**THE LUCY CRANWELL LECTURE 1989**

"LOOKING AT PLANTS WITH THE EYES OF A MOA"

given by Dr Ian Atkinson, Botany Division, DSIR,
at the Conference Centre, University of Auckland
on 4 October 1989

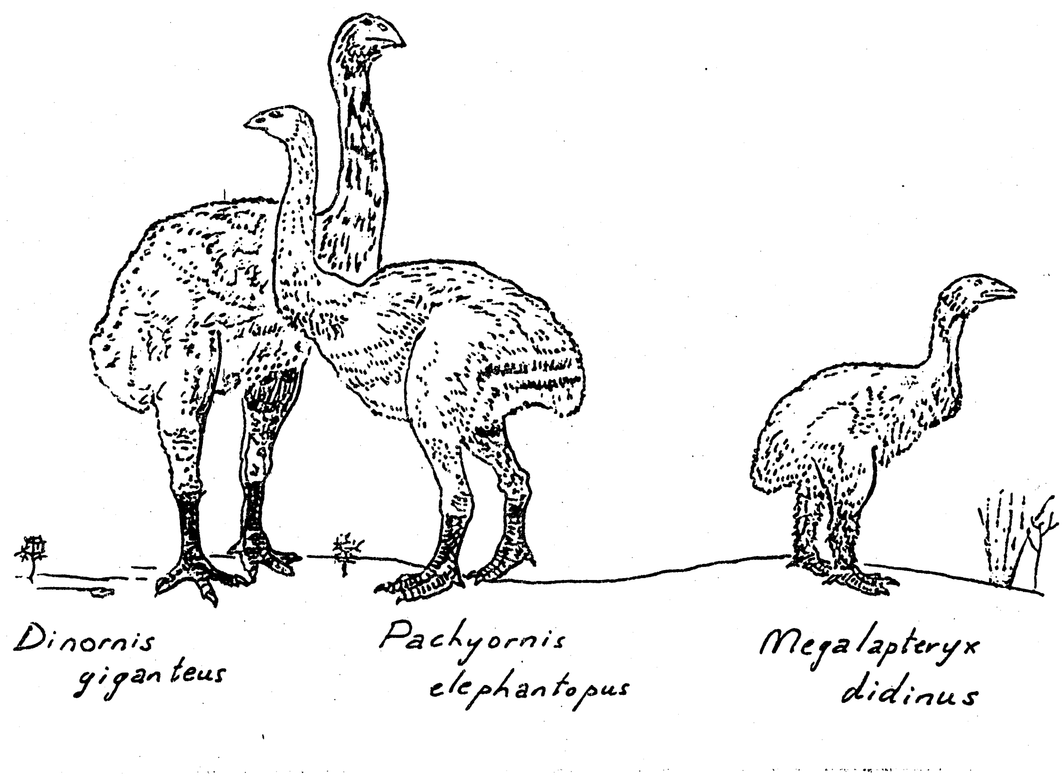
When Anthony Wright asked me to give this talk I cannot pretend that I thought it was a great idea. But now I have to say that I am grateful for the invitation because in the first place Lucy Cranwell was a real pioneer botanist and I feel honoured to be able to pay tribute to her with this talk. Mind you, I am not absolutely certain that she will approve of everything I tell you tonight.

My second reason for being grateful is that I do not have many opportunities to think about moas and the effects they may have had on plants. Such work is not seen as a readily marketable product and the fact that understanding the effects of moas on plants does have practical implications for conservation management is unlikely to convince Treasury officials that we should do such work.

And my third reason for being grateful is that it is 13 years since I talked about this subject in Auckland - and that occasion was when Michael Greenwood and I gave our first paper on divaricating plants. This gives me a chance to pay tribute to Michael because it was he who first suggested to me that these strange plants might owe their peculiar characteristics to moas. What I am talking about tonight goes well beyond divaricating plants but it is mostly work that Michael and I have done together and it was his creative insight that started it off.

## Some features of moas

If we are to speculate about the way in which moas looked at plants, we need to know a little more about these animals.



(i) They appear to have been mainly herbivorous but they probably did eat small animals when opportunities arose. At present our knowledge of their diets is based on analyses of less than 20 gizzards.

(ii) There were about 11 different species of moas with weights ranging from 20 to over 200 kg.

(iii) The various species of moa are unlikely to have eaten identical arrays of plant species. When feeding on the same plants, however, it is possible that different parts (e.g. buds, leaves, twigs, flowers, fruit) were eaten by different moa species.

(iv) There is no unequivocal evidence that moas moved in flocks - but movement in small family groups or as single individuals are both likely.

(v) Fertile alluvial flats would have been favoured places to feed and, according to one estimate, densities up to at least 30 averaged-sized moa to the square kilometre may have occurred.

(vi) Notwithstanding the use of certain favoured areas, moas occurred in a very wide range of habitats up to at least 1800 m (6000 ft) altitude in places. For example, dunes like those at the mouth of the Karamea River would have been visited by moas, vegetation on the alluvial flats each side of the river would have been more intensively used, and some species of moa ranged into the hills and mountains forming the river's catchment. They visited swamp margins where they ate flax among other plants. They penetrated into infertile mountain areas such as the granite country of the Hope Range, North-west Nelson. And one or two species even roamed up into the mountain tops such as Mt Owen, also in North-west Nelson.

(vii) Moas would have been very dependent on their eyesight when searching for food even if they did have a sense of smell. Most birds have exceptional colour vision but, on the basis of work done with emus, moas may well have been insensitive to colours at the two ends of the visible spectrum, i.e. violet, indigo and deep red or coppery colours. Blue, green and yellow colours would have been distinguished easily.

## Evolutionary responses of plants to herbivores

Overseas studies have demonstrated a variety of adaptations among plants that have apparently evolved in response to the browsing of both invertebrate and vertebrate herbivores. These include both modifications to growth forms as well as chemical adaptations:

| | | | | |
|---|---|---|---|---|
| <u>Growth form responses</u>: | (i) | spines on stems | e.g. | *Rubus*, boxthorn |
| | (ii) | prickles on leaves | e.g. | holly |
| | (iii) | stinging hairs | e.g. | nettles |
| <u>Chemical responses</u>: | (iv) | mechanical deterrents | e.g. | silica in grasses |
| | (iv) | chemical deterrents | e.g. | alkaloids, tannins |

The ways in which plants co-existed with moas through millions of years of evolutionary time were numerous but three basic modes of co-existence can be distinguished: avoidance, tolerance and deterrence.

<u>Coexistence with moas: avoidance</u>

1. <u>On islands</u>. Most if not all outlying islands (>50 km from mainland) were never reached by moas so that broad-leaved palatable plants such as the Chatham Island forget-me-not (*Myosotidium hortensia*) or *Stilbocarpa polaris* were able to evolve in the absence of large browsing animals.

   Almost all the offshore islands (<50 km from mainland) were connected by land during the last glacial period when sea-level was low. However a majority of these islands were too small to support viable populations of moas with the result that some palatable plants, e.g. large-leaved milk tree (*Streblus banksii*) may have always been more common on islands than on the mainland.

2. <u>On cliffs</u>: Many plants growing on cliffs escape browsing by introduced mammals because they are not reachable, e.g. mountain fivefingers (*Pseudopanax* spp.). This kind of protection would also have operated during moa times.

3. <u>As epiphytes</u>: Lilies such as *Collospermum hastatum* and orchids such as *Drymoanthus adversus* are all examples of plants that would frequently not have been reachable by moas because of the inaccessibility of their epiphytic position.

4. <u>As hemi-parasites</u>: The native mistletoes are generally very palatable to possums but their habit of growing from the branches of trees would have often placed them beyond the reach of moas.

5. <u>Protection from other plants</u>: Sometimes one can observe how a palatable plant such as *Parsonsia heterophylla* has escaped browsing by introduced mammals because it has grown through or among other woody species that have been avoided by these animals. Unbrowsed specimens of mountain

fivefingers (*Pseudopanax colensoi*, *P. ternatus*), for example, can sometimes be found among stands of bog pine (*Halocarpus bidwillii*), an unpalatable species.

6. Low-nutrient foliage: The nutrient content of many plants growing on infertile soils would have been so low that moas would have not spent much time browsing them. For instance, a manuka scrub community with an understorey of umbrella fern (*Gleichenia cunninghamii*) and club moss (*Lycopodium cernuum*) could hardly be expected to have supported any significant numbers of moas.

7. Rapid growth. On fertile soils, rapid height growth by plants is possible and this would have enabled some species to quickly grow above the heights that moas could stretch to when feeding. Whau (*Entelea arborescens*) is perhaps the fastest growing of all native trees; possibly it relied on this characteristic to avoid browsing by moas to some extent.

8. Camouflage: When this trend evolves, long before a stage is reached when a plant can be said to be camouflaged, there will be intermediate stages when the plant is less apparent to a would-be browser. *Pittosporum obcordatum* is a good example of a plant that seems to have developed adaptations that increase its chances of being missed by a herbivore using sight to find its food. Juveniles less than 50 cm tall are more or less umbranched but the long narrow bronze-coloured leaves with prominent whitish mid-ribs are borne at an angle that makes them look like leafless twigs, unsuitable for browsing. In its next stage of growth the plant becomes divaricate.

   *Pittosporum patulum* also has narrow purplish-bronze leaves and a habit of growth that makes it extremely difficult for a human eye to discern its presence in the beech forest understories where it grows. If indeed this habit reduced the frequency with which it was found and eaten by moas, it does not now save it from deer, goats or possums because they can use their sense of smell to locate this palatable plant.

   The native jasmine (*Parsonsia capsularis*) is still another plant whose dark bronze-coloured foliage and habit of growth make it difficult to see as a juvenile on the forest floor. But as it grows taller to a metre or more in height, normal green foliage is produced and the plant is easy to see.

   Camouflage or reduced apparency is not restricted to plants of the lowland and montane zone. On greywacke screes at higher altitudes there occur a number of specialist scree plants some of which are very palatable to hares, rabbits, deer or chamois. A few of these may have been camouflaged to a moa's eyes. Thus the penwiper (*Notothlaspi rosulatum*) in the cabbage family (Cruciferae) has very dark coloured leaves that from 2 or 3 metres away look like the shadows cast by rocks in a coarse scree. *Lignocarpa diversifolia* is a scree plant in the carrot family (*Umbelliferae*) that has very grey leaves matching the grey colour of the coarse screes where it grows.

9. <u>Mimicry</u>: A remarkable case of mimicry is the manner in which the very palatable (to browsing mammals) *Alseuosmia pusilla* mimics the unpalatable mountain horopito (*Pseudowintera colorata*). Michael Greenwood and I presume that this is an adaptation that once allowed the alseuosmia to escape browsing by moas. However, we have no proof that moas actually did avoid eating mountain horopito.

   Perhaps the most amazing case of mimicry among New Zealand plants is that of the creeping vine *Muehlenbeckia ephedroides* which, when growing on a gravel beach or riverbed, looks exactly like a very low mound or patch of withered and dead stems. Only when the stems are turned upside down is it possible to see that they contain chlorophyll and are very much alive.

   *Helichrysum depressum* is another riverbed plant whose greyish stems and foliage give a strong impression that the plant is dead. Both *H. depressum* and *M. ephedroides* are eaten by stock and rabbits.

   Another possible instance of mimicry is that of *Celmisia lyallii* which in growth form looks very like an aciphylla. There are at least two problems with this example. *C. lyalli* is not browsed by sheep and in fact appears to have become much more abundant in areas like the McKenzie country since stock were introduced. This of course does not demonstrate that it was not once eaten by moas. The other problem is that the supposed mimicry is generalised in the sense that, so far, it has not been possible to relate it to a particular species of *Aciphylla*.

   There is no question in my mind that there are many cases of mimicry among New Zealand plants but most are either unrecognised or have not been properly described.

<u>Coexistence with moas: tolerance</u>

1. <u>Vigorous resprouting</u>: Some plants, even though they may be heavily browsed by cattle, goats, deer or some other mammal, are able to repeatedly recover from such loss of foliage simply by resprouting new shoots. Examples are kohuhu (*Pittosporum tenuifolium*), fivefinger (*Pseudopanax arboreus*) and ngaio (*Myoporum laetum*). It is more than likely that some species tolerated moa browsing in the same way.

2. <u>Reduced leaf size</u>: Many forest understorey plants are small-leaved even though their branch systems are not divaricate. Furthermore, their leaves are not closely spaced along the stems. Examples are *Coprosma colensoi*, *C. spathulata* and *Neomyrtus pedunculata*. The advantage of this growth habit is that, for a given bite size, a moa would have obtained less foliage compared with a large-leaved plant or one in which many small leaves are

bunched together.

3. Leaf loss: The loss of leaves and their replacement by photosynthetic stems can also be seen as a way in which greater levels of browsing could be tolerated. Examples are *Clematis afoliata*, *Rubus squarrosus*, *Carmichaelia* spp and *Chordospartium stevensonii*. This is not to suggest that moas were necessarily the primary selective force in bringing about leaf loss in all these cases.

Coexistence with moas: deterrence

1. Fibrous unpalatable leaves: Examples of this growth characteristic can be seen in the lancewoods. The very fibrous long linear leaves of juvenile lancewood (*Pseudopanax crassifolius*) are in marked contrast to the more "normal" looking adult leaves that generally do not begin to develop until 2 or more metres height above ground. It is interesting to note that the marginal teeth on the leaves of lancewood are represented as very prominent spinous teeth in the juvenile leaves of the toothed lancewood (*P. ferox*), a species that generally occurs on more fertile soils than ordinary lancewood. It is even more interesting to note that the Chatham Island lancewood or hoho (*P. chathamica*) is without any distinctive juvenile form and its leaves lack teeth of any kind.

   Many other plant species that grew within the feeding heights of moas have fibrous leaves, tree ferns for example, but it is unlikely that all such species have developed such leaves in response to moa browsing.

2. Leaves of high tensile strength: It is a remarkable fact that the leaves of juvenile cabbage trees (*Cordyline australis*), produced while the plant is still unbranched, are extremely difficult to pull off the stem. If browsed by moas in the past, they would have had to have been cut off piece by piece. In contrast, the adult leaves are fairly easily pulled from the plant. Kiekie (*Freycinetia banksii*) is another example where the leaves are difficult to remove from the stem because of their high tensile strength.

3. Divaricate growth form: The case for considering this growth form as an adaptation to moa browsing has been well documented even though there are some who believe that the form owes its origin to climatic factors. The growth form occurs in many different families and genera, particularly *Coprosma*, *Pittosporum* and *Olearia*. Most are shrubs but in the 9 cases where the adult is a tree, the transition in branching pattern and foliage from juvenile to adult is quite remarkable, matai for example. Why the divaricate habit should become less important in mature trees, whose crowns are fully exposed to weather conditions, than in the juvenile growing in the shelter of a forest or scrub understorey, has never been explained by adherents of the climatic explanation.

of introduced mammal. This does not prove that they were all eaten by moas (although Colin Burrows' analyses of moa gizzard contents shows clearly that some were) but it does show that we are looking at a generally palatable group of plants. The interlaced and sometimes rigid branching, the reduction in leaf size and number around the periphery of the plant, and the tough difficult-to-break stems, would have all acted as deterrents to moa browsing.

Perhaps one of the most remarkable features of this group is their wide habitat distribution. They are sometimes (but not always) prominent in the understoreys of lowland and montane forests, they occur on the coast, around swamps and in salt marshes, they are very common on fertile river flats, some occur on infertile soils, and a few occur in the subalpine zone. Such a distribution coincides very well with the distribution of moas as judged from the various subfossil deposits where moa bones have been found.

4. <u>Tangled vine form</u>: This form is well expressed in pohuehue (*Muehlenbeckia complexa*) and has some major similarities with the divaricate growth form: small leaves often well spaced along the stem, combined with tough stems that are both difficult to break and difficult to extract from the body of the plant. Juvenile leafless bush lawyer (*Rubus squarrosus*) shows the same habit of growth although this species has stem spines which would have been a further deterrent to browsing.

5. <u>Spines, spiny leaves</u>: The speargrasses (*Aciphylla* spp.) have segmented leaves, each segment modified to form a long spine. The largest and most spiny species are typically associated with stony watercourses or streambanks where nutrients are high. The speargrasses of the alpine zone are not only much smaller in size but much less spiny as well.

Judged by the interest shown in speargrasses by browsing animals today, e.g. takahe, hares, deer, etc, it appears likely that it is the nutrient-rich base of the plant that has greatest food value. The long spines would have made feeding on these plants by moas a delicate matter (given the probable vital importance of eyesight to these birds in searching for food) and in this connection it is interesting to note that the larger speargrasses have a ring of spiny stipules surrounding the base of the plant - possibly a second line of deterrence. One can speculate that moas used their heavily armoured feet and legs to tread down the leaves of a speargrass in order to reach into the base of the plant.

The small pointed mucrons at the tips of totara leaves may have functioned as deterrents to moa browsing in the past. The totara species associated with soils of moderate fertility (*Podocarpus totara* and *P. hallii*) have well developed prickly mucrons. *P. acutifolius* frequently grows on fertile alluvium and its leaves, particularly those of the juvenile, have sharper mucrons than any other species of totara. In contrast, snow totara (*P.*

alluvium and its leaves, particularly those of the juvenile, have sharper mucrons than any other species of totara. In contrast, snow totara (*P. nivalis*) that commonly grows in strongly leached soils of the montane and subalpine zone, has leaves that lack mucrons.

6. Chemical repellents: A very large number of our native plants contain chemical compounds that appear to be effective in either repelling herbivores or at least greatly reducing the extent to which a plant is eaten. The oil glands of kanuka (*Kunzea ericoides*) and *Olearia solandri* are one example, the toxins contained in the foliage of taraire (*Beilschmiedia taraire*) and rangiora (*Brachyglottis repanda*) are another. The gymnosperms are frequently rather unpalatable, presumably because of their high content of tannins, phenols and other distasteful compounds.

   It should be emphasised, however, that at present we have no real evidence to show that these various compounds were developed as a direct response to browsing by moas. Some, for example, may be an adaptation to insect browsers - and others may trace their origin to a time in geological history when the major herbivores were dinosaurs.

## Concluding remarks

First, I must reiterate that some of the ways in which particular species of plants could have coexisted with moas in the past are fortuitous results of other adaptations and in no way owe their origin to moas. But with certain features there are many pointers to moas as the primary selective factor in their origin. We should hardly be surprised at this in view of the widespread occurrence in other parts of the world of structural and chemical characteristics in plants that allow those plants to withstand herbivores, either vertebrate or invertebrate.

Second, whether the explanations for some of these apparently moa-induced adaptations are indeed correct or not, the plant features themselves do require an explanation - they are unusual features insofar as most plants do not possess them. When next you go tramping in the bush, do not accept these features as commonplace just because you have seen them many times before. Try to look at them through the eyes of a moa.