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LIGHT CONDITIONS AND THE EVOLUTION OF HETEROBLASTY (AND THE DIVARICATE FORM) IN NEW ZEALAND

Summary: Heteroblasty, changes in vegetative phenotype during ontogeny, is unusually common in the New Zealand flora. Some feature(s) unique to the New Zealand situation must have influenced the evolution of this strategy. Similarities were examined between the ontogenetic changes in phenotype and growth strategy in *Elaeocarpus hookerianus, Carpodetus serratus* and *Pseudopanax crassifolius*. Variation in hypothesised light capture efficiency of juvenile and adult forms can be related to changes in the light environment that these growth forms experience. Heteroblasty is hypothesised to have evolved as a result of the change from a low light intensity environment below the canopy of high altitude conifer/broad-leaved forests, to a high light intensity environment above the canopy. The differences in architecture between juvenile *E. hookerianus* and *C. serratus* on the one hand, and *P. crassifolius* on the other hand, are likely to be related to their adaptation to heterogeneous moderate light intensity and homogeneous low light intensity, respectively. The divaricate form characteristic of many New Zealand shrubs may have arisen following the development of heteroblastic trees with a divaricate juvenile, and the subsequent loss of the adult state. This paper provides hypotheses which future research can scientifically test.

Introduction

The New Zealand flora has two unusual features: the divaricate form common to many shrubs (10% of all endemic woody species; Greenwood and Atkinson, 1977); and the high proportion of tree species with heteroblastic vegetative growth (200 tree species; Cockayne, 1912). The divaricate habit describes a collection of phenotypic characteristics, most commonly: small leaves, wide branch angles, and thin interlacing stems forming a dense canopy (Greenwood and Atkinson, 1977; Atkinson, 1992; Wilson and Galloway, 1993; Kelly, 1995). Heteroblastic changes during ontogeny of New Zealand trees may include transition in both leaf and branch phenotype (Philipson, 1964; Gould, 1993; Day, Gould and Jameson, 1997). The prevalence of the divaricate habit and heteroblasty in New Zealand has encouraged speculation on their possible selective advantages since the flora was first studied (Diels, 1897; Cockayne, 1912). Because these strategies are not restricted to particular families, and a genus may group members both with and without these features (Philipson, 1964), remarkable convergent evolution must have occurred. Furthermore, there are species which display both a heteroblastic habit and a

juvenile with a divaricate form (Philipson, 1964). This has prompted a search for some feature(s) peculiar to the New Zealand situation that may have influenced evolution. Here it is proposed that New Zealand's forests provided light conditions where heteroblastic development is favoured.

The current theories for the evolution of heteroblasty and the divaricate habit are outlined in Table 1. Other than some of the climate and micro-climate hypotheses, the theories make *a priori* assumptions of adaptive strategy: the suggested mechanism for evolution relies purely on speculation about the interaction between selection pressure and phenotype. These theories are difficult to test because the conditions proposed to give rise to evolutionary change can not be repeated. An alternative approach combines the concepts of ontogenetic and phylogenetic contingency (Watson, Geber and Jones, 1995). Plant phenotype depends on the interaction between genotype and environment during ontogeny (environment is envisaged in its broadest sense including climatic and edaphic conditions as well as influence from other biota: competition, herbivory, parasitism, etc.). Plant genotype - or more precisely constraints on development - depends on the interaction between

Table 1: *Theories for the evolution of the divaricate form and heteroblasty in the New Zealand Flora*

Trait	Selective Pressure	Outline of hypothesis	References
Divaricate form	Climate	Divaricates evolved resistance to water stress either during the last ice-age when water was scarce or in response short droughts in the current forest environment	Diels, 1897; Cockayne, 1912; Rattenbury, 1962; Wardel, 1963; McGlone and Clarkson, 1993
	Microclimate	Divaricates evolved a plant canopy with a microclimate providing: - resistance to frost or wind damage - advantage in high light intensity	Kelly and Ogle, 1990; McGlone and Clarkson, 1993 Kelly, 1995
Heteroblasty	Hybridisation	Heteroblastic species arose through hybridisation between two homoblastic relatives	Godley, 1985
Divaricate form and heteroblasty	Moa browsing	The divaricate form is resistant to Moa browsing; adult foliage of heteroblastic species occurs above Moa height	Greenwood and Atkinson, 1977; Mitchell, 1980; Atkinson and Greenwood, 1989; Batchelor, 1989

genotype and environment over phylogeny. Therefore, examining the form and function of a plant in its current environment provides information about selection pressure(s) of the species' phylogenetic environment (Watson *et al.*, 1995). This approach assumes that species with adaptive advantage in a given environment also have a competitive advantage, and thus the composition of the community will tend toward an association of species each with competitive advantage within a particular environmental niche (Horn, 1971). Hypotheses for the evolution of species can be constructed based on the function of a plant in its current environment. If many species have evolved a similar habit in the same environment, then this method of hypothesis construction is particularly useful (Givnish, 1987). To construct evolutionary hypotheses using this method one must: 1) identify the current environment of species with similar habit; 2) investigate the function of the habit in the environment; and 3) identify the features of the environment to which the habit is particularly suited.

This paper does not attempt to refute theories for the evolution of heteroblasty or the divaricate habit proposed by others: these have been widely discussed (Table 1). Instead it expands a hypothesis which proposed that optimisation of light capture influenced the evolution of the divaricate form (Kelly, 1995; Day *et al.*, 1997; Day, *in press*, a, b). Heteroblasty is examined using this same premise. The developmental strategies of three native New Zealand trees, *Elaeocarpus hookerianus* Raoul (pokaka), *Carpodetus serratus* J.R. et G. Forst.

(putaputaweta, marble leaf) and *Pseudopanax crassifolius* (Cunn.) C.Koch. (lancewood), provide evidence to support this theory. Hypotheses presented here provide a basis for future experimentation.

Species

Three species, *E. hookerianus*, *C. serratus* and *P. crassifolius*, were chosen to represent the diversity of New Zealand tree species which undergo abrupt heteroblastic change, principally because the development and physiology of these species have been examined in some detail (Gould, 1993; Clearwater and Gould, 1995; Day, *in press*, b; Day and Gould, 1997; Day *et al.*, 1997; Day, Gould and Jameson, *in press*). Both *C. serratus* and *E. hookerianus* have a divaricate juvenile form, however, juvenile *C. serratus* leaves are larger than those of most divaricating species. Juvenile *P. crassifolius* and *C. serratus* have open canopies in forest conditions, whereas *E. hookerianus* has a denser habit. *C. serratus* and *P. crassifolius* are found throughout New Zealand while *E. hookerianus* distribution is restricted to cooler, low light and low nutrient habitats (Leathwick, 1995). The crown shape and branch pattern of adults of these species are similar, it is their juvenile forms which differ in appearance.

Three distinct phases of growth, which differ in both architecture and growth pattern, develop during *E. hookerianus* ontogeny (Day *et al.*, 1997). Juvenile

plants have small leaves which range from obovate to linear-lanceolate, and thin branches with wide branch angles and a zig-zag stem arrangement (the angle between contiguous internodes is often not 180º). Horizontal branches lack apical control of axillary shoot outgrowth (Day and Gould, 1997). Vertical axes arise both from other vertical axes and horizontal axes often low within the canopy. These axes commonly abort resulting in a dense canopy of interlacing vertical and horizontal axes. Vertical extension of the canopy occurs slowly. The transition to adolescent and adult forms requires the dominance of a single vertical axis over all others (Day *et al.*, 1997). Adolescent plants differs from both juveniles and adults, they have an open branch canopy and strong vertical extension. The adult canopy is dense and shoot extension is greatest in the horizontal direction. Adult leaves are larger and more uniform in morphology, branches are stouter, and branch angles less obtuse than juvenile plants (Day *et. al.*, *in press*).

C. serratus juvenile plants also have wide branch angles, zig-zag stem arrangement and thin stems (Day, *in press*, b). Leaves range in length from 10 - 30 mm and are uniform in morphology. Horizontal branches arise from the single vertical axis in groups of three, resembling a rosette of branches, separated by sections of vertical stem with no horizontal axes. Axes of horizontal branches twist producing a horizontal and evenly spaced leaf distribution (Day, *in press*, b). Branches are not interlaced and the canopy is open in forest conditions but may be dense in an open environment. Adult leaves are larger than for juveniles, and branches are stouter with more acute

branch angles and no zig-zags. The twisting of axes to a horizontal plane, and the rosette arrangement of horizontal axes is not evident in adult trees.

P. crassifolius contrasts with the previous species in that the juvenile has a single vertical axis with no horizontal lateral axes. Leaves are long (up to 1 m) and narrow (less than 2 cm) with a massive mid-rib providing mechanical support (Gould, 1993). The cuticle and hypodermis are well developed. Leaves commonly are angled at 45º from horizontal and their azimuth is preferentially orientated toward forest canopy gaps (Clearwater and Gould, 1995). The adult is branched, and the leaves are shorter (15 - 20 cm), broader (2 - 3 cm), and more randomly oriented with respect to azimuth and angle from horizontal than juvenile plants (Gould, 1993).

Common to the ontogeny of these species is heteroblastic change. If heteroblasty evolved under the same selection pressures, then similarities in phenotypic change during ontogeny should inform us about these pressures. There are three major similarities between the species (Table 2): (1) a multilayer juvenile leaf arrangement; (2) an increase in leaf width during ontogeny; and (3) a tall, narrow, cylindrical canopy as a sapling which broadens during the transition to adult form.

Leaf distribution and growth strategy

While acknowledging that many environmental properties influence species succession, Horn (1971) devised a simple theory, based on the comparison

Table 2: *Changes in architecture of* E. hookerianus, C. serratus *and* P. crassifolius *during ontogeny*

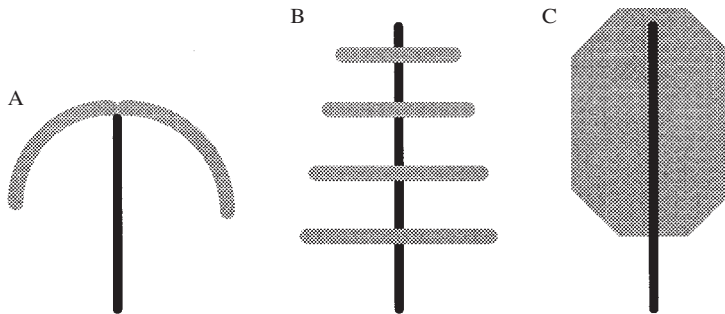| | Change during ontongeny | | |
	E. hookerianus	*C. serratus*	*P. crassifolius*
Leaf length	Increase	Increase	Decrease
Leaf width	Increase	Increase	Increase
Leaf Area Index (LAI)	Increase	Increase	Increase
Phenotypic plasticity	Decrease	Decrease	Little change
Stem diameter	Increase	Increase	Increase
Ratio of canopy diameter: height	Decrease (juvenile to adolescent)	Decrease (seedling to sapling)	Decrease (seedling to sapling)
	Increase (adolescent to adult)	Increase (sapling to adult)	Increase (sapling to adult)
Branch density	Decrease (juvenile to adolescent) Increase (adolescent to adult)	Little change	Increase
Vertical apical dominance	Increase (juvenile to adolescent) Decrease (adolescent to adult)	Decrease	Decrease

Figure 1: *Diagrammatic representation of monolayer (A) and multilayer (B, C) leaf distributions. A multilayer may have leaves arranged in foliage layers (B) or randomly throughout the canopy (C). Black line, zero order axis; grey, foliage.*

between the efficiency of light capture of two leaf distributions, which could explain many of the changes. A monolayer leaf distribution (all leaves contained within a single layer) was compared with a multilayer distribution (leaves distributed randomly throughout the canopy or in foliage layers) (Fig. 1). A multilayer leaf distribution captures more light than a monolayer distribution when incident light intensity is greater than approximately 50% of full sunlight (Horn, 1971). Many features enhance the light capture efficiency of a multilayer (Table 3), particularly: narrow or lobed leaves (which reduce self shading of lower leaves); optimisation of the leaf area index (LAI = plant leaf area divided by the ground area shaded by the canopy) to 1.6; and plasticity (Horn, 1971). Plasticity may be expressed in phenotype, in anatomy (ie: sun and shade leaves), or in physiology (ie: photosynthetic induction state).

In forests, early succession species commonly have multilayer leaf distributions and late succession species have monolayers. However, some mid to late succession species are multilayered. These species Horn (1971) terms persistent multilayers, because they persist in shaded environments where they presumably capture light less efficiently than monolayers. Persistent multilayers may remain in the forest community if light conditions are heterogeneous; for example forest canopy gaps are reasonably frequent (creating a rapid change in light quality and quantity), or if the forest canopy consists of a patchwork of species (the quality and quantity of light alters with position in the understorey). Thus a stable forest community may have species with a range of leaf distribution types from monolayers to persistent multilayers. This range is similar to a range of growth strategies from 'pessimistic' to 'optimistic' described by Takahashi (1996). Some architectural and growth strategy properties of these extreme forms of forest tree growth type are

presented in Table 3. Basically, trees with a 'pessimistic' growth strategy are shade-tolerant, have large leaves and show little plasticity. An 'optimistic' growth strategy is plastic, leaves and branches are small and have short longevity, and architectural changes occur during ontogeny particularly in canopy shape from narrow to broad. Persistent multilayer trees with an 'optimistic' growth strategy are likely to be 'oskars' (Silvertown, 1987). These plants persist in the forest understorey waiting for the appearance of a canopy gap to which they respond by growing rapidly.

Where within this range of architectural type and growth strategy do *E. hookerianus*, *C. serratus* and *P. crassifolius* lie? The three species have properties in common with an 'optimistic' growth strategy: multilayered leaf distribution; narrow leaves (which broaden during ontogeny); a change in canopy shape during ontogeny from narrow to broad (Gould, 1993; Day, *in press*, b; Day *et al.*, 1997). *E. hookerianus* and *C. serratus* also have small leaves and exhibit extensive phenotypic plasticity in response to changing light conditions (Day, *in press*, b; Day and Gould, 1997). Conversely, *P. crassifolius* has some properties of the 'pessimistic' growth strategy, namely large leaves with great longevity, and low phenotypic plasticity.

Plasticity

Forest trees that exhibit plasticity during their ontogeny are likely to follow the persistent multilayer growth strategy (Horn, 1971). Plasticity describes the ability of plants to alter state (phenotype, anatomy or physiology) in response to changes in environmental conditions (Bradshaw, 1965; Schlichting, 1986; Scheiner, 1993; Padilla and Adolph, 1996). In forest environments, plants are

Table 3: *Architectural and growth strategy properties of the extreme forms of forest tree growth types*

	Pessimistic/Monolayer	Optimistic/Persistent multilayer/Oksar	Reference
Leaf size and morphology	Large, broad and entire	Narrow or lobed	Horn, 1971
Number of stems and leaves	Few	Many	Horn, 1971
Stem diameter	Stout	Thin	Horn, 1971
Leaf and branch longevity	Long	Short	Kikuzawa, 1995; Takahashi, 1996
Plasticity	Low	High	Canham, 1988; Thompson, Huang and Kriedemann, 1992; Takahashi, 1996
Heteroblastic change	Small	Large	Hansen, 1996
Leaf arrangement	Monolayer	Multilayer	Horn, 1971
Canopy shape as sapling	Flat and spreading	Tall and thin	Horn, 1971
Change in ratio of canopy diameter : height	Little change	Decrease (seedling to sapling) Increase (sapling to adult)	Horn, 1971; King, 1981; Givnish, 1988
Energy requirement (ecological compensation point)	Low	High	Osmond, 1987; Canham, 1988; Givnish, 1988; Thompson *et al.,* 1992
Allocation of production to leaves	High	Low	Whittaker and Woodwell, 1968; Nicola and Pickett, 1983
Major light source	Homogeneous, low intensity	Heterogeneous, high intensity	Horn, 1971
Absolute shade tolerance	Tolerant	Intolerant	Horn, 1971
Shade shed	Deep	Light	Horn, 1971
Response to high light intensity	Little response	Maximise height extension	King, 1981; Thompson *et al.,* 1992; Takahashi, 1996
Response to low light intensity	Reduce growth in all directions	Optimise architecture for light capture	Takahashi, 1996
Successional stage	Late	Mid/Late	Horn, 1971

most likely to express plasticity in response to changes in the light environment (Lee and Richards, 1991). The boundaries within which the state of the plant may vary is set by the genotype, and the environment determines the actual state within these limits (Watson *et al.*, 1995). A plant with wide boundaries has much plasticity.

Plasticity is assumed to provide adaptive advantage in a heterogeneous environment because a plant may optimise its state to the prevailing environment without genetic constraints (Lee and Richards, 1991). In a heterogeneous environment there are four potential strategies of growth that plants may follow; random, conditional, multiple, and uniform (Lloyd, 1984; Schlichting, 1986). A random growth strategy is unlikely to be advantageous to plants in any conditions. If the environment changes frequently (e.g. seasonally) or the change is unpredictable (e.g. the opening of forest canopy gaps), a conditional strategy may be favoured. With this strategy, traits are labile and are conditional on the prevailing environment conditions. This is what is generally understood as plasticity. Alternatively, if the change in

environment is predictable and occurs less frequently (e.g. once or twice during ontogeny) then a multiple strategy may be advantageous. A multiple strategy arises when a conditional strategy becomes genetically fixed during evolution to become part of ontogenetic development rather than a direct response to environmental change. Heteroblasty is an example of a multiple growth strategy. A uniform strategy is favoured when plants grow in a homogeneous environment. Plants in a heterogeneous environment may follow a uniform growth strategy when: they are unable to detect the environmental change; the time required for detection and response to environmental change is large in relation to the rate of change of the environment; there is a large asymmetry in the time spent in different environments; or the performance advantage of different phenotypes is not great enough to cover costs (Padilla and Adolph, 1996). Costs in this respect might include the cost of reproductive fitness, cost of transforming between states, or cost of maintaining the genetic and cellular mechanism required for a plastic response (Scheiner, 1993).

E. hookerianus, *P. crassifolius* and *C. serratus* plants have a multiple phenotypic strategy. They show genetically fixed heteroblasty during ontogeny in canopy shape, leaf morphology and branching pattern (Philipson, 1964; Gould, 1993; Day *et al.*, 1997) regardless of the environment in which they grow. *E. hookerianus* plants also display a loss of conditional plasticity during ontogeny (Day *et al.*, 1997; *in press*). The heteroblastic change in these species is, however, partially labile because the age or tree height at which the change occurs may be influenced by environmental conditions. The first branch of *P. crassifolius* may arise between 1.8 - 7.0 m from ground-level depending on the forest cover (McGlone and Clarkson, 1993). *E. hookerianus* transition height varies between 2 - 4 m depending on the environment in which the plant grows (Rumball, 1963). Using the argument above, the multiple heteroblastic strategy common to many New Zealand native trees suggests these plants experience a predictable environmental change, and spend a substantial portion of ontogeny in each environment.

The juvenile forms of both *E. hookerianus* and *C. serratus* have a conditional growth strategy (Day, *in press*, b; Day and Gould, 1997). In response to a change in light conditions (either a comparison between open and shaded environments, or seasonal changes in environmental conditions), these species change leaf morphology and size, axis length, canopy and foliage density, and horizontal axis branching pattern. Plants have two shoot types (with either expanded or unexpanded internodes), two axis types (horizontal and vertical) with different architecture, small leaves, and many shoot apices within a small canopy volume. These features allow plants to respond rapidly to changes in environmental conditions. The conditional strategy of these juvenile plants suggests they experience a heterogeneous environment.

In contrast to the other species, juvenile *P. crassifolius* plants display little phenotypic plasticity. Clearwater and Gould (1995) show that leaf orientation of juvenile *P. crassifolius* plants optimise capture of low intensity light rather than high intensity light. The homogeneous nature of this low intensity light in the forest understorey may provide advantage for a uniform growth strategy. Alternatively, these plants may show physiological plasticity. While the architecture of these plants may not be labile, plants may alter growth rate in response to a change in environment. Many New Zealand broad-leaved forest plants increase their growth rate rapidly in response to an increase in light intensity (Bieleski, 1959; Wardle, 1991).

Consequences of the growth forms

The growth strategy of juvenile *E. hookerianus* and *C. serratus* plants is energetically expensive. Production costs for the 'optimistic' growth strategy are high because many axes and leaves are produced and their longevities are low (Takahashi, 1996), and because plasticity entails higher costs than a uniform growth strategy (Schlichting, 1986). Juvenile *E. hookerianus* and *C. serratus* plants display a number of features which suggest they compensate for these expenses by enhancing light capture and minimising expenditure on support costs. Light capture is enhanced by the multilayer leaf distribution (if incident light is of moderate to high intensity), by the low leaf area index (LAI) of plants in forest conditions (which minimises self shading of leaves in the lower canopy), and by the wide branch angles. Wide branch angles are characteristic of plants in which enhancing light capture is important (Fisher, 1986), because wide angles help space leaves evenly in the plant canopy to reduce self shading (Day, 1998). The productive use of captured light is likely to be enhanced by a low light compensation point, this trait is characteristic of many New Zealand forest species (Bieleski, 1959; Wardle, 1991). Furthermore, plasticity allows plants to capture light efficiently when there is a change in the environment conditions (Lee and Richards, 1991). For example, juvenile *E. hookerianus* plants produce small leaves and short axes within the plant canopy during early spring to enhance light capture and minimise expenditure when light conditions are poor, and produce longer leaves and axes on the edge of the plant canopy when light conditions improve (Day and Gould, 1997). Support costs are minimised by producing a high proportion of leaves on short shoots within the canopy, and by restricting horizontal extension (horizontal axes require more support than vertical ones; Givnish, 1986), thereby reducing expenditure on secondary thickening of stems. The growth strategy of juvenile *E. hookerianus* and *C. serratus* suggest these plants have evolved to take advantage of a heterogeneous, moderately high energy light environment.

In contrast to *E. hookerianus* and *C. serratus*, juvenile *P. crassifolius* plants have low costs. While the large leaves are expensive to produce and support (Gould, 1993), they are retained for a long period of time. Plants produce few leaves and no branches. The leaves of juvenile plants, with their massive mid-rib and extensive hypodermal layer (Gould, 1993), perform functions similar to the combined functions of branches and leaves of other species. The form of juvenile *P. crassifolius* has evolved to provide advantage in the low energy,

homogeneous light source of the forest understorey (Clearwater and Gould, 1995).

The heteroblastic change characteristic of the three species is expensive, principally as a consequence of maintaining the cellular and genetic machinery required for a change in architecture. To compensate for this cost, plants must experience a predictable environmental change during ontogeny, must spend a reasonable proportion of ontogeny in each environment, and the ratio of productivity to costs of a multiple strategy must be greater than for a uniform strategy. Many features which characterise the heteroblastic change in *E. hookerianus*, *C. serratus*, and *P. crassifolius* suggest the environmental change experienced by these plants during ontogeny is from low to high light intensity. The change from narrow to broad leaves, the increase in LAI and canopy diameter, the decrease in branch angles, and the decrease in the rate of vertical extension (from sapling to adult), imply that adult plants do not function in a low light intensity environment where minimising self shading is a priority. Changes in leaf anatomy of *E. hookerianus* (Day *et al*, 1997), particularly the development of a hypodermal layer of cells which reduces the light energy entering the leaf, enhances this suggestion.

New Zealand forests

Previous sections have suggested that the conditions required for the selection of heteroblasty during evolution include a predictable change during ontogeny in light intensity from a homogeneous low energy or heterogeneous moderate energy environment to a higher light intensity environment. The current environment of New Zealand heteroblastic trees must be examined to determine whether it conforms to this hypothesis. Furthermore, features of the environment must be identified which

are different or more extreme than similar environments around the world to account for the large proportion of heteroblastic trees in New Zealand.

Wardle (1991) groups New Zealand forests into six types. Conifer/broad-leaved or mixed forests of the lower altitude are generally tall, floristically complex and two-tiered with an upper layer of predominantly podocarp species and a lower canopy of broad-leaved species. Upper montane mixed forests are shorter and floristically poorer than lower altitude forests, and the canopy often forms a dense wind-roof. Most high altitude forests and forests in drier areas are dominated by beech species. Coastal forests commonly contain similar species to low altitude mixed forests, but canopy trees are shorter and deformed by salt winds. The remaining two forest types are exotic forests and scrublands. Scrublands exist in poor sites where scrub is the tallest vegetation that can develop in that particular environment, or form an early stage of succession after disturbance.

In New Zealand forests, Wardle (1991) identifies 118 species of tree, of which Eagle (1978) presumably describes 100. These 100 species were classified as heteroblastic (if a juvenile form was pictured or described) or homoblastic, and their presence scored in each of the five non-exotic forest types described above (Table 4). Scoring was based on the following rules: if a species distribution was lowland/montane it was scored in low-altitude mixed forest only; if a species distribution was montane/sub-alpine it was scored in high-altitude mixed forest only; if a species distribution was montane only it was scored in both low and high altitude mixed forest; if a species distribution was in more than one forest type (e.g. coastal and lowland) it was scored in all forest types in which it was distributed; Wardle (1991) was used to identify those species in beech forests. Chi-squared analysis (Systat 6.0 for Windows, Chicago) indicated that the distributions

Table 4: *The distribution of heteroblastic and homoblastic New Zealand tree species in five forest types*

	Scrub	Coastal forest	Low altitude mixed forest	High altitude mixed forest	Beech forest
Number of species					
Heteroblastic species	7	1	35	10	0
Homoblastic species	10	20	54	9	5
Individual χ^2 values for each cell					
Heteroblastic species	0.17	5.54	0.46	1.63	1.80
Homoblastic species	0.09	3.01	0.25	0.89	1.01
χ^2 for each forest type	0.26	8.55	0.71	2.52	2.81

Table 5: *Comparison of environmental optima of beech, heteroblastic, and homoblastic tree species*

	Number of species	Mean annual solar radiation (MJ m^{-2} day^{-1})	Mean annual temperature (°C)	Mean July minimum temperature (°C)
Beech species	5	11.47 ± 0.31	9.43 ± 1.05	0.54 ± 1.34
Heteroblastic species	8	11.94 ± 0.25	11.04 ± 0.83	2.78 ± 1.06
Homoblastic species	20	12.07 ± 0.16	11.42 ± 0.52	3.01 ± 0.67
ANOVA		$F_{2,30} = 1.52$, NS	$F_{2,30} = 1.53$, NS	$F_{2,30} = 1.39$, NS

of homoblastic and heteroblastic trees in the five forest types was different ($2x2$ $\chi^2(4) = 14.73$, $p < 0.005$). This result was confirmed using general linear model analysis corrected for the Poisson distribution. The greatest discrepancies in species distribution was in coastal and beech forests, where heteroblastic species were under-represented, and in high altitude mixed forest where heteroblastic species were over represented (Table 4). Another analysis was conducted using data from Leathwick (1995). In a broad sense and with a limited data set, the distribution of homoblastic and heteroblastic species does not differ with respect to optimal solar radiation, mean annual temperature or mean July minimum temperature (Table 5). The 33 tree species (Leathwick, 1995) were classified as beech species, heteroblastic species and homoblastic species as in the previous analysis, and the environmental optima for each species estimated from the figures presented by Leathwick (1995) before comparison by ANOVA (Systat 6.0 for Windows, Chicago).

The analyses above may suggest that heteroblasty in New Zealand trees evolved in high altitude mixed forests. The large increase in light intensity from the understorey to the canopy of this forest type provides an obvious candidate for the environmental change responsible for the evolution of heteroblasty. This change is predictable, and occurs at a height at which many species would experience the change. The canopy of high altitude mixed forest often reaches of 6 - 10 m (Wardle, 1991), the height reached by many of New Zealand's small trees. While not exclusive to this forest type, it may be this feature, the low stature of high altitude mixed forest allowing many different species to experience both low and high light intensity environments, which is primarily responsible for the evolution of heteroblasty in so many New Zealand tree species.

Many heteroblastic trees do not grow in high altitude mixed forests (Table 4). Furthermore, none of the heteroblastic trees with a divaricate juvenile grow in these forests (Greenwood and Atkinson, 1977). Therefore conditions must exist in low altitude mixed forests which provide advantage for plasticity in juvenile habit and an 'optimistic' growth strategy. A number of possibilities exist which might provide a heterogeneous light environment in the understory.

(1) Heterogeneity in the species composition of the canopy may provide an increase in the quality and quantity of light reaching the understorey as sunflecks (Chazdon, 1988). Sunflecks provide a heterogeneous light environment. While finding that a substantial proportion of light reaching the understorey of a lowland podocarp forest is in the form of sunflecks, MacDonald and Norton (1992) conclude that the quality and quantity of sunflecks was similar to evergreen forests overseas.

(2) Both the frequency and size of forest canopy gaps may be such that many plants experience the heterogeneity in light environment that light gaps provide. Again, there is no evidence that gaps are large or form frequently in New Zealand beech forests (Stewart, Rose and Veblen, 1991) or high altitude mixed forests (Ogden *et al.*, 1991) compared with forests overseas. However, perhaps relevant here is the ability of juvenile plants to wait for a gap to form before undergoing change to adult architecture (Wardle, 1991). In New Zealand forests where temperatures are mild, drought unlikely and herbivore pressure low, juvenile plants may survive for more years than similar plants overseas and therefore may be more likely to survive until a gap forms. If this were so, then an 'optimistic' growth strategy is likely to provide advantage over a 'pessimistic' one.

(3) The New Zealand vegetation may provide a high proportion of forest margin environments. Wardle (1991) comments on the patchiness of forests in a number of different locations, patches surrounded by rocky areas in mountain and volcanic areas, patches of high altitude forest where it grades into beech forest, low altitude forest, scrublands or grasslands.

Scrublands and forest margins provide a particularly heterogeneous light environment and provide an ideal light environment for plants with conditional and multiple growth strategies.

Hypothesis for the evolution of the divaricate habit

There are many vegetative features which characterise the divaricate habit. Recently, two studies have elucidated features which differentiate divaricates from other plant forms (Atkinson, 1992; Kelly, 1995), and may illustrate the functional advantage of the divaricate habit. Both papers conclude that climate is likely to have shaped phenotypic selection. The defining characteristics of divaricates are narrow leaves, a small leaf width/internode length ratio, large branch angles and high branch density (Atkinson, 1992; Kelly, 1995). Effectively these features position small leaves randomly within a dense branch canopy with large distances between leaves. As Kelly (1995) points out, this architecture closely resembles the optimal multilayer leaf distribution described by Horn (1971).

Wardle (1991) argues that the lax filiramulate (low branch density divaricate) form, characteristic of forest-grown divaricate plants, evolved from larger-leaved relatives in forest conditions. The denser divaricate form represents phenotypic adaptation to extreme conditions - of which Wardle (1991) suggests grazing and wind might be the most important - following movement from the forest to more open conditions. Evolution of the divaricate habit might have progressed thus:

(1) Forest trees evolved heteroblastic vegetative development (ie: evolved a multiple growth strategy), perhaps in response to the change in light intensity above and below the canopy of high altitude mixed forests. That adult plants develop a juvenile phase rather than juvenile developing an adult phase is implied by recent genetic evidence suggesting adult forms are ancestral and that juveniles arise, in part, through a repression of the adult developmental programme (Poethig, 1990; Bai and Sung, 1995; Weigel and Nilsson, 1995).

(2) Species may have dispersed to lowland mixed forests where a heterogeneous understorey light environment provided advantage to juveniles with plasticity, a lax divaricate habit (particularly wide branch angles and low LAI), and 'optimistic' growth strategy.

(3) As plants moved to more open conditions a number of changes may have occurred: evolution favoured those plants which could flower at a lower height, ie, in the juvenile or adolescent state (adolescent *E. hookerianus* has this ability; Philipson, 1964; Day *et. al.*, *in press*); the adult state was lost through genetic mutation when it became energetically disadvantageous (ie: a multiple strategy provides no advantage in a homogeneous light environment, and height might prove disadvantageous in open conditions); the lax divaricate form evolved a denser canopy in response to harsh climatic conditions (Wardle, 1991).

Evidence for this series of events is circumstantial at best. Heteroblastic trees exist in forests and forest margins but not in open conditions. Plants with a divaricate habit and trees with a juvenile divaricate habit exist side by side. Species with a lax divaricate form in forest conditions develop a dense branch canopy in open conditions. Confirmation of the hypothesis will require extensive genetic and physiological experimentation. The type of experiments that might prove this hypothesis include: following the movement of heteroblastic trees and divaricate plants between different vegetation systems over phylogeny using pollen deposits; comparing the functional advantages of the lax divaricate and divaricate habit in lowland forest, forest margin and open conditions; identifying anatomical or physiological traits of divaricate plants which suggest a forest origin; and investigating the cytology of related divaricate shrubs and heteroblastic trees in an attempt to identify a consistent genetic mutation which may have led to the loss of the adult vegetative phase.

The movement of plants with divaricate form from forest to open conditions is likely to have succeeded because plants had the plasticity to grow successfully in a different environment and adapt to new stresses. The move from open to forest conditions is unlikely because the plasticity necessary to accomplish this move would not have developed in the relatively homogeneous open environment. Furthermore, thin stems are unlikely to have evolved in open conditions, they only provide advantage to the plant if energy efficiency is important and if potential sources of shearing forces (e.g. wind) are low.

The divaricate form of some forest understorey plants would adapt well to open conditions. The multilayered leaf distribution is suitable for high light intensities, and the small leaves would reduce water loss in the low-humidity environment. Other

features could have easily evolved. Plants in open conditions are likely to require less plasticity because the light environment is more homogeneous. The increase in canopy density may create a micro-climate within the canopy which may provide protection against frost, wind, or a decrease in humidity (Kelly and Ogle, 1990; McGlone and Clarkson, 1993; Kelly, 1995). Associated with this we might expect differences in architecture within the canopy compared to the canopy edge (characteristic of divaricate shrubs growing in open areas; Greenwood and Atkinson, 1977). Furthermore, the interlacing of branches may provide advantage in windy conditions. The thin stems and open canopy of forest divaricates would be highly susceptible to wind, whereas the many points of contact between stems resulting from the interlacing branches may provide support for the plant much as scaffolding provides support.

Conclusions

The light capture efficiency of monolayer and multilayer leaf distributions (Horn, 1971), the difference between 'pessimistic' and 'optimistic' growth strategies (Takahashi, 1996), theories for the evolution of phenotypic plasticity (Bradshaw, 1965; Lloyd, 1984; Schlichting, 1986; Scheiner, 1993; Padilla and Adolph, 1996), and an examination of the light environment in New Zealand's mixed forests provide the basis for this discussion of the evolution of heteroblastic development in some New Zealand trees. It is suggested that the multilayered leaf distribution, large phenotypic plasticity and the narrow cylindrical canopy shape that characterise sapling *E. hookerianus* and *C. serratus* provided advantage to these species during evolution. Despite an expensive ontogenetic strategy, these plant canopy properties would maximise light capture for low expenditure on support structures in a moderately high intensity, heterogeneous light environment provided by sun flecks, forest canopy gaps, forest margins, or shrublands. Juvenile *P. crassifolius* differ from the above species in the extent of phenotypic plasticity displayed, however the multilayered leaf distribution, narrow cylindrical canopy shape, and low provision for support structures remains. Expenditure provides long-lived, expensive leaves rather than branches. Clearwater and Gould (1995) suggest these plants have adapted to a homogeneous, low intensity light environment.

The evolution of heteroblasty requires: phenotypic plasticity to provide the necessary genetic basis for the development of a multiple

growth strategy; a predictable change in environmental conditions during ontogeny, for example the change in light intensity from the understorey to the canopy of high altitude conifer/ broad-leaved forest; and growth for a reasonable portion of ontogeny in each environment. These features ensure that the benefits of a change in architecture during ontogeny exceed the costs.

A hypothesis is proposed for evolution of the divaricate habit whereby forest light conditions influenced the evolution of heteroblastic trees with a lax divaricate juvenile form, and the move to more open conditions encouraged the ability to flower while in the juvenile state, the loss of the adult form, and an increase in plant canopy density in response to harsh environmental conditions.

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