylla* Ait. Unpubl. M.Sc. thesis, University of Canterbury.

DEVEREUX, I. 1967. Oxygen isotope paleotemperature measurements on New Zealand Tertiary fossils. *New Zealand Journal of Science* 10: 988-1011.

ELDER, N. L. 1950. Balls Clearing and Hutchinson Bush. *Bulletin of the Wellington Botanical Society* 23: 2-8.

FALLA, R. A. 1974. The moa. *Nature Heritage* 1: 69-74.

FINERAN, B. A. 1964. Some plant records from Port Pegasus, Stewart Island. *New Zealand Journal of Botany* 2: 380-384.

FINERAN, B. A. 1969. The flora of the Snares Islands, New Zealand. *Transactions of the Royal Society of New Zealand (Botany)* 3: 237-70.

FINERAN, B. A. 1973. A botanical survey of seven mutton-bird islands, south-west Stewart Island. *Journal of the Royal Society of New Zealand*. 3: 475-526.

FLEMING, C. A. 1975. The geological history of New Zealand and its biota. pp. 1-86 *in* KUSCHEL, G. (ed.) 1975 *Biogeography and Ecology in New Zealand*. Dr W. Junk B. V. Publishers, The Hague.

GODLEY, E. J. 1961. "Fauna and Flora" pp. 1-14 *in* Sinclair, K. (Ed.) *Distance Looks Our Way*. Paul's Book Arcade.

GODLEY, E. J. 1975a. Kowhais. *Nature Heritage* 5: 1804-1806.

GODLEY, E. J. 1975b. Flora and vegetation. pp. 177-229 *in* KUSCHEL, G. (Ed.) 1975. *Biogeography and Ecology in New Zealand*. Dr W. Junk B. V. Publishers, The Hague.

JOHNSON, P. N.; CAMPBELL, D. J. 1975. Vascular plants of the Auckland Islands. *New Zealand Journal of Botany* 13: 665-720.

KIRK, T. 1899. *The Student's Flora of New Zealand and the Outlying Islands*. Wellington, New Zealand.

KEEN, Lynette R., (unpublished) 1970. Significance of leaf size for water relationships in some closely related supecies. M.Sc. thesis, University of Auckland.

KNOTT, N. P. 1956. Possible effects of fertilization upon forage production and game use. *Proceedings of the Annual Conference of the Western Association State Game and Fish Commissioners* 36: 207-9.

LIVINGSTONE, D. A. 1974. Extract from INQUA report to the U.S. National Academy of Sciences. *Soil News* 22: 46-48.

MEDWAY, D. G. 1967. Avian remains from new caves in the Taumatamaire district. *Notornis* 14: 158-160.

MEDWAY, D. G. 1971. Sub-fossil avian remains from the Awakino-Mahoenui area. *Notornis* 18: 218-219.

MILLER, G. R. 1968. Evidence for selective feeding on fertilized plots by red grouse, hares and rabbits. *Journal of Wildlife Management* 32: 849-853.

MILLS, J. A.; MARK, A. F. *In press*. Food preferences of takahe in Fiordland National Park, New Zealand, and the effect of competition from introduced red deer. *Journal Animal Ecology*.

MOAR, N. T. 1970. A new pollen diagram from Pyramid Valley swamp. *Records of the Canterbury Museum* 8: 455-461.

MOSS, R. 1972. Food selection by red grouse *(Lagopus lagopus scoticus Lath.)* in relation to chemical composition. *Journal of Animal Ecology* 41: 411-428.

OLIVER, W. R. B. 1910. The vegetation of the Kermadec Islands. *Transactions of the New Zealand Institute* 42: 118-175.

OLIVER, W. R. B. 1949. The moas of New Zealand and Australia. *Dominion Museum Bulletin* No. 15.

OWEN, M. 1975. Cutting and fertilizing grassland for winter goose management. *Journal of Wildlife Management* 39: 163-167.

PHILIPSON, W. R. 1963. Habit in relation to age in New Zealand trees. *Journal of the Indian Botanical Society* 42A: 167-179.

RATTENBURY, J. A. 1962. Cyclic hybridization as a survival mechanism in the New Zealand forest flora. *Evolution* 16: 348-363.

SCARLETT, R. J. 1974. Moa and man in New Zealand. *Notornis* 21: 1-12.

SIMMONS, D. R. 1968. Man, moa and the forest. *Transactions of the Royal Society of New Zealand* (General) 2: 115-127.

SIMPSON, G. 1945. Notes on some New Zealand plants and descriptions of new species (No. 4). *Transactions of the Royal Society of New Zealand* 75: 187-202.

SORENSEN, J. H. 1951. An annotated list of the vascular plants. *In* Botanical investigations on Campbell Island. *Cape Expedition Series Bulletin* No. 7 (Part II): 25-38.

SYKES, W. R. 1969. The effect of goats on vegetation of the Kermadec Islands. *Proceedings of the New Zealand Ecological Society* 16: 13-16.

TAYLOR, B. W. 1955. The flora, vegetation and soils of Macquarie Island. *Australian National Antarctic Research Expeditions Reports* (Botany) Series B Volume II: 1-192.

TAYLOR, G. MARIE, 1961. A key to the coprosmas of New Zealand—Part 2. *Tuatara* 9: 43-64.

TAYLOR, G. MARIE, 1975. Divaricating shrubs. *Nature Heritage* 6: 2118-2127.

THOMAS, J. R.; COSPER, H. R.; BEVER, W. 1964. Effects of fertilizers on the growth of grass and its use by deer in the Black Hills of South Dakota. *Agronomy Journal* 56: 223-226.

TUCKER, J. M. 1974. Patterns of parallel evolution of leaf form in new world oaks. *Taxon* 23: 129-154.

WARDLE, P. 1963. Evolution and distribution of the New Zealand flora, as affected by Quaternary climates. *New Zealand Journal of Botany* 1: 3-17.

WARDLE, P. 1964. Facets of the distribution of forest vegetation in New Zealand. *New Zealand Journal of Botany* 2: 352-366.

WELTY, J. C. 1975. *The Life of Birds* 2nd ed. W. B. Saunders Co., Philadelphia.

WENT, F. W. 1971. Parallel evolution. *Taxon* 20: 197-226.

YALDWYN, J. C. 1958. Notes on the environment and age of the subfossil deposits of the Martinborough Caves. *Records of the Dominion Museum* 3: 129-133.

TABLE 1. *Distribution of Divaricating Plants in Relation to Some Ecological Factors*
(*Compiled by I. A. E. Atkinson and A. P. Druce*)

Species[1]	Altitudinal zone[2]	Geographical district[3]	Soils	Vegetation types[19]	Non-divaricate relatives
VIOLACEAE					
Melicytus micranthus	Lowland	Eastern and southern N.I., eastern S.I., Nelson	Recent soils from alluvium	Podocarp forests	*M. ramiflorus**
Hymenanthera alpina	Coastal, lowland to alpine	North and South Islands	Recent soils from rock, talus, alluvium and volcanic ash	Shrubland, open communities	*H. obovata*
H. sp. (*H. angustifolia* agg.) (stems flexuose, 2n = 32)[4]	Lowland, montane	North and South Islands	Recent soils from alluvium	Forest margins	
H. sp. (*H. angustifolia* agg.) (stems rigid, 2n = 64)[4]	Lowland, montane	North and South Islands	Recent and gley recent soils from alluvium	Scrub	
POLYGONACEAE					
Muehlenbeckia astonii	Coastal, lowland	N.I., Wellington coast; eastern S.I.	Weakly and moderately leached soils	Shrubland, open communities	*M. complexa*
PITTOSPORACEAE					
Pittosporum anomalum	Montane, subalpine	North and South Islands	Moderately leached soils	Shrubland	*P. eugenioides*
P. divaricatum (incl. *P. lineare*)[5]	Lowland, montane	Eastern N.I.; eastern S.I.	Moderately leached soils	Beech forests	
P. obcordatum	Lowland	Eastern N.I.; eastern S.I.	Recent soils from alluvium	Podocarp forests	*P. tenuifolium*
P. rigidum (incl. *P. crassicaule*)[6]	Coastal, lowland to subalpine	North and South Islands	Strongly leached soils	Forest, scrub	
P. turneri juvenile	Lowland, montane	North Island volcanic plateau	Recent soils from volcanic ash	Forest margins	*P. patulum*
ELAEOCARPACEAE					
Elaeocarpus hookerianus juvenile	Lowland, montane	North and South Islands	Weakly and moderately leached soils, gley soils	Forest	*E. dentatus*
Aristotelia fruticosa	Lowland to subalpine	North and South Islands	Weakly and moderately leached soils	Forest margins, scrub, shrubland	*A. serrata**
MALVACEAE					
Plagianthus betulinus juvenile	Lowland, montane	North and South Islands	Weakly leached soils	Forest	
P. divaricatus	Coastal	North and South Islands	Saline gley recent soils	Shrubland	
Hoheria angustifolia juvenile	Lowland	North and South Islands	Weakly leached and recent gley soils	Forest	*H. sextylosa*
ESCALLONIACEAE					
Carpodetus serratus juvenile	Lowland, montane	North and South Islands	Weakly and moderately leached soils, gley soils	Forest, scrub	
PAPILIONACEAE					
Sophora microphylla juvenile	Lowland, montane	North and South Islands	Weakly leached soils	Forest, forest margins, scrub	*S. tetraptera**
S. prostrata	Lowland, montane	Eastern South Island	Weakly leached soils	Grassland, open communities	
MORACEAE					
Paratrophis microphylla juvenile	Lowland	North and South Islands	Weakly leached soils	Forest	*P. banksii*
ICACINACEAE					
Pennantia corymbosa juvenile	Coastal, lowland	North and South Islands	Weakly leached soils	Forest, scrub	*P. baylisiana*

TABLE 1.—continued.

Species[1]	Altitudinal zone[2]	Geographical district[3]	Soils	Vegetation types[19]	Non-divaricate relatives
RHAMNACEAE					
Discaria toumatou	Coastal, lowland, montane	Eastern N.I., eastern S.I.	Weakly leached soils	Shrubland, open communities	
RUTACEAE					
Melicope simplex	Lowland	North and South Islands	Weakly leached soils	Forest	*M. ternata**
ARALIACEAE					
Pseudopanax anomalus	Lowland, montane	North and South Islands	Weakly and moderately leached soils	Forest, scrub	*P. simplex**
CORNACEAE					
Corokia cotoneaster	Coastal, lowland, montane	Eastern N.I., eastern S.I.	Weakly leached soils	Forest margins, shrubland, open communities	*C. buddleioides**
MYRSINACEAE					
Myrsine divaricata	Lowland to subalpine	North and South Islands	Weakly to strongly leached soils	Forest, scrub	*M. salicina**
RUBIACEAE					
Coprosma acerosa (incl. *C. brunnea*)[7]	Coastal, lowland to montane	North and South Islands	Recent soils from alluvium, volcanic ash, sand, talus and rock	Open communities	*C. repens**
C. areolata	Coastal, lowland	North and South Islands	Weakly leached soils	Forest, scrub	
C. ciliata s.s.	Subalpine	Western N.I., western S.I.	Strongly leached soils	Forest, scrub	
C. crassifolia	Coastal, lowland	Eastern N.I., eastern S.I.	Weakly leached soils	Forest, shrubland	
C. intertexta	Lowland to subalpine	S.I. Marlborough to Central Otago	Weakly to moderately leached soils	Shrubland	
C. obconica	Lowland	Northern South Island	Recent soils from alluvium, limestone and dolomite	Shrubland	
C. propinqua	Coastal, lowland to montane	North and South Islands	Recent, gley recent soils and other weakly leached soils	Open communities, shrubland, forest margins	*C. robusta**
C. rhamnoides (incl. *C. polymorpha*)[8]	Coastal, lowland	North and South Islands	Weakly and moderately leached soils	Forest, shrubland, scrub	
C. rigida	Lowland, montane	North and South Islands	Recent and gley recent soils, rendzina soils	Forest, forest margins	
C. rotundifolia	Lowland	North and South Islands	Weakly and moderately leached soils	Forest, scrub	
C. rubra	Lowland	Eastern N.I., eastern S.I.	Weakly and moderately leached soils	Forest, scrub	
C. rugosa	Lowland to subalpine	North and South Islands	Recent soils from alluvium, colluvium and volcanic ash	Open communities, shrubland	*C. tenuifolia**
C. virescens	Lowland	Eastern N.I., eastern S.I.	Weakly leached soils	Forest	
C. wallii	Lowland	Eastern N.I. (Wairarapa); S.I.	Weakly leached soils	Forest margins, shrubland	
C. sp. (aff. C. ciliata)[9]	Montane, subalpine	Eastern South Island	Moderately leached soils	Shrubland	

TABLE 1.—*continued.*

Species[1]	Altitudinal zone[2]	Geographical district[3]	Soils	Vegetation types[19]	Non-divaricate relatives
C. sp. (aff. *C. parviflora*, mtn. sp.)[10]	Lowland to subalpine	North and South Islands	Moderately and strongly leached soils, gley soils	Forest, scrub	
C. sp.[11]	Montane, subalpine	North and South Islands	Moderately and strongly leached soils, gley soils	Forest margins, shrubland	
C. sp. ("violet drupe")[12]	Lowland	Eastern North Island	Recent and recent gley soils from alluvium	Scrub	
COMPOSITAE					
Olearia capillaris	Montane, subalpine	North and South Island	Weakly leached soils	Scrub	*O. arborescens**
O. divaricata[13]	Montane, subalpine	South Island	?	Shrubland, open communities	
O. fragrantissima	Lowland	Eastern South Island	Weakly leached soils	Shrubland, forest margins	
O. laxiflora[14] ?	Lowland	South Island (Westland)	?	Forest margins, open communities	
O. serpentina[15]	Lowland, montane	S.I.: Nelson, Marlborough	Moderately and strongly leached soils	Forest	
O. virgata (volcanic plateau var.)[20]	Montane, subalpine	N.I.: volcanic plateau	Recent and gley recent soils from volcanic ash	Shrubland	*O. traversii*
O. sp. (*O. virgata* var. *implicita*)[16]	Lowland, montane	S.I.: Nelson, Westland	Recent and gley recent soils from alluvium	Shrubland	
O. sp. (*O. virgata* var. *rugosa*)[16] ?	Montane	Eastern South Island	Moderately and strongly leached soils	Grassland, shrubland	
O. sp. (aff. *O. hectorii*)[17]	Lowland	Eastern North Island	Recent soils from volcanic ash and mudstone; rendzinas	Forest margins	
O. sp. ("Glenhope")[18]	Lowland (370 m)	S.I.: Hope R. near Glenhope	Recent soil	?	
PODOCARPACEAE					
Podocarpus spicatus juvenile	Lowland, montane	North and South Islands	Weakly and moderately leached soils	Forest, scrub	*P. ferrugineus*

[1] Nomenclature follows Allan (1961) unless otherwise indicated.

[2] Limits for montane, subalpine and alpine zones follow Wardle (1964).

[3] "Eastern N.I." includes areas west of the main ranges where rainfall is less than 1000 mm.

[4] Beuzenberg (1961). Flexuose species: CHR 244118. Rigid species: CHR 86719.

[5] Cooper (1956).

[6] Considered by A.P.D. to be probably one species.

[7] Considered by A.P.D. to be one species as did Kirk (1899).

[8] Treated by Taylor (1961) as a single species.

[9] Both morphological differences and geographical separation suggest this is a separate taxon. CHR 279335

[10] Following the suggestion of Cheeseman (1925). CHR 277354.

[11] An undescribed species. CHR 179689-91.

[12] An undescribed species discovered by A.P.D. in 1966. CHR 159320.

[13] Cockayne (1909).

[14] Kirk (1899).

[15] Simpson (1945).

[16] Qualitative differences suggest specific rank.

[17] Reported as an undescribed species by Elder (1950). CHR 158932.

[18] An undescribed species discovered by A.P.D. in 1975. CHR 285845.

[19] As used here, scrub is distinguished from forest by having most stems less than 10 cm d.b.h. Shrubland is distinguished from scrub by having a woody cover of less than 80%.

[20] CHR 279559.

* Known to hydridize in the wild with the corresponding divaricating species.

TABLE 2. *Distribution of Divaricating Plants in the New Zealand Coastal Flora**

Region	Total species of indigenous woody plants	No. of divaricating species		Source of information
		endemic to region	not endemic	
1. Kermadec Islands	20	—	—	Oliver 1910; Sykes 1969.
2. Three Kings Islands	52	—	2	Baylis 1958.
3. Chatham Islands	36	1 +	2	Druce, unpub. 1976.
4. Subantarctic Islands†	19	—	1	Cheeseman 1909; Sorensen 1951; Taylor 1955; Fineran 1969; Johnson and Campbell 1975.
5. Northland coast	69	—	4	Atkinson, unpub.
6. Egmont coast	47	—	4	Druce, unpub. 1976.
7. Wellington coast	49	—	7	Druce, unpub. 1976.
8. Stewart Island coast	23	—	4	Cockayne 1909; Fineran 1964, 1973.

* For the purpose of this analysis, coastal species are those present in vegetation canopies *fully exposed* to wind-carried salt, usually less than 0.5 km from the sea.
† Antipodes, Auckland, Campbell, Snares and Macquarie Islands.
+ *Coprosma acerosa* var.

To test the null hypothesis that there is no difference between the incidence of divaricating plants on islands (regions 1–4 above) compared with their incidence on comparable parts of the mainland (regions 5–8 above):

$$\chi^2 = 22.52 \text{ with 1 d.f.}$$
$$P < 0.005 \text{ and the null hypothesis is rejected.}$$