DO NEW ZEALAND FOREST TREES REGENERATE FROM SPROUTS?

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Observations in South Island lowland forests show that a high proportion of the angiosperm tree species, young or old (as well as many shrubs), produce basal stem sprouts (Table 1). This discussion is confined to the trees some of which (e.g. *Fuchsia excorticata, Griselinia littoralis, Melicytus ramiflorus, Myrsine australis*) very often have some sprouts, while others (*Alectryon excelsum, Myoporum laetum, Pittosporum tenuifolium, Sophora microphylla*) appear to have them only under certain specific conditions. The sprouting phenomenon is well known for forest trees in temperate Northern Hemisphere regions, e.g. in eastern North America (Burrows 1990). There the evolution of the sprouting behaviour, found in many angiosperms and a few gymnosperms, is ascribed to the long-term influences of, and consequent natural selection by: (i) browsing and bark-eating animals such as porcupines, woodchucks or deer; and/or (ii) periodic fires. The destructive influences have caused selection of those plant forms which are most easily able to recover from the damage. They do so by activation of dormant buds and, in some species, the sprouted stems form thickets at the base of parent trees. Although there can be disadvantages to the sprouts from being attached to parents, through transfer to them of fungal or bacterial diseases, in many species the sprouts are known to give rise to new young trees. If the main stems of parent trees die they can be replaced by one or more of the sprouts.

Do any of the New Zealand tree species with basal sprouts actually regenerate in this way? Also, what selective force(s) could have led to this type of growth behaviour of trees in our forests?

The field evidence for regeneration from sprouts

In the list in Table 1 I have marked those species which I know from first hand experience to be capable of replacing themselves from sprouts if the main stems are killed. Others may do so. *Cordyline australis* is very well known in this respect, but below are examples of observations on other species. Many shrub species could also be cited, but they merit a separate article.

Alectryon. Sprouts may grow into new trees, when young trees are sawn off at the base.

Aristotelia serrata, Beilschmiedia tawa, Corynocarpus, Griselinia littoralis, Hoheria sexstylosa and *Sophora microphylla*. As for *Alectryon*.

Melicytus ramiflorus. When old, somewhat rotten trees are felled by wind, well-grown sprouts around the base develop into new trees. Trees burnt to the ground also regenerate from sprouts.

Fuchsia excorticata. As for *Melicytus.*

Myrsine australis. Trees damaged near the base produce abundant sprouts. Roots also produce sprouts. These both give rise to small clumps of trees.

Schefflera digitata. Young trees broken down by goats are replaced by basal sprouts.

Weinmannia racemosa. If trees with basal sprouts are knocked down by falling podocarp trees they can regenerate from the sprouts.

In several areas on the Port Hills near Christchurch affected by fires in recent years, *Melicytus* and *Fuchsia* trees which were reduced to stumps by the passage of a fire have produced sprouts which grow vigorously. It is clear from the field evidence that the same trees have regenerated in the same way several times before. This knowledge has wider implications for forest recovery following fire (or logging). In virtually all Banks Peninsula forest remnants there is evidence that these areas have been comprehensively burnt. Charcoal fragments occur on the ground surface, charred logs are commonly present and many of the tall podocarps have fire scars on their stems. The big podocarps survived the fires which destroyed much of the lower forest growth and it is likely that at least some individuals of species like *Melicytus, Fuchsia, Griselinia, Alectryon* and *Myrsine* recovered from the ashes by sprouting from the base of burnt stems. One problem for regeneration of these Banks Peninsula trees or shrubs by this means now is continued browsing by feral goats, possums or domestic stock which can kill off all of the new sprouts.

Gymnosperms are not altogether missing from the list of lowland tree species which produce sprouts (Table 1) but the big podocarps do not seem to do so. Sprouting is evident in *Lagarostrobos colensoi* (silver pine) (cf Moar 1955), and also in the shrubby species *Phyllocladus alpinus* and *Halocarpus bidwillii,* all in high rainfall areas and under sodden ground conditions.

Possible evolutionary causes

It might be thought possible that the avian browsers in our fauna (the larger moa and some other birds) had some influence on the widespread development of the sprouting habit among our angiosperm tree species. We know that deer, goats or cattle eat basal sprouts on these trees and, once the browsing is relaxed, the trees respond by producing more sprouts. Bark chewing by possums, goats or horses and cuts made by the hooves of the larger ungulates can also cause buds to be activated, giving rise to new sprouts. It is difficult to imagine, however, that moas or other browsing birds (kokako, kereru, kakapo) could have had similar effects to these. Neither Atkinson & Greenwood (1989), nor Batcheler (1989), writing of the possible influences of moas on evolution of the form of New Zealand plants, have mentioned basal sprouting. It seems safe to say that, although moas may have eaten the basal sprouts on angiosperm trees, they probably were not responsible for the evolution of this phenomenon.

In comparison with other regions, we in New Zealand have tended to think of our flora and vegetation as having been relatively free from fire influences during their evolutionary development. However there is a growing body of evidence that fire has been fairly frequent throughout the Quaternary period, both in glacial and inter-glacial times (Molloy 1969, 1975, 1977; Molloy *et al* 1963; McGlone 1981, 1989; McGlone & Topping 1973; McGlone *et al* 1984; Burrows & Russell 1990; Burrows *et al* 1993). Therefore it seems quite possible that fire has been a selective force affecting some of the properties of our woody plants.

Coping with fire

Manuka (*Leptospermum scoparium*) and kanuka (*Kunzea ericoides*) with tiny, wind-dispersed seeds (and inability to produce basal sprouts) are usually cited as the New Zealand examples of species adapted to allow vegetation recovery after fire (cf. Burrows 1973; Burrows *et al* 1979). Undoubtedly they are our best examples of species conforming to the Mutch hypothesis of the advantage to plants of being burnt. Mutch (1970) proposed that the extreme flammability of many plant species over vast areas of the world (e.g. the Boreal conifer forests of the Northern Hemisphere; the savanna grasslands of Africa or South America; the grasslands of the North American Great Plains; heathlands of Europe; many kinds of Australian vegetation including *Eucalyptus* forests; the Californian chaparral scrub; the Mediterranean maquis, etc) has arisen by natural selection because of the benefits to these plants of being burnt. They burn very readily through their content of gums, resins, oils and/or by possessing abundant dry fuel. A fire removes various adverse influences (such as browsing or seed-eating pests, or diseases, or toxic effects of litter) and the ground is open and free of competitive plants which would otherwise prevent seedling establishment. The nutrients released by burning of plants and litter are available to boost the growth of seedlings which arise from seeds dispersed from unburnt sites or originating from various forms of seed bank (cf. Burrows 1990).

Leptospermum and *Kunzea* are good examples of highly flammable plants, containing oil and having abundant fuel. After a fire they spring up densely, following wind dispersal of their seeds, but the density of the resultant stands inhibits their own regeneration thereafter, as subsequently germinated seedlings are suppressed by light- and root-competition.

Another, more economical strategy for recovery from fire is to regenerate by sprouting from underground stems or roots, or from surviving stumps. Many plants in temperate or tropical fire-prone vegetation do this. Many New Zealand species in a range of vegetation types also do this, e.g. in: grasslands (*Festuca novae-zelandiae, Poa cita, Chionochloa* spp. and many dicotyledon herbs); fernlands (*Pteridium esculentum, Gleichenia dicarpa*); wetlands (*Baumea* spp., *Empodisma minus* and other herbs); and shrublands (*Discaria toumatou, Coprosma* spp., *Corokia cotoneaster, Hymenanthera alpina* and others). These species can also regenerate from seeds or (the ferns) from spores.

I suggest that we should also add many angiosperm and some podocarp forest trees to the list of species which can counter the destructive influence of fire. If they are scattered emergents in mixed forest big podocarps like matai

(*Prumnopitys taxifolia*) and kahikatea (*Dacrycarpus dacrydioides*) can avoid the worst effects of fire by having tall, clean stems which are bypassed by the fire without much damage. Mountain totara (*Podocarpus hallii*) avoids fire in many places by living in rocky or bouldery habitats. Various angiosperm trees (and shrubs) could recover from fire by resprouting. Thus it seems to me that fire may well have shaped the development of the sprouting habit of these trees. Those individuals which survive by sprouting pass their genes on to new generations through their seeds.

Many kinds of attribute allow plants to resist, evade, avoid or recover from fire. They are very well expressed in the Australian and southern African floras (cf Gill 1975; Gill *et al* 1981; White 1976). Although *Fuchsia excorticata* and *Melicytus ramiflorus* can regenerate from burnt stumps, as far as I know there are no New Zealand trees with such well-developed lignotubers as those of many *Eucalyptus* or *Banksia* species. Nor do I know of any with the very long shallow roots giving rise to sprouts, such as those found in *Maytenus boaria* (from Chile), *Robinia pseudoacacia* (North America) or *Eleagnus angustifolia* (Western Asia). A few New Zealand trees and shrubs proliferate vegetatively by means of root sprouts, e.g. *Myrsine australis, Phyllocladus alpinus* (the latter on wet sites), but only on a relatively small scale.

Some of the less spectacular fire-countering phenomena are well developed in New Zealand, not least the sprouting habit of woody plants, a phenomenon little-mentioned in our ecological literature. Although our trees do not exhibit some of the more extreme means of fire resistance, post-fire recovery, or even dependence on fire for reproduction, seen in the Australian and southern African floras, the sprouting habit serves them well under our conditions. It could also be put into use when propagating the species concerned.

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Table 1 Tree Species of South Island Lowland Forests Which Produce Basal Sprouts

Canterbury	Good evidence for regeneration of new trees	Additional Species in Westland-Buller-Nelson-Marlborough	Good evidence for regeneration of new trees
Alectryon excelsum	yes	*Ascarina lucida*	
Aristotelia serrata	yes	*Beilschmiedia tawa*	yes
Carpodetus serratus	yes	*Dysoxylum spectabile*	
Cordyline australis	yes	*Lagarostrobos colensoi*	
Corynocarpus laevigatus	yes	*Melicope ternata*	
Fuchsia excorticata	yes	*Myrsine salicina*	
Griselinia littoralis	yes	*Pittosporum colensoi*	
Hedycarya arborea		*Pseudopanax edgerleyi*	
Hoheria sexstylosa	yes	*Pseudowintera axillaris*	
Melicytus ramiflorus	yes	*Quintinia acutifolia*	
Myoporum laetum		*Weinmannia racemosa*	yes
Myrsine australis	yes		
Pennantia corymbosa			
Pittosporum eugenioides			
P. tenuifolium			
Pseudopanax arboreus			
P. crassifolius	yes		
Schefflera digitata	yes		
Sophora microphylla	yes		