A PHYSIOLOGICAL INVESTIGATION
OF THE
ADAPTIVE SIGNIFICANCE OF JUVENILITY
IN
Pennantia corymbosa Forst.

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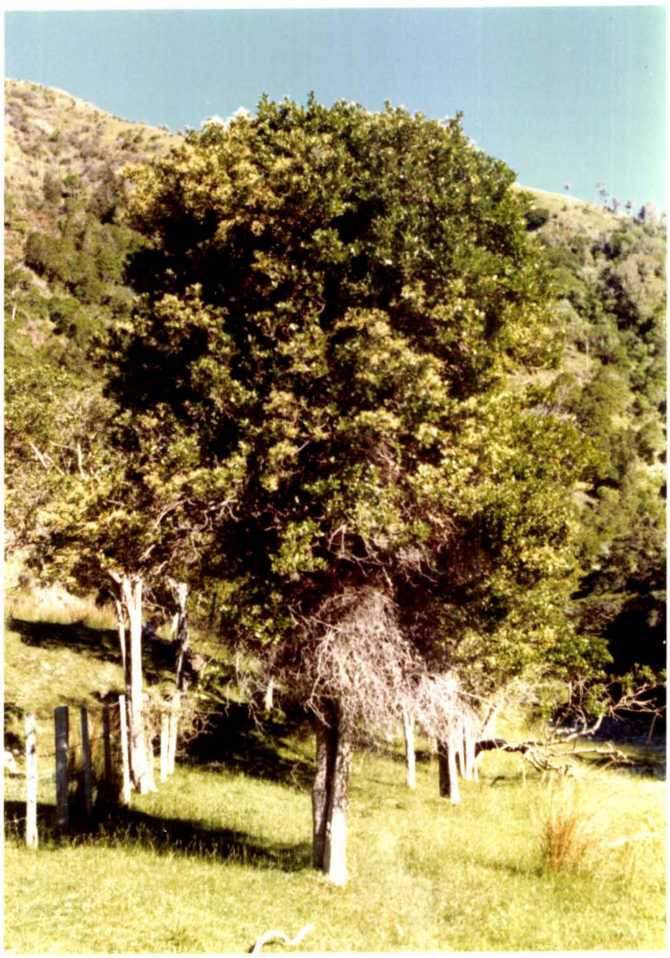

Mature Specimen of Pennantia corymbosa Forst.

ABSTRACT

The responses of the juvenile and adult growth forms of Pennantia corymbosa Forst. to a range of light intensities, leaf temperatures, shoot water potentials and wind velocities were investigated.

Results tend to indicate that the small-leafed divaricating juvenile is better adapted to open habitats than the adult. Responses to light intensity were similar for both growth forms. Measurements of photosynthetic rates at various light intensities after pretreatment at low and high irradiances revealed little difference in response between juvenile and adult, with both showing a similar increase in photosynthetic rates and light saturation points after the pretreatment light intensity was increased. Granal stacking in chloroplasts from juvenile and adult leaf palisade was reduced after growth at the higher pretreatment light intensity to the same extent in juveniles and adults. Solarization, despite the presence of a hypodermis, was greater in the adult, while the activity of Ribulose -1,5- diphosphate carboxylase was greater in the juvenile.

The indication that the juvenile is better adapted to open habitats is also supported by the results of experiments into the response of photosynthetic rates to a range of temperatures. The data revealed a higher mean temperature optimum for the juvenile than for the adult leaves ($21^{o}C$ c.f. $18^{o}C$).

The hypothesis that the juvenile might be better adapted to edaphic water stress was tested by withholding water for 14 days and measuring the rates of photosynthesis and transpiration as shoot water potential decreased. Rates of photosynthesis and transpiration declined in both juvenile and adult leaves as shoot water potential decreased. However,

the juvenile was able to maintain a higher rate of photosynthesis at comparable low water potentials than the adult which indicates that the juvenile is the more drought tolerant of the two.

Leaves of the juvenile also retain water better than those of the adult under moderately windy conditions. When plants were grown in a wind tunnel at wind speeds of up to 12 m sec^{-1} stomatal closure (as measured using a leaf diffusion resistance meter) occurred at lower wind speeds in the juvenile than the adult leaves.

The results obtained during this investigation thus support the hypothesis that the small-leafed divaricating juvenile of Pennantia is better adapted to a dry, exposed habitat than is the large-leafed orthotropic adult.

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"Wind is a most important factor in New Zealand"

Leonard Cockayne (1911)

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CHAPTER I

INTRODUCTION

A feature of the New Zealand flora is the prevalence of small-leafed (leptophyllous* and nanophyllous*) species with semi-divaricating and divaricating* habits. According to Greenwood and Atkinson (1977) there are 54 species from sixteen families that have a more or less divaricating growth habit, which constitutes approximately ten percent of the indigenous woody flora.

That the proportion of divaricating nanophylls in the New Zealand flora is atypically high is suggested by the paucity of recordings of like plants in other floras. However, the growth habit is not unique to New Zealand as divaricating plants do occur elsewhere, particularly in xeric environments.

Carlquist (1965) has noted the presence in Madagascar of a plant (Decaryia madagascariensis) with divaricating, thorny branches, while Bartlett and Bartlett (1976) have recorded a thorny divaricating shrub (Candalia microphylla) from Patagonia. Tucker (1974) lists 53 divaricating species from the species from the desert and chaparral communities of California and Arizona, though in these cases leaf size is much larger than that of most New Zealand divaricating species. Thus it is apparent that nowhere else are small-leafed divaricating plants such a large proportion of the woody flora.

The large number of distantly related plant families that contain divaricating species indicate the existance of strong selection pressures in favour of divarification at some stage during the evolutionary history of the New Zealand flora. The New Zealand flora has been geographically isolated since the Cretaceous (Fleming, 1962) and possibly the Permian (Darlington, 1965) thus giving ample time for selection pressures to operate.

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*See Glossary for definition

The occurrance of a large number of woody plants which exhibit heteroblastic development* is another feature of the indigenous flora, the life cycles of which have long been familiar to botanists (Hooker 1853, Kirk 1878). Eleven of the heteroblastic species have divaricating juveniles. These belong to nine genera in eight unrelated families (Philipson 1963).

Rumball (1961) conducted a survey of the distribution of heteroblastism by country from which it appears that, although the survey was not complete, the incidence of heteroblastism, like divarication, is atypically high in the New Zealand flora. Rumball (1961) reported two interesting Australian species, Flindersia maculosa and Eremocitrus glauca both from the Rutaceae, that are thorny xerophytic shrubs while juvenile and develop into the tree form later. The habit of Flindersia maculosa, leafy and slender at the top but bearing a mass of tangled branches and very few leaves at the base, is very similar to Eleocarpus hookerianus, an indigenous species with a divaricating juvenile. The presence of heteroblastic species with microphyllous+ non-divaricating juveniles in the Réunion, Maurice and Rodriques group of islands has been reported by Friedmann and Cadet (1976). Unfortunately the proportion of species with microphyllous juveniles is not indicated.

A characteristic of heteroblastic development in indigenous species is the length of duration of the juvenile stage, which may last up to 60 years as in the case of the divaricating juvenile of Eleocarpus hookerianus (Bulmer 1958). It appears that there has been strong selection for an attenuation of the developmental processes that result in the adult plant. Thus it is again evident that there has been strong selection pressure in favour of the divaricating growth habit. The question then arises as to the nature of the selection pressure and therefore the type of environment to which divarication and juvenility is an adaptation.

+ Technically nanophyllous

* See Glossary for definition

Juvenility in the New Zealand flora (and as a consequence divarication) was first studied experimentally by Leonard Cockayne (1899, 1900, 1901) who raised seedlings of many indigenous plants. Cockayne (1929) in FLORA AND VEGETATION OF NEW ZEALAND states that in 106 cases considered the juvenile is the more mesophytic* and in seventeen cases the more xerophytic* plant when compared to the adult. Cockayne included the eleven species of divaricating juveniles in the xerophytic category. Cockayne (1911) deduced that divaricating shrubs are xerophytes because:

> "The ecological factors governing this growth-form appear to be wind, in the first place, and then various other xerophytic stimuli, of which soil must play an important part."

Leonard Cockayne (1911) did not consider the present day New Zealand climate to differ from others to a degree that would allow for the evolution of the divaricating growth habit to such a unique extent. Cockayne considered that the divaricating habit is a xeromorphic growth form resulting from adaptation to "steppe climates" that he hypothesized occurred during the Pleistocene when conditions were cooler and drier than at present.

Rattenbury (1962) supported Cockayne's hypothesis of divarication as an adaptation to a harsh Pleistocene climate. However, he considered that cold climatic conditions resulting in low soil temperature which would retard root absorption combined with strong winds, rather than low soil moisture, could have led to the evolution of divarication during the Pleistocene.

Wardle (1963) considers that the concentration of divaricating, small-leafed, species in forest and mesic scrub communities does not support Cockayne's hypothesis. Instead he suggests that divaricating jubenile forms are adapted to present day fairly dry forest environments, and that their xeromorphy enables them to survive on drier sites while the development of adult foliage is related to the development of larger root systems.

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* See Glossary for definition

Dansereau (1964), while discussing the prevalence of leptohyllous species in the indigenous flora, found it difficult to see the ecological significance of having small leaves with regard to the present climate, and considered such forms to be non-disadvantageous at the present but advantageous at some time during the past.

Denny (1964) from her studies on the habit heteroblastism of Sophora microphylla found that dryness and long days bring about a phenotypic response which results in more divarication, that genotypic populations have developed in areas where the environment is dry. Furthermore where the plants are from a shaded or damp habitat there is little divarication. The presence of two species of Sophora that show marked divarication (along with many other divaricating species) in Canterbury and Central Otago which has the driest climate in New Zealand combined with dry "Northwesters" suggested to Denny that divaricating plants are adapted to fairly dry continental-type climates which still exist.

Went (1971) suggested a non-adaptative explanation. He proposed that a particular chromosome segment carrying the genes controlling divarication was transferred asexually between families, perhaps by an insect vector.

Evidence that small-leafed juveniles (although not associated with divarication in this instance) are an adaptation to edaphic water stress is presented by Friedmann and Cadet (1976) who conducted a survey of the geographical distribution of heterophyllous species in the Réunion, Maurice and Rodriques Islands. There was found to be a significant relation between the occurrence of heterophylly and the xeric condition of the enviornment to which it was concluded microphylly is an adaptation.

Several workers have suggested that divarication could possibly be an adaptation against browsing by moas. This theory has been recently discussed by Greenwood and Atkinson (1977) in some depth. However, the theory must remain speculative due to the difficulty of investigating such an hypothesis experimentally.

The anatomy and physiology of divaricating plants, and in the case of divaricating juveniles the corresponding adults, has been investigated over the last 50 years or so, with the aim of determining the habitat to which the divaricating growth habit is an adaptation.

Fitzgerald (1923 quoted by Rumball 1961) claimed that the juvenile leaves of Paratrophis microphylla, Plagianthus betulinus and Pennantia corymbosa are more xeromorphic both internally and externally than those of the adult. The criteria for xeromorphy used by Fitzgerald are not known as they were not mentioned by Rumball and the original thesis is not available.

Johnston (1948) compared the anatomy of juvenile and adult leaves of Carpodetus serratus taken from shaded and open habitats. Using the criteria for xeromorphy described by Maximov (1928) (i.e., smaller and thicker leaves, closer venation, increased stomatal density and strongly developed palisade mesophyll) he found that the adult "shade" leaves were more xeromorphic than the juvenile "shade" leaves, while the reverse was found for the juvenile and adult "sun" leaves. However, adult "shade" leaves were sampled from the forest margin and juvenile "shade" leaves from the forest floor, thus it is possible that the degree of xeromorphy in adult "shade" leaves was due to differences in humidity. Therefore it is only valid to compare "sun" leaves in which the juvenile is more xeromorphic. Johnston also found that the transpiration rate in "sun" leaves was greater for the juvenile than the adult, which Maximov (1928) describes as a xeromorphic characteristic. Johnston noted that the differences in the anatomy and physiology of "sun" and "shade" leaves of Carpodetus were similar to the differences in juvenile and adult leaves. Furthermore, he concluded that the juvenile leaves were more plastic, reacting more completely when exposed to similar environmental conditions as the adult.

Keen (1970) investigated the anatomy and physiology of small and large-leafed plants in the genera Coprosma, Melicope and Plagianthus. Leaf anatomy studies showed that all the small-leafed plants are xeromorphic, while the large-leafed plants are typical mesomorphs. From elementary physiological studies Keen concluded that the small-leafed species are not necessarily more drought resistant than the large, but are better adapted to grow under conditions of physiological drought, mainly because of a reduced internal resistance to water movement, more efficient heat exchange processes and a greater resistance to wilting.

It is evident that further research on heteroblastic species is needed to determine the adaptive significance of divarification and juvenility in the indigenous flora. By selecting a divaricating juvenile it is possible to make a comparative investigation between divaricating and non-divaricating plants of the same species, thereby minimizing genetic differences and concentrating on developmental changes.

To gain information on the habitat to which a plant species or ecotype is adapted it is possible to monitor the response to a range of combinations of environmental parameters. Physiological changes are an accurate indication of the effect that a given set of parameters is having on the plant because of the rapidity of functional responses to changes in environment. Therefore the emphasis in this investigation is physiological, with some anatomical and biochemical work where considered appropriate.

The responses of rates of photosynthesis and transpiration to changes in factors of the environment are easier to interpret than the responses of other plant characteristics. Such responses have a definite application to describing the adaptation of plants to their environment, (Jarvis 1969). Thus investigations into the effects of a range of defined environments on the rates of photosynthesis and/or transpiration have been under taken to test for physiological differences between divaricating juvenile and non-divaricating adult plants.