

## An introduction to plant demography with special reference to New Zealand trees

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**Abstract** An outline of the scope and origins of plant demography emphasises the link between numerical and evolutionary approaches. The rules governing thinning in monocultures and some general features of plant competition in mixtures are described. Plant demography can be applied at several levels — that of the genetic individuals or that of the modular components of which plants are usually composed. This dual population structure puts a new emphasis on the morphological changes occurring in competing mixtures.

Various approaches to the definition of strategies are discussed. Plants with short life cycles and abundant production of small seeds are contrasted with long-lived species producing fewer larger seeds. This 'r-K' continuum is used as a broad framework, although Grime's (1979) two dimensional strategy model may be more realistic.

The concept of the 'regeneration gap' has been a persistent theme in forest ecology in New Zealand, and its explanation has generally been presumed to lie in past climatic change. However, population age and size frequency distributions reflect demographic processes, which must be properly explored before extrinsic causes can be ascribed to particular structures. The steady state climax theory is an inappropriate concept on which to build an understanding of the demography of canopy trees in New Zealand. A kinetic model, in which disturbance is accepted as a selective force to which different tree species have become differentially adapted, accepts regeneration gaps localised in space and time as demographic phenomena. A model of cohort structure in kauri is used to illustrate the dangers inherent in drawing conclusions about population 'status' from a small sample of diameters and approximate ages. The difficulties of applying transition matrix models emphasises our lack of basic demographic information for most New Zealand trees. The errors inherent in determining tree population age structures are addressed.

The regeneration strategies of the beeches (*Nothofagus* spp.) and the podocarps (Podocarpaceae) are outlined primarily in relation to seed size and seed production periodicity. The beeches conform well to the predator satiation theory of mast seeding, but the podocarps (and other bird-dispersed trees) present additional problems. More information on the interactions between tree fruiting behaviour and the avifauna is needed for satisfactory evolutionary accounts.

The existence of 'advance growth' seedling populations in New Zealand forests is well known, but there is little information on dormant buried seed banks. Some information about the sizes of seed banks in New Zealand forests is provided, and it is concluded that they are probably of similar magnitude to those in other temperate forests, and warrant more rigorous study.

**Keywords** *Agathis*; cohort; demography; disturbance; forest dynamics; mast seeding; *Nothofagus*; *Podocarpus*; regeneration gap; seed bank; strategy; transition matrices; tree ages; thinning

### INTRODUCTION

This paper presents, on the one hand, an introductory treatment of plant demography, and on the other, a specific discussion of several areas of forest dynamics which are pertinent to New Zealand trees. This wide scope has required brief treatment of many topics and whole areas of the general subject, such as life tables and survivorship curves, have been omitted. Similarly left out are some topics of relevance to demographic studies on New Zealand trees, in particular the role of introduced mammals. I have chosen rather to comment on specific problems, and to present some conceptual models and speculations which I believe to be worth pursuing.

Although quantitative description is a precursor to most studies, my intention here is to introduce a way of approaching plant ecology in New Zealand which will look beyond description. In the last two decades formative concepts of plant ecology such as 'succession' and 'climax' have been subject to re-evaluation, and new organising concepts ('models') have been introduced. Emphasis has

shifted from community composition to the population dynamics of the constituent species, and to evolutionary explanations. This approach asks new questions and requires data which cannot be gathered on a single visit to a study area, no matter how thoroughly it is quantified at that time. Data on growth rates, mortality, longevity, and seed production require long-term studies. Sadly, current research funding procedures often inhibit protracted research, but valuable work on some aspects (e.g., seed banks and seedling survivorship) can be done on a shorter term.

The New Zealand literature contains enough information for reviews of some topics. John Wardle (1984) has collated demographic data for the beeches, and preliminary reviews of maximum recorded longevities and stand basal-areas have been attempted (G. M. Wardle 1984). However, in general, the literature contains only scattered and anecdotal references to demographic parameters. I am conscious of adding to that anecdotal literature in parts of this essay, but I do so in the hope of stimulating more rigorous approaches to the subject.

The first parts of the paper cover the origins of the subject, emphasising that its few quantitative models and generalisations have arisen largely from applied research on agricultural systems. It is my belief that when these generalisations are more widely appreciated they will be found to have value in the study of complex vegetation. Other concepts and some analytical techniques have been borrowed from zoology, and the concept of modular structure — individual plants as metapopulations of sub-units with demographic properties — derives from classical plant morphology. A recent evolutionary emphasis has focussed on seed production and survival at different stages during the life cycle, leading to varied attempts to define life cycle strategies.

The latter part of the paper deals selectively with aspects of the demography of New Zealand forests. Old arguments about regeneration are briefly reviewed in the light of modern approaches, and the role of disturbance is emphasised. Mast seeding — so widespread in the New Zealand flora — is discussed, and some new information on seed banks presented. Quantitative models (transition matrices) of population growth and community change require (among other things) estimates of individual longevities. Age structure is a fundamental demographic characteristic, and the errors associated with obtaining it for long-lived trees warrant detailed consideration.

Finally, I present a model of cohort structure which I believe to be widely applicable to New Zealand trees. Disturbance sets in train sequences of birth and mortality which may take several gen-

erations — a thousand years — to become obliterated. Regeneration strategies of several canopy dominants are discussed with this model in mind, using the simplifying r-K terminology of MacArthur & Wilson (1967).

## THE ORIGIN AND SCOPE OF PLANT DEMOGRAPHY

Demography is the science dealing with populations; its raw materials are estimates of numbers (population density), age frequency distributions, and schedules of birth rates and death rates. Plant demography emphasises the numeric and evolutionary approach to natural plant populations, especially in the comparative study of life cycles.

The potential to increase in numbers is inherent in all organisms, and is especially noticeable in plants, which often have prodigious seed outputs. The contrast between the *potential* for population increase, and the *observed* stability in many populations was one of the key observations leading Charles Darwin to the theory of evolution by natural selection:

“In a state of nature almost every full-grown plant annually produces seed .... hence we may confidently assert that all plants .... are tending to increase at a geometrical ratio — that all would rapidly stock every station in which they could exist — and that this geometrical tendency to increase must be checked by destruction at some period of life” (Darwin 1859).

Although John Harper traces the origins of the science of plant demography to the work of Darwin (Harper 1967; see also Allan 1977) there is no doubt that he himself established the discipline a century later. Harper's (1977) book is a work of Darwinian magnitude which comprehensively surveys the literature and defines the scope of the subject. The central theme relates to the numerical properties of plant populations: seed production, dormancy and germination; seedling growth and survival; reproductive schedules and life expectancies; life tables and population flux models. Except in man-made situations, plants rarely grow as monospecific populations, so that in mixed communities the interactions between species — the effects of neighbours of a different kind — must be considered. Moreover, numerical properties such as seed set, dispersal, and seedling survival are clearly influenced by pollinators, pathogens, predators, and herbivores, so that in considering the causes of particular mortality or dispersal patterns (for example), we encounter the whole biotic complex ‘from the plants’ point of view’. Thus, the rather grimly actuarial core of the subject has widened and a more

holistic approach has given renewed impetus to the comparative study of plant life cycles, viewed as 'strategies' ensuring the survival and reproduction of species populations in mixed communities (Grime 1979). Several authoritative reviews of parts of the subject (Solbrig 1980) and an introductory text (Silvertown 1982), are available.

## CONCEPTS DERIVED FROM THE EXPERIMENTAL STUDY OF HERBACEOUS SPECIES

### Thinning in monocultures

Much work of relevance to forest demography has been undertaken on agricultural crops with applied ends in view. From such studies some well documented generalisations have arisen, and can be briefly summarised as follows (White 1980):

- (1) The asymptotic relationship between density and yield implies that over a wide range of planting densities there is a convergence in time towards a similar total biomass per unit area (this may be conceived as the 'carrying capacity' for that particular crop).
- (2) This arises because plants have indeterminate 'modular' growth — at low density a population is, on average, composed of fewer larger individuals than it would be at a higher density.
- (3) The partitioning of the biomass between individuals is not equal, some plants capture more resources than others so that a 'competitive hierarchy' develops.
- (4) The size (weight) frequency distributions which develop in such situations are often log-normal or highly skewed (Ogden 1970).
- (5) At very high densities, and/or late in population development, some of the suppressed fraction of the population may die.
- (6) This time and density-dependent mortality is referred to as 'self thinning' and the rule governing the relationship between surviving plant density and population biomass is defined by:

$$w = kd^{-3/2}$$

where  $w$  = mean plant weight,  $d$  is density and  $k$  is a constant.

More detailed treatments of (6) above are given by Harper (1977), White (1980), and Silvertown (1980). The observation that as a population increases in biomass the smaller individuals succumb and the released resources are captured by the dominants, may not be very surprising, but the ubiquity of the simple mathematical relationship is. It has been shown to hold for plant populations ranging from annual herbs to forest trees. It seems that the thinning rule (or '3/2 power law' as Yoda et al. (1963) referred to it) is one of the general

principles of plant population biology (White 1980). I anticipate that it will be found to have equal generality in understanding the development of mixed stands of natural forest vegetation, where highly skewed size frequency distributions appear to be common.

### Competition in mixtures

The interactions between herbaceous species in mixtures have been studied extensively, especially by agronomists concerned with the effects of weeds on crop yields. The most elegant experiments are those in which the total density has been held constant, and the proportions of a pair of species varied ('replacement series' experiments; Harper 1977, p. 225). In most such experiments the mixtures are not more productive than pure stands of their highest yielding component (Trenbath 1974). This result is at first sight rather surprising; one might expect that mixtures of plants with different seasonal patterns of development (phenologies) or with different shade tolerance (allowing stratification) would be more productive on an annual basis than pure stands of either, but in only a few cases has this been experimentally demonstrated.

The importance of competition between species in determining their local success and broad distribution patterns has been generally acknowledged for many decades (see, for example, Darwin 1859; Chapter III), and is embodied in the concepts of 'realised' and 'fundamental' niches (Hutchinson 1965). However, the experimental, analytic, and numeric approach to plant populations, as monocultures or in mixtures, is relatively recent and as yet few studies on forest vegetation in New Zealand have taken cognisance of the demographic generalisations derived from simpler experimental populations.

### Modular structure

The analogy between a bud and a seed is surprisingly close. A plant (such as a tree) is composed of a family of interconnected buds, each one of which may be capable of reproducing the form of the whole. The plant grows by the germination of buds adding more of the basic modular units of which it is composed (shoot systems, leaf clusters, or even individual leaves, for example). If the interconnecting structures degenerate — as in many rhizomatous species — we speak of 'vegetative reproduction', but (except perhaps where specialised dispersal structures are involved) the process differs in no fundamental way from the normal growth process. Thus individual plants are composed of modular units which themselves have demographic properties; interactions between

plants, or between branches within a plant modify the balance between birth and death of modules, influencing the size and morphology of the genetic individual. This peculiarly botanical concept of demography at two levels, that of the subunits of which plants are composed ('modules' or 'ramets'), and that of the distinct genetic individuals ('genets'), has been stressed by White (1979, 1980). It is congruent with the architectural approach to plant structure adopted by Halle et al. (1978) and with the more physiological 'pipe model theory of plant growth' proposed by Shinozaki et al. (1964).

Although it is the survivorship of genets which determines evolutionary fitness, for many purposes the demography of the ramets may be more meaningful than that of the genets. For example, the number of flowering spurs (modules) in an orchard will predict fruit yield much more accurately than will the number of trees. Likewise it is normal to use the tiller as the basic unit in grassland communities because it is usually impossible to determine the limits of genetic individuals.

## THE CONCEPT OF STRATEGY

The best known framework in which to discuss life-cycle strategies is that proposed by MacArthur & Wilson (1967). Their conceptual model emphasised the numerical aspects of population growth and stability, distinguishing (as extremes of a continuum) two contrasting types of life history: those of organisms adapted for dispersal, colonisation and rapid population growth, and those of organisms adapted for persistence and reproduction in stable populations. The terms to describe these two types of population growth they took from the logistic model of population growth:

$$\frac{dn}{dt} = \frac{rN(K-N)}{K}$$

in which  $r$  is the instantaneous rate of population growth (unlimited by density) and  $K$  is the carrying capacity.  $N$  is the population size at any given time ( $t$ ). Thus  $r$ -strategists are species capable of rapid reproduction in open environments — for example, weeds with short adult life-cycles producing abundant small well-dispersed seeds.  $K$ -strategists are long-lived species of stable communities with fewer larger seeds producing more competitive shade-tolerant seedlings capable of replacing the adults *in situ* when the latter die. There are several valid objections to the idea that selection favours a suite of characters which together determine either  $r$  or  $K$ , but the terminology is a useful shorthand and draws attention to the idea that some plants are adapted for dispersal (in space or time), others for

persistence, and no plants are successfully adapted for both extremes of environmental stability (Silvertown 1980).

Detailed studies of the  $r$ - $K$  hypothesis in plant populations are few, but have led to insights into regional patterns of reproductive behaviour (e.g., McNaughton's (1975) work on *Typha*) and into the detailed genotypic composition of populations in heterogeneous environments (*Taraxacum*; Solbrig & Simpson 1974, 1977; see also reviews by Stearns 1976, 1977). Thus, we can usefully speak of forest pioneer species such as *Leptospermum scoparium* or *Aristotelia serrata* as 'r-types' in contrast to, say, miro (*Podocarpus ferrugineus*) or tawa (*Beilschmiedia tawa*) which are more  $K$ -adapted, despite the considerable ecological differences between the species in these pairs. Likewise it may be useful to contrast related taxa: in several respects *Leptospermum scoparium* may be regarded as more  $r$ -adapted than *L. ericoides* (shorter life cycle, shorter stature, greater ecological amplitude, greater seed production(?), lesser shade tolerance); using similar criteria for 'climax' species we may say that mountain beech (*Nothofagus solandri* var. *cliffortioides*) appears to be more  $r$ -adapted than silver beech (*N. menziesii*). This theme will be expanded upon later in this paper.

Grime (1979) has advocated description of strategies in a strictly botanical framework which relies not so much on genetic attributes which determine population growth as on growth responses to environmental gradients which determine total biomass. He recognises two types of environmental gradients. The first are gradients of stress, phenomena which restrict photosynthetic production, such as shortages of light, water, or minerals. The second are gradients of disturbance, which cause destruction of plant biomass, such as the activities of herbivores or pathogens, wind-damage, frost, drought, or fire. On this basis he defines three basic strategies: competitors ( $C$ ) are plants adapted to low stress, low disturbance habitats; ruderals ( $R$ ) are adapted to low stress but high disturbance, and stress-tolerators ( $S$ ) to intense stress but low disturbance. The model is conceived as a triangle with these extreme strategies at its corners; many plants fall nearer to one corner than another, but most are intermediate to some degree. In so far as it is two dimensional and implies more attention to plant attributes (such as the ability to increase in biomass while declining in number), Grime's model may be more satisfactory than the simple  $r$ - $K$  continuum for herbaceous species. I have found it difficult to apply to trees because in forest the environmental gradients of stress (light intensity) and disturbance are linked.

A third approach to the concept of strategy relies not so much on numerical attributes of population

growth, or on defining critical environmental gradients, but rather examines the energy allocation patterns of different types of life cycles. This approach regards organisms (plants or animals) as having a certain limited amount of time or energy available for allocation during their life cycles (Cody 1966). The ways in which such resources are allocated in competition, reproduction, or the avoidance of predators for example, represent 'decisions' made by natural selection, and we can refer to the resulting temporal sequence of growth and behaviour as the life cycle strategy (Harper & Ogden 1970).

## ASPECTS OF THE DEMOGRAPHY OF NEW ZEALAND TREES

### Introduction

The most characteristic feature of the native vegetation of New Zealand is that it is forest — almost everywhere except in the high mountains, the native flora comprises woody plants with long life-cycles: the beeches normally live for two to three centuries (J. Wardle 1984), the podocarps and kauri (*Agathis australis*) for at least twice this span and sometimes much longer (Katz 1980, G. M. Wardle 1984). Large organisms which live for centuries may follow the same rules as those which are more ephemeral, but they present special difficulties of experimentation and observation.

Although there has recently been much interest in the dynamics of forest communities, especially in the role of disturbance at different scales in north American and tropical forests (Whitmore 1984, White 1979, Pickett & White *in press*), the demography of trees is still largely unknown. Work on populations of mainly annual herbaceous species, in contrast, has blossomed in both the American and the European literature (e.g., in recent issues of the *Journal of Ecology*). In a survey of the New Zealand literature I found very few papers concerned solely or largely with the presentation of plant demographic data, but many which contain information of relevance to understanding the population dynamics of particular species. Some more strictly demographic data are included in theses (e.g., Burgess 1984, Makepeace 1980, Micheau 1984) but these relate primarily to herbaceous weeds, complementing northern hemisphere studies rather than forming the basis for an indigenous plant demography. To review that literature would mean setting arbitrary limits and I have chosen rather to comment on some specific demographic problems in New Zealand, and to point out those areas where demographic data are most urgently required. With a relatively well-stud-

ied flora, and an extensive literature describing the forests, New Zealand ecologists seem well placed to take advantage of a new conceptual framework and make significant contributions to the demography of canopy dominants in mixed evergreen forests.

### Regeneration gaps and forest dynamics

Early research in forest dynamics in New Zealand was strongly influenced by the imported idea of a gradual and orderly succession to a predetermined and stable climax community (Clements 1916, Tansley 1935). Although climax forests were allowed to fluctuate in space and time as different shade-bearing or tolerant species replaced each other as a result of the vagaries of reproduction and site (Jones 1945), catastrophic perturbation was considered to be a deviation from the normal course of events. In such forests it was expected that all-aged populations would be present, with large numbers of juveniles and progressively fewer individuals in larger size classes — demographically stable populations comprising a climax community in equilibrium with regional climate.

When Cockayne (1928), Holloway (1954), and later workers entered the evergreen conifer-broadleaf forests of New Zealand they frequently found sapling and small tree densities which they regarded as inadequate for the regeneration of canopy dominants such as kahikatea (*Dacrycarpus dacrydioides*), rimu (*Dacrydium cupressinum*), cedar (*Libocedrus bidwillii*), totara (*Podocarpus totara*), matai (*P. spicatus*), and kauri (*Agathis australis*). It followed that such forests were successional to the true climax (Cockayne 1928, Robbins 1962) or that they were in disequilibrium with the climate (Holloway 1954, P. Wardle 1963a). The poor representation of the sapling and small tree classes was referred to as the 'regeneration gap'. The observation that regeneration was abundant in disturbed areas was incompatible with a strictly climatic explanation for the so-called 'regeneration gaps' (Molloy 1969), but seems to have been generally dismissed on the grounds that such sites were 'successional'.

Several recent independent studies on populations of *Libocedrus bidwillii* (Veblen & Stewart 1982, Norton 1983a, Clayton-Greene 1977) emphasise that all-aged populations should not be expected in stands which have not been disturbed recently. "The absence of young *L. bidwillii* from some old stands is a result of its regeneration ecology; given the presence of young trees nearby under the same climate but on more recently disturbed sites such stand structures cannot be attributed to a change of climate" (Veblen & Stewart 1982). Essentially identical arguments have been advanced

for kauri forests (G. M. Wardle 1984) and for the dense podocarp forests of the central North Island (literature reviewed in Morton et al. 1984).

Consequently, although I do not dismiss the possibility that past climatic changes have influenced population structures, I lay stress on localised rather than regional effects. The concept of a regeneration 'failure' is only valid if we expect regeneration to be continuous, as implied by the 'climax' or 'steady state' models. I believe these models are inappropriate as a demographic framework for New Zealand forests because of the prevalence of disturbance. On the other hand a 'mosaic regeneration' or 'kinetic' model (Whitmore 1975, Veblen et al. 1980), in which stochastic disturbance is accepted as a selective force to which different tree species have become differentially adapted, can readily accept (indeed, would predict) regeneration gaps localised in space and time.

### Disturbance

The evidence for localised, or sometimes quite widespread, forest destruction in New Zealand, on a time scale which is relevant to the demography of the canopy dominants, is much stronger than the evidence for significant climatic changes on similar time scales. Storm damage to forests has been frequently reported (e.g., Reid 1948, Elder 1965, Thomson 1936, Forster 1931, Mason 1950, Ure 1970, Clayton-Greene 1977, Shaw 1982). Drought years, resulting in widespread forest mortality have been discussed by Grant (1984) and Jane & Green (1983); fire damage by Molloy et al. (1963), Dick (1956), McQueen (1951), Esler & Astridge (1974), Clayton-Greene (1975), and McGlone (1983); vulcanism by McKelvey (1963) and Burke (1974); earthquakes, avalanches, and snow damage by Robbins (1958), J. Wardle (1984), and Mark et al. (1964) respectively, and widespread outbreaks of wood boring and leaf eating insects by Conway (1949), Rawlings (1953), Dugdale (1965), Milligan (1974), and others (reviewed by J. Wardle 1984).

Following a much more comprehensive survey of the (mainly North American) literature White (1979) concluded that disturbances of various types, sometimes correlated in occurrence and usually showing continuous gradients in magnitude, were a normal feature of most landscapes. This view has found wide acceptance (Whitmore 1984). Many disturbances have an endogenous component, in the sense that species have evolved strategies which promote, resist, or avoid disturbance at different stages of community development. These different strategies comprise the dynamics of the community. Although it has long been recognised in New Zealand that vegetation patterns, and population structures, are not precisely predictable from envi-

ronmental variables without a knowledge of stand history (e.g., Holloway 1954), only recently has adaptation to varying spatial patterns and temporal frequencies of disturbance been viewed as the prime cause of life cycle phenomena such as longevity, seed dispersal, and shade tolerance.

### Even-aged stands

Relatively even-aged stands, associated with regeneration gaps, are well known in many widespread forest communities in New Zealand (e.g., *Leptospermum* spp. Esler & Astridge 1974; *Nothofagus* spp. J. Wardle 1984). In these stands *Leptospermum* or occasionally *Nothofagus* may act as 'nurse crops' for the establishment of conifers. A narrow age range in a mature conifer population may consequently imply a seral origin.

On a scale of one or a few hectares, many, possibly most, canopy dominants in New Zealand forest can occur in more or less even-aged stands with regeneration gaps: e.g., rimu (*Dacrydium cupressinum*) and various podocarps (Herbert 1980, Katz 1980); *Libocedrus* (Clayton-Greene 1977, Veblen & Stewart 1982, Norton 1983b); kauri (Mirams 1957); all the beech (*Nothofagus*) species (J. Wardle 1984); kamahi (*Weinmannia racemosa*) and rata (*Metrosideros robusta*) (Stewart & Veblen 1982). Most of these species also have seedlings which are relatively 'light demanding' either for establishment (kamahi) or for recruitment into larger size classes (the beeches). In some respects the regeneration behaviour of kauri, rimu, and the beeches is similar to that of kanuka (*Leptospermum ericoides*). I suggest that their populations come and go at different places on the landscape in a mosaic fashion, with the spatial and temporal scale of that mosaic different for different species. Our intrinsic difficulty in grasping patterns on this time scale has been exacerbated by the greatly reduced area of the lowland forests. Even supposedly shade tolerant climax species, such as tawa (*Beilschmiedia tawa*), may grow in stands with much more restricted age ranges than would be expected if regeneration and mortality were continuous; highly skewed size frequency distributions are associated with approximately normal age frequency distributions (C. J. West pers. comm.).

The concept of 'relatively even-aged' deserves further comment because the size and density relationships of even-aged populations of both herbs and trees have been shown to follow well-defined rules, as reviewed earlier. In natural situations 'even-aged' has meaning only in the context of the 'normally attainable age', best regarded as the age at which those few survivors which reach dominance in the stand tend to die (Harper & White 1974). Relatively even-aged refers to the situation

where a site is 'fully stocked' with seedlings over a time period which is considerably less than the normally attainable age. Thus, the normally attainable age for mountain beech (*Nothofagus solandri*) is probably about 250 years, although the majority die earlier and maximum longevity is in excess of 300 years (J. Wardle 1984). Stands often develop from suppressed seedlings following damage to canopy trees by wind, snow, drought, insect and fungal attack, etc., and the age-range of the subsequent population will reflect the age-range of the 'advance growth' seedlings, commonly 20 or 30 years (J. Wardle 1970a; cf. Kirkland 1961). In the case of kauri normal age is probably six or seven centuries, although some trees live for twice this span (Ecroyd 1982, Ahmed 1984). Seedlings of kauri become established in pioneer *Leptospermum* stands arising after fire, but the establishment period may be quite restricted (< 60 years; Mirams 1957, Lloyd 1980). Later recruits commence life at a competitive disadvantage and are likely to succumb to competition before the original cohort reaches maturity. These examples suggest that a stand can be regarded as even-aged or a cohort defined, if most of the individuals in it fall within an age range of not much more than ten percent of the normally attainable age. While strict definition of these terms is not feasible, the above discussion emphasises the need for accurate age frequency distributions and better data on normally attainable (and maximum) ages.

### Mast seeding

Periodic massive seeding may be a strategy for keeping safe-sites fully stocked with long-lived seedlings and may also provide enhanced opportunity for long distance dispersal and colonisation of sites which are spatially and temporally restricted (see p. 767 for example involving red beech). The more usual explanation for irregular synchronous seed production is that it is an adaptation to satiate seed predators with more seeds than they can consume in mast years. The intervening years of starvation prevent the predator populations building up (Silvertown 1980). Wardle (1984) has summarised data on mast-seeding in the beech species, showing that 'full' mast years are often widespread within species. The evidence for synchronous masting between species is less clear, but there is some agreement. In further conformity with the predator satiation model all the species show greatly reduced proportions of unsound seeds (ovule mortality) in mast years (J. Wardle 1984, table 9.2). Masting appears to be 'triggered' by a hot dry summer in the preceding year. While this may be the original 'cause' of the mast seeding habit, as pointed

out by Silvertown (1980), if, as a result, predator satiation occurs, selection will operate to enhance the synchrony and magnitude of the effect by acting against those individuals which seed out of season.

Erratic seed production is generally regarded as characteristic of trees with seeds which lack specialised dispersal agents (Silvertown 1980). However, in New Zealand masting is well documented for some long-lived herbs, and for some bird-dispersed tree species. Connor (1966) has described periodic flowering in snow tussock (*Chionochloa rigida*) and shown that this is also initiated by prior hot summers, and is generally in synchrony with beech. Synchronous masting has also been documented for other large sub-alpine herbs including other *Chionochloa* spp., *Aciphylla* spp., *Phormium* spp., and *Celmisia* spp., (Mark 1968, Mark 1970).

We might expect the masting habit to be absent from species which produce animal-dispersed fruit with protected seeds, since satiation of the dispersal agents would be a poor strategy. However, most of the podocarps have bird-dispersed seeds, and several members of the family show pronounced masting (Fig. 1). In the case of rimu in Westland, masting is synchronous and occurs usually at about 5 year intervals, though there is a tendency for good years to come in pairs (James & Franklin 1978). The Westland seed production sequence is in synchrony with that at Pureora in the North Island over the period for which records are available (1961–67;  $r = 0.91$ ;  $P < 0.01$ ). Widespread synchrony is a feature of the predator satiation model, but climatic explanations are also possible. Beveridge (1964) notes that a large percentage (80%) of the annual rimu seed crop is destroyed in the crowns and suggests that weta (*Hemideina* sp.) may be responsible. Franklin (1968) notes that more seeds have fleshy receptacles in mast years, suggesting that bird dispersal will be enhanced in such years when the female trees may be brightly coloured with ripe fruits. Thus we can envisage a situation in which masting confers advantages in pre-dispersal survival, and the risk of dispersal-agent satiation is off-set against the advantage of the tree's enhanced attractiveness to such agents.

The case of tawa (*Beilschmiedia tawa*) is particularly instructive since this large fleshy drupe is dispersed almost solely by New Zealand pigeons (*Hemiphaga novaeseelandiae*) and its germination success is considerably improved once its fleshy mesocarp has been removed by these birds (cf. Myers 1984). Tawa seeds (the embryo and cotyledons) are attacked by the lepidopteran larva *Cryptaspasma querula*, with infestations reaching high levels in poor fruit years, but falling in years of abundant fruit production suggesting predator

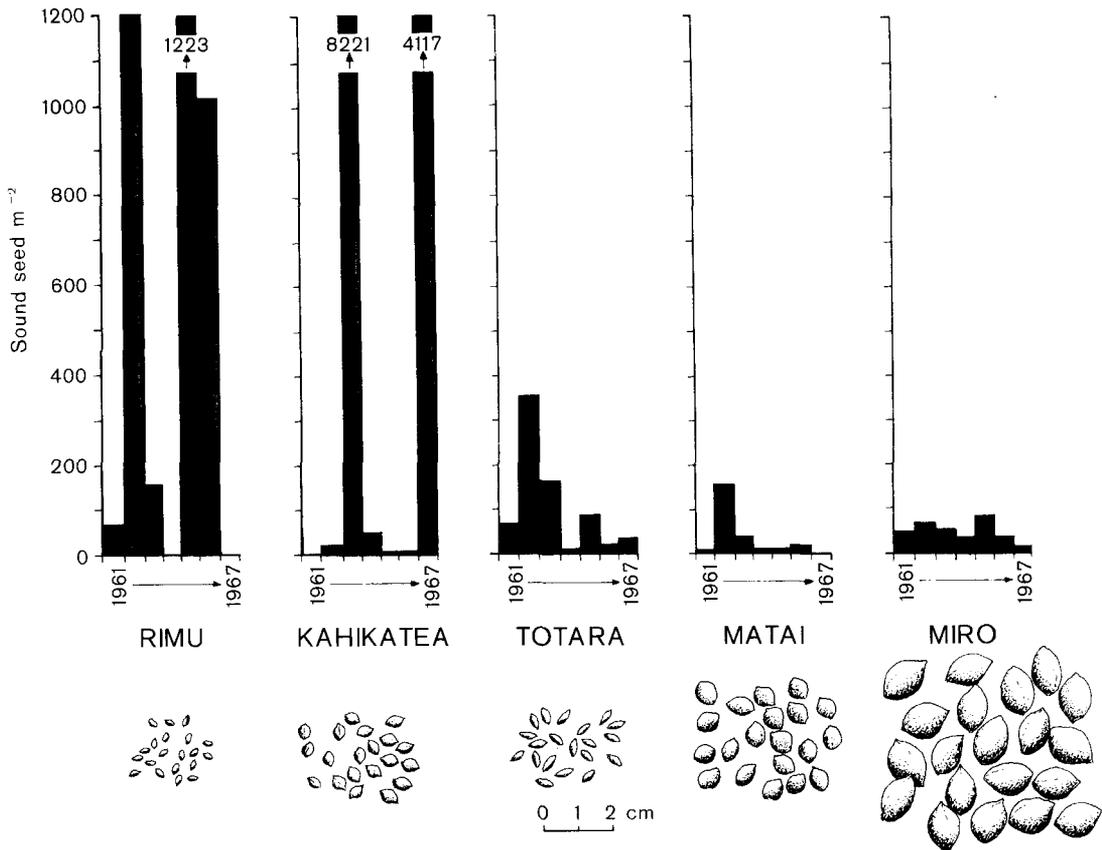


Fig. 1 Periodicity of seed production and seed size in the five most common canopy podocarps. Redrawn from data in Beveridge (1973) and Preest (1963).

satiation (C. J. West, pers. comm.). The most notable feature of tawa fruit production, however, is its spatial variability between locations within any forest region, even in 'good' years. This suggests that the spatial scale of masting synchrony required to satiate the local *Cryptaspasma* population may be quite small, while some asynchrony between locations will prevent pigeons becoming satiated and keep the dispersal system working.

These speculations are based on inadequate data, and I offer them mainly to stress the many fascinating co-evolutionary interactions between seed predators, fruit eating birds, trees, and shrubs in the primaevial forests. Sadly, these subjects are now difficult to study; both tree and native bird populations have been much reduced, and the picture has been further confused by introduced birds and mammals which destroy large proportions of the seed crops of some species (Beveridge 1964). However, much basic information about seed production schedules remains to be gathered and is

essential if the demography of the tree species populations comprising the spatio-temporal mosaic of the remaining lowland forests is to be comprehensively understood.

#### Seed banks

One important aspect of the forest demography which is easily studied is the size and composition of the buried seed bank. Although the ecological significance of 'advance growth' seedling populations has long been recognised, surprisingly little has been published on seed banks in New Zealand, perhaps because under laboratory conditions many native tree species do not have long-lived seeds. While this may be generally true for small experimental samples, it does not follow that some seeds do not remain viable in natural soils for long periods. Beveridge (1964), Herbert (1976), and Bathgate (1981) all imply that miro, matai, and rimu seeds can remain viable under forest litter for

at least two years. Bathgate (1981) recorded the equivalent of 100 viable seeds per m<sup>2</sup> of rimu at a depth of 6–12 cm in a soil column taken from beneath a 55 year old rimu stand in terrace forest. Herbert (1976) collected forest duff from seven sites in Pureora and Tihoi state forests, and from a total of less than half a cubic metre of duff raised about 20 000 individual seedlings comprising 45 species of indigenous plants. On a per metre squared basis he obtained from 50 to 1000 native tree seedlings in different areas. High seed numbers were found in the forest/shrub ecotone where shrub hardwoods such as *Coprosma* spp., *Pseudopanax* spp., and *Carpodetus serratus* were common. Herbert also records that c. 100 seedlings per m<sup>2</sup> germinated subsequently from the areas cleared of duff, suggesting a considerable residue of viable seeds in the surface soils. In student class studies in the Kauaeranga valley, Coromandel, we have consistently recorded a larger seed bank in the surface 3 cm of the soil ('A' horizon) than in the loose litter. Our seed-bank estimates, from a variety of shrubland and forest communities, have been in the range 500–3000 viable native shrub and tree seeds per m<sup>2</sup>. In soil samples collected from other forest areas (Swanson, near Auckland; and Waipoua, Pureora, and Whirinaki State Forests) over a five year period we have recorded total germinable seed values in the range 150–600 per m<sup>2</sup>. Critical discussion of these values must await their formal publication, but I mention them to illustrate that New Zealand forests do have seed-banks, and that these are of a similar magnitude to those found in temperate forest communities elsewhere in the world (Harper 1977). There is here a whole field of plant ecology almost untouched in New Zealand.

Two features of our seed-bank studies have impressed me. The first is the great spatial variability in viable seed numbers in the soil — our mean estimates for any area (derived from separate small samples, usually 10 × 10 × 10 cm) have huge standard errors. The second is the consistency with which certain species occur. For example 'gap colonisers' with bird-dispersed seeds, such as *Coprosma australis*, *C. robusta*, *Aristotelia serrata*, *Geniostoma ligustrifolium*, *Carpodetus serratus*, and *Fuchsia excorticata* seem to maintain small seed banks (10–100 per m<sup>2</sup>) throughout a wide range of forest communities. *Fuchsia* especially seems likely to have long-lived seeds as its seedlings appear in soil samples from sites far removed from living parent trees and in areas where the species has been destroyed as a mature tree by browsing animals. These 'forest nomads' contrast with early successional species, characteristic of larger scale disturbance, and with small wind dispersed seeds, such as the *Leptospermum* spp., and *Weinmannia race-*

*mosa* which have larger (?temporary) seed banks close to mature stands, but do not maintain a ubiquitous presence. Manuka (*Leptospermum scoparium*) differs from kanuka (*L. ericoides*) in maintaining a colossal seed bank in its old capsules on the trees. We have estimated this to be up to 300 000 viable seed per m<sup>2</sup> in mature stands where the soil seed bank (of manuka) was a mere 100 seeds per m<sup>2</sup>. Kanuka in contrast does not retain its capsules, and we have found soil seed banks ranging from 166 to 2867 per m<sup>2</sup> in a three year study at Swanson.

Detailed demographic work on seed quantity, periodicity, and dispersal in space and time is badly needed for almost all our native trees and shrubs. With the exception of the beeches most of the data available are scattered through the literature and largely anecdotal.

## SOME METHODOLOGICAL AND RELATED CONSIDERATIONS

### The determination of tree ages

The problems of determining the age structure of a forest stand fall into two categories: (1) the problems of aging a single tree; and, (2) those of predicting the age-structure of a population from size or diameter data.

Tree ages are usually determined from ring counts of increment cores. It is usually assumed that the rings are annual or that false (intra-annual) or missing rings are sufficiently infrequent as to constitute an acceptably small error. These assumptions appear reasonable, at least in montane and sub-alpine forests where seasonal differences in climate are very pronounced (P. Wardle 1963b, Norton 1984). However, an accurate annual ring-count from a core or cross-section depends upon careful surface preparation and cross-dating between several trees (Dunwiddie 1979; Ogden 1980; Norton 1983b, c). Even if the annual rings on the core have been accurately counted, in order to obtain the age of the tree, additions must be made for any 'missing radius' when the core does not bisect the pith, and for the variable time taken (by the seedling) to reach coring height. Various techniques and assumptions are possible in the calculation of these additions; but most studies do not mention them. The errors involved may be considerable, as discussed for *Libocedrus* by Dunwiddie (1979). Even when ages are based on cross-sections it is difficult to get absolute accuracy.

### The relationship between size and age

The age of a tree derived from an increment core must be regarded simply as an estimate. Moreover,

diameter measurement is also subject to error, especially in the case of large trees with irregular moss-covered boles. In consequence, there is an unavoidable error factor built into the age:diameter model — age:diameter scatter diagrams contain more error variance than their formal statistics suggest. However, even neglecting this underlying worry, the development of competitive hierarchies in relatively even-aged stands means that in many cases age and diameter are not closely related. For example: rimu (Herbert 1980, June 1982); *Libocedrus bidwillii* (Clayton-Greene 1977, Norton 1983a); kauri (Lloyd 1960, Ogden 1983a); tawa (Ogden & West 1981). Even where this relationship is statistically significant — as it usually is if both large and small trees are included in the sample — it may be misleading as a predictor of age from diameter due to the wide age variance included in any diameter class. It is quite conceivable that a small sample of inaccurately aged trees from widely separated size classes would provide a highly significant age:diameter relationship but obscure a multiple cohort structure derived from several distinct waves of regeneration. Such a structure would not necessarily be revealed in a size frequency distribution; if each cohort developed the log-normal size frequency characteristic of a monoculture and thinned through time, then a composite size frequency distribution would be heavily weighted by the most recent cohort, and the older modes immersed (Fig. 2). As Harper (1977) has stressed "It is wholly unrealistic and very dangerous to assume any relationship between the size of trees and their age, other than the vague principle that the largest trees in a canopy are likely to be old".

### Size frequency distributions

Although past mortality may be difficult to deduce, some information about the history of a stand is contained in an age frequency-distribution. As discussed earlier, the difficulty lies in obtaining such a distribution without relying on untenable assumptions and inadequate samples. Trunk diameter frequency distributions are more readily obtained and predictions of the future of tree populations (and accounts of stand history) have generally relied upon their interpretation (Daubenmire 1968). Because reproductive behaviour in perennial plants appears to be more specific to size than age, it may be that such predictions are best based on size rather than age, but a reliable predictive model must incorporate also size specific growth, fecundity, and mortality rates. To estimate these requires observations on marked individuals over many years.

Skewed size frequency distributions, with a predominance of small stems and progressively fewer

in larger classes, can represent stable self-replicating 'climax' populations (size = age), or even-aged thinning hierarchies (size  $\neq$  age). Obtaining age estimates from a substantial number of trees should separate these extreme possibilities, but could not eliminate the potential confusion between the first (stable) situation and a population migrating into an area. In both cases young trees would be numerous and old trees rare; evidence of past mortality patterns would be needed to determine the demographic status of the stands. For example, in the case of mangroves (*Avicennia marina*) on mud flats at Ohiwa harbour, size frequency distributions and Leslie matrix analyses strongly suggested an invasive status, but early aerial photographs provided the supporting evidence (Burns & Ogden 1985).

A further difficulty arises because small scale disturbance may mean that populations may sometimes comprise copses of even-age scattered in a multiple-aged matrix, determined by safe-site frequency and dispersal characteristics (Horn 1981). The size frequency distribution thus becomes site/age specific and dependent upon the relative scales of the vegetation mosaic and the sampling unit. Composite size frequencies based on several stands often appear much more 'stable' (log-normal) than do those of individual stands (Ogden 1971, Wardle 1984). Selective small scale sampling appears to have emphasised the regeneration-gap in the New Zealand gymnosperms (e.g., P. Wardle 1963a).

### Transition matrices

The application of transition matrix models in forest ecology has been described by Enright & Ogden (1979). The Leslie matrix model (Leslie 1945, Usher 1973) requires standard life-table data derived from the survivorship, growth, and fecundity of marked individuals. It can be applied to age- or size-class data (Werner & Caswell 1977). In its simplest form it assumes exponential population growth and stable transition probabilities, but nevertheless it provides a useful tool for comparing different populations and assessing the vulnerability of different stages to perturbation (Bierzychudek 1982).

In the multi-species model, the rows and columns of the transition matrix refer not to the different stages in a population, but to the different species in a community (Horn 1975). This matrix defines the probability of any species being replaced by an individual of its own kind or by another species. Horn's model relies upon a tree by tree replacement process, so that there is no change in the total population size of all species, only the proportions may vary. It is analagous to the 'ratio-diagram' method (Harper 1977, p. 285) in the sense

**Fig. 2** Diagram to illustrate how a small core sample may give a misleading impression of the age structure of a stand, and how a size frequency distribution may obscure cohort structure due to the development of size hierarchies in each cohort.

a) Age-diameter relationship generated by: (1) assuming the population is composed of individuals of three ages (cohorts) only — 100, 500, and 900 years; (2) assuming these three cohorts have continuous but non-overlapping size class distributions; (3) sampling two trees from each size class; (4) applying an error term (+ or -) which varies at random within the limits given, increasing from smaller to larger (older) trees.

b) Age-diameter relationship assuming that each cohort represents a pulse of regeneration with relatively little regeneration between. The dots are roughly proportional to the density. Larger dots indicate how a small sample of cored individuals from different diameter classes might suggest a linear age-diameter relationship.

c) Hypothetical proportions of the total population in each cohort (based on a logarithmic decay).

d) Hypothetical proportions within each cohort assuming each commences with a highly skewed size frequency distribution and progresses towards normality in old age. (The proportions in the different classes are arbitrary but not atypical).

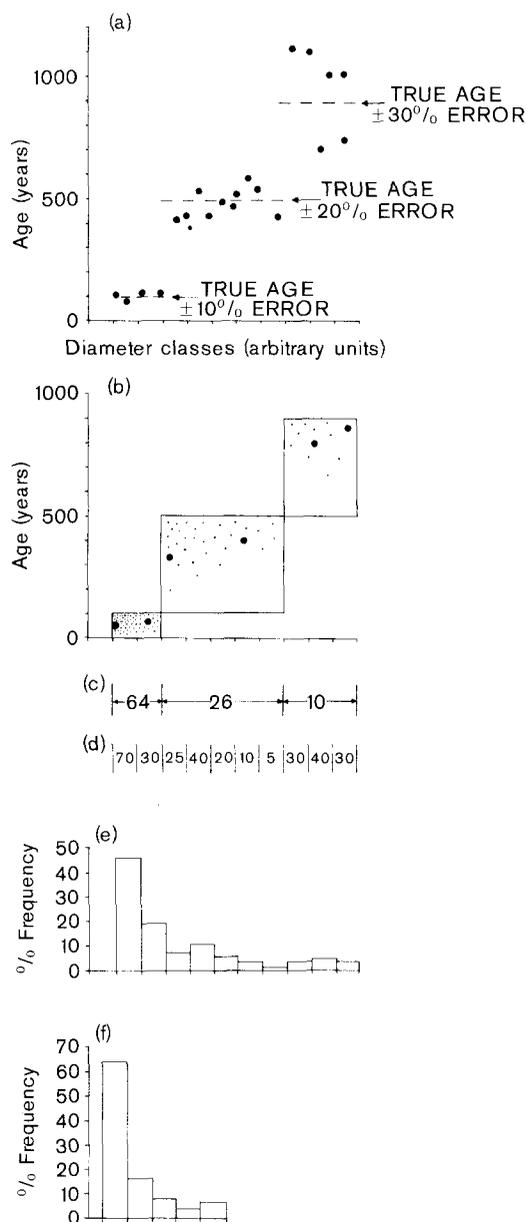
e) The product of (c) and (d). Size frequency distribution illustrating how the cohort modes become immersed in the overall distribution.

f) As (e), but lumping adjacent size classes, and reducing horizontal scale.

Note that if the cohort size ranges overlap the likelihood of failing to pick out the modes in the composite size frequency distribution increases. Also, if the error of age estimation (a) is considered the likelihood of not detecting the cohort structure from cores also increases.

that we must imagine each species being replaced in its new proportions and the process repeated from generation to generation.

The field problem is how to estimate the transition probabilities. The most reliable approach must be to collect data from marked individuals or plots over a long time period (Stephens & Waggoner 1970). Shorter-cut approaches have relied upon the relative proportions of saplings (variously defined) beneath mature trees of each species (Horn 1975, Fox 1977). Enright (1978) calculated replacement probabilities from the measured (or estimated) mortality rates of mature trees and the relative proportions of saplings considered capable of capturing the released site (Enright & Ogden 1979). I have analysed data collected by Lloyd (1971) in which transition probabilities were based upon a subjective choice of the 'seedling most likely to succeed' in 11 214 plots with defined dominants (Ogden 1983b). Barden (1980) tackled the job more directly by identifying the 'gap-makers' and their associated 'gap-fillers' in canopy gaps in the southern Appalachians, and a similar approach has been tried by Smale & Kimberley (1983) in New Zealand.



The assumptions made in the selection of replacements are clearly central to the results obtained. This problem deserves more attention. Weighting sapling abundances by their survivorships appears necessary but the volume of data required is formidable. Moreover, survivorships are site specific; saplings of some species, abundant beneath an intact canopy, may fare badly in sudden gaps, and be out-competed by more responsive species. For example, Smale & Kimberley (1983)

show that saplings of kohekohe (*Dysoxylum spectabile*) are more abundant than those of tawa (*Beilschmiedia tawa*) beneath an intact canopy of these species, but the latter captures proportionally more of the gaps created by tree-fall. From a small sample of gaps with identified gap-makers they describe a reciprocal relationship between the two species, but their data also imply that the stable proportions are mediated by gap frequency, with tawa maintaining a lower proportion in the absence of gaps.

Different tree species have different longevities, so that their populations interact asynchronously. In lowland mixed-podocarp forest in New Zealand, emergent rimu (*Dacrydium cupressinum*) may live for 800 years, probably three times as long as most individuals of *Beilschmiedia* or *Weinmannia* comprising the hardwood canopy beneath. This difference in 'turnover time' can be readily built into the model (Horn 1975) — if the data are available. An associated problem is that the fall of a giant tree usually eliminates not one, but several, adjacent canopy and subcanopy trees and initiates a "micro-succession" (Forcier 1975) or "serule" (Daubenmire 1968) in the gap it creates. Not all the species involved reach the canopy, but a decision to exclude some species on the grounds of stature is liable to be arbitrary and to direct attention away from the details of the process. Finally, in diverse stratified forest many species are rarely represented, and for this reason alone the reliability of the transitions estimated for them may be low.

## REGENERATION MODELS FOR SOME CANOPY DOMINANTS

### A model of cohort structure in a kauri population

In this section I present a conceptual model for the development of population structure in a species which is relatively light demanding at some phase of juvenile growth, but capable of canopy dominance and great longevity. The model is developed specifically with reference to kauri, but should be regarded as an example illustrating one possible explanation for most of the observed phenomena rather than a definitive statement. I believe the model is broadly applicable to other canopy dominant gymnosperms in New Zealand.

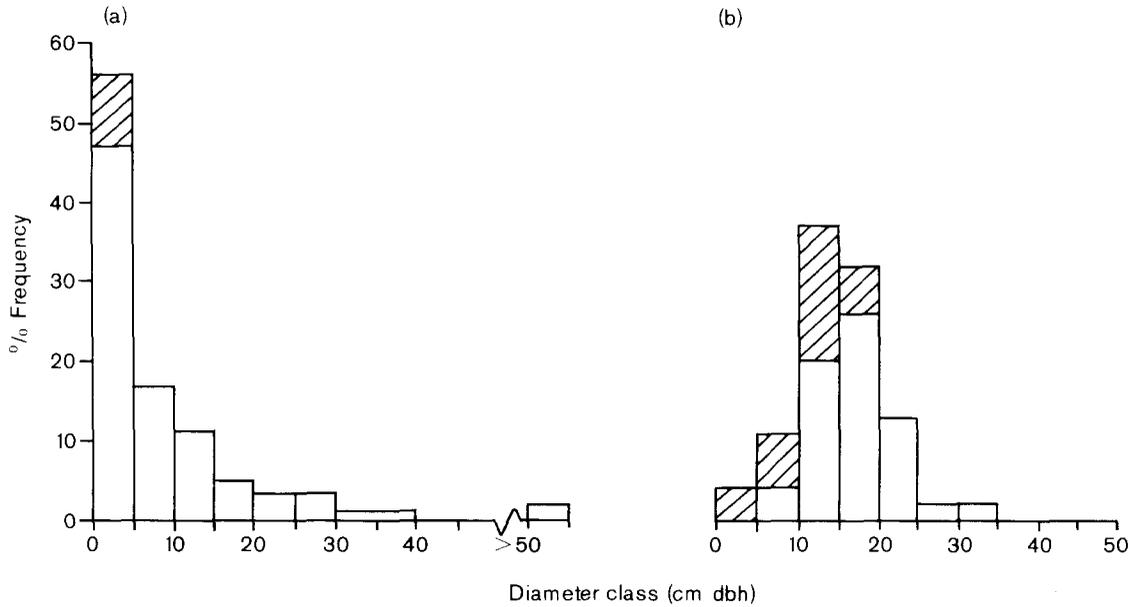
The succession from burned forest to a dense stand of young kauri — known as a 'ricker' — has been described several times (reviewed by Ecroyd 1982). Near Auckland, pioneer *Leptospermum* communities act as nurse crop for *Phyllocladus trichomanoides* and kauri, with the latter eventually overtopping and outliving the former. A typical ricker stand is partially described in Fig. 3. This

kauri population is 100–120 years old, and has a weak age: diameter relationship. It is an example of an 'even-aged' thinning monoculture — later additions are in the highly suppressed class and are likely to be eliminated in future. The associated *Leptospermum ericoides* population is senile. Juvenile kauri populations of this type are frequent throughout Northland, following the large-scale burning which occurred during the latter half of the nineteenth century.

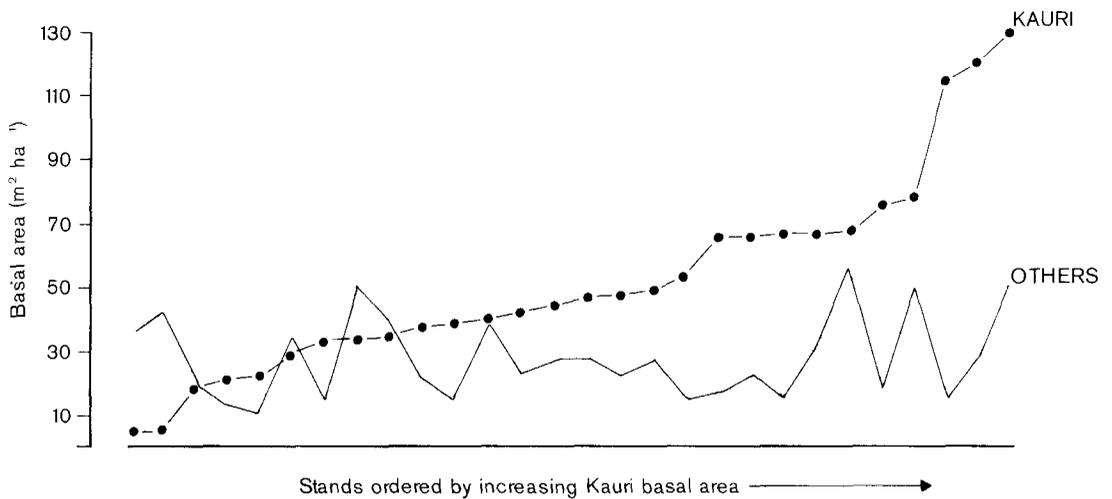
The density of these ricker stands is far greater than that of the mature forest. Kauri regeneration is absent and thinning continues as basal area and height increase. Early light demanding species are gradually eliminated and a sub-canopy usually including larger seeded, more shade tolerant species, such as *Podocarpus ferrugineus*, *Nestegis* spp. and *Beilschmiedia* spp., develops. A dramatic change in growth form occurs when the tree is 50–60 cm dbh; the conical ricker sheds its lower branches and develops an open spreading crown above its associates. If stands are ranked in order of increasing basal area, the associated species (taken together) show no trends (Fig. 4); a high basal area of kauri does not depress its associates, nor a low value allow them to expand. This situation mirrors that described for *Araucaria hunsteinii* in New Guinea (Enright 1982). Perhaps these ancient associations between conifers and hardwoods demonstrate niche partitioning by vertical stratification and differential longevity? Whatever the evolutionary explanation, mature kauri associations carry a prodigious quantity of timber.

Although this whole sequence, taking 600 to 1000 years, has never been studied quantitatively, several ecologists have commented on the apparent "lack of regeneration" in kauri forest (Ecroyd 1982). However, a quantitative survey of 25 mature unlogged kauri stands revealed abundant seedlings of different sizes in the majority (Ahmed 1984).

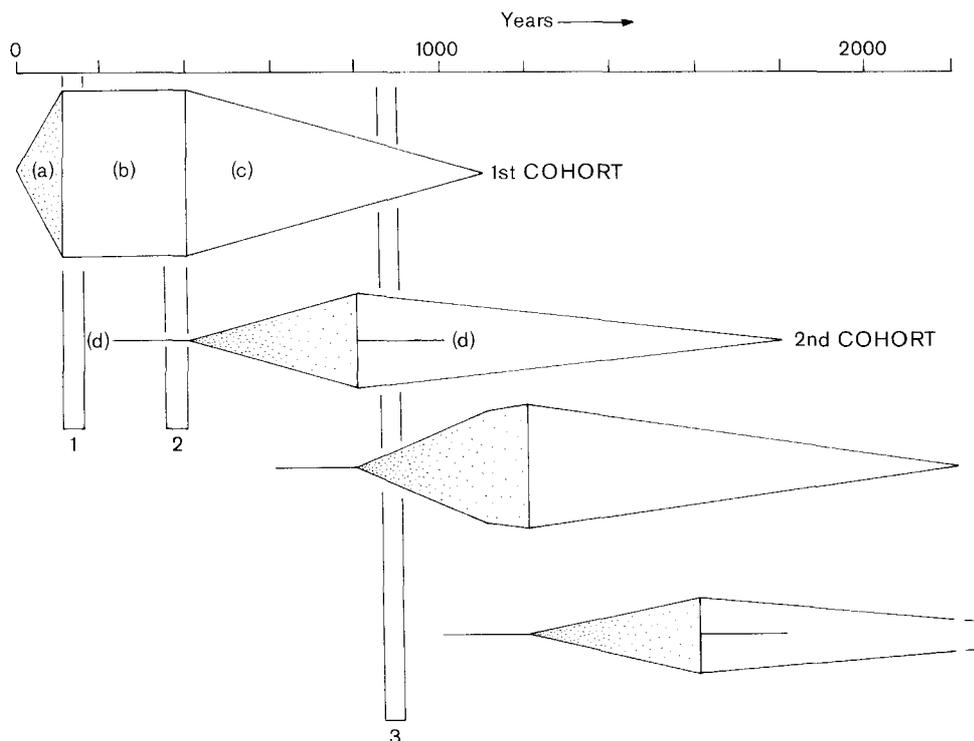
These observations are embodied in the pictorial model presented in Fig. 5. Each lozenge shaped block may be taken to represent the total quantity (biomass; approximated by basal area) of a cohort in a particular area. The first cohort has a phase of seedling recruitment (in the *Leptospermum* nurse crop) while its biomass increases, then a phase of relatively 'constant' biomass while it thins. During this phase seedlings may be present on the forest floor, but they are ephemeral and recruitment is unusual. The population may at first follow the  $-3/2$  thinning rule. Figure 4 suggests that a truly constant biomass is never achieved. Ultimately however, even the canopy dominants begin to die and the biomass of the cohort declines. In so far as the cohort is relatively even aged, the canopy mortality could be roughly synchronous on the



**Fig. 3** Size frequency distribution for (a) kauri and (b) kanuka in a typical ricker stand. Redrawn from Ogden (1983a). Shaded area represents dead stems.



**Fig. 4** Basal area of kauri and associated species in 28 stands taken from throughout the range of kauri. Data from Ahmed (1984) and G. M. Wardle (1984).



**Fig. 5** A pictorial model of possible cohort structure in a kauri forest. Each lozenge shaped block represents the total quantity (biomass) of a cohort. The first cohort can be divided into: (a) a recruitment phase, during which seedlings are recruited and biomass increases; (b) a thinning phase, during which population density declines but total biomass remains constant (or increases); (c) a senescent phase during which biomass declines. Seedlings of the second cohort (d) may be present during the phase of maximum biomass, but are not recruited until the first cohort enters the senile phase. The recruitment phase of the second (and subsequent) cohorts is longer and characterised first by seedling establishment and later by growth of existing young trees. A thinning phase may not be so clearly distinguished. Columns 1, 2, and 3 represent 50 year time spans. These three instants at which we view the population reveal very different age (and size) class structures. For further explanation see text.

same scale. I postulate that a point is reached when annual mortality exceeds annual increment, and gaps become a feature of the canopy. The sheer size of the dying kauris ensures that, at least temporarily, these gaps extend to the forest floor, where the light environment consequently improves. At Trounson Kauri Park, G. M. Wardle (1984) has described canopy gaps of c. 0.05 ha in area created by the fall of single kauris which destroyed several subcanopy trees. Such gaps frequently contained kauri seedlings, often on rotting wood.

These results suggest that some self-replacement of kauri can occur in the gaps. This is modelled in Fig. 5 as a second cohort, 'filling in' the biomass lost by the first. We can envisage this as occurring by way of seedling recruitment in gaps at first, but later, as the second generation gets larger, occurring

primarily by vegetative growth. With the time scales postulated in Fig. 5 the second generation would itself begin to senesce before the demise of its parental population, so that 'space' would become available for a third 'wave' of recruits. Indeed, the model is sufficiently general that we could envisage the second cohort being represented by a second species without necessarily influencing the success of the third cohort. If such a second species had a significantly shorter life span than kauri, more than one generation may be interpolated between successive kauri cohorts, perhaps influencing soil fertility or other features in a way which would stabilise the oscillation (Beveridge 1977).

Figure 5 is also designed to draw attention to the different time perspectives of humans and kauris(!). Each numbered bar represents a 50 year 'window'

on the population. Viewed at time 1 we see a competitive hierarchy such as that in Fig. 3. At time 2 we see a dense high-volume kauri stand, with small seedlings but no recruitment, and showing the first signs of 'over-maturity'. At time 3 three overlapping generations are present, but, because we see sizes (not ages) this may not be apparent. Each cohort has developed a competitive hierarchy, so that a wide range of size classes, from scattered ancient veterans (1st cohort) to abundant seedlings and saplings (3rd cohort) will be present. The varied size frequency distributions recorded in mature stands by Ahmed (1984) may simply reflect different stages of this long process (and/or the spatial scale of the mosaic).

Wardle's work suggests that although a proportion of the large gaps created by falling kauris will be re-occupied by kauri, some will be lost to other species (G. M. Wardle 1984). Moreover, kauri may often fail to establish in the smaller more ephemeral gaps created by the death of associates. Thus, it is possible to envisage, following the gradual demise of the first cohort, a sequence of progressively more depleted and less synchronous waves of regeneration. As with *Athrotaxis* in Tasmania (Ogden 1985), the longevity of kauri appears as part of a strategy for retaining possession of individual sites, and maintaining a mosaic of regenerating patches in the landscape. A millenium or more will be required for even two such 'cycles' on a site, during which time, fires, storms and cyclones will have stochastically destroyed larger forest areas in the vicinity, to initiate ricker populations and rejuvenate the sequence.

### Regeneration strategies in podocarps

The controversy which surrounds this subject — alluded to earlier when discussing 'the regeneration gap' — permeates forest ecology in New Zealand, and has been at the root of much argument between those who would preserve the remaining forests dominated by this family, and those who would exploit them for timber (Morton et al. 1984). However, strictly demographic data, so crucial to the arguments, are remarkably few. Dense stands can certainly arise following fires or other disturbances (Cameron 1955, 1960; McKelvey 1963). In medium density forest, gap regeneration cycles involving hardwoods have been described (Beveridge 1973, 1983) and similar patterns can occur on a somewhat larger scale giving rise to a mosaic of more or less even-aged stands in different phases of development (Mead & Dijkstra 1983). This situation is congruent with the model described for kauri, but the species differences within the canopy-forming podocarps (including *Dacrydium* spp.) add a further dimension. Sometimes environmental con-

ditions, particularly drainage, may dictate which species dominates the first cohort following disturbance, with, for example, totara (*P. totara*) on drier sites and kahikatea on wet. In other situations the occurrence of nearby seeding trees may play a role in the initial composition. However, not all species are equally probable at all stages — some of the podocarps are 'r' types with abundant (if erratic) production of small seeds and light-demanding seedlings, while others annually produce fewer larger seeds giving rise to slower growing, more shade tolerant seedlings ('K' types) (Fig. 1). The comparative demography of matai and miro would make a rewarding study.

Returning to the kauri model, we can imagine a first cohort dominated by one species, but containing several. Competition might alter the species proportions as the stand developed, totara, for example, might outcompete rimu in the initial struggle (Cameron 1960). The subsequent pattern of senescence would also have species related features, matai, for instance, may be longer-lived than the other species but susceptible to butt and heart rots, miro more vulnerable to wind-throw following canopy opening on the death of rimu. Our understanding is inadequate to model the possibilities, but in the absence of large scale disturbance the second cohort would be less synchronous than the first, and its specific composition show a shift towards 'K' types, as suggested by McKelvey for the West Taupo forests (McKelvey 1963; Fig. 6).

Data from dense mixed podocarp forest from work by Katz (1980) at Whirinaki and Herbert (1980) at Tihoi are summarised in Fig. 7. Both studies show similar relative ages for the different species, which seems to imply a common pattern of 'successional' development, but may simply reflect the different survivorships and longevities of the species. For example, although 50 percent of both the matai and rimu in the logging trials at Okurapoto (Whirinaki) became established in a 100 year period (5–600 years ago) most of the remaining matai were older (up to 750 years old) and most of the remaining rimu younger (to 350 years old). Thus, if the stand originated with the oldest matai some 750 years ago, it follows that many rimu, and most of the kahikatea and miro, germinated and developed beneath a pre-existing podocarp canopy, or in gaps created in such a canopy. In so far as the whole process continued over at least 450 years — rotten (old) and small (young) trees were excluded from the samples — it may be misleading to refer to these stands as 'even-aged' and attempt to force them into 'cohorts'. A transition matrix model would rest on fewer assumptions and have predictive power, but would depend upon reliable

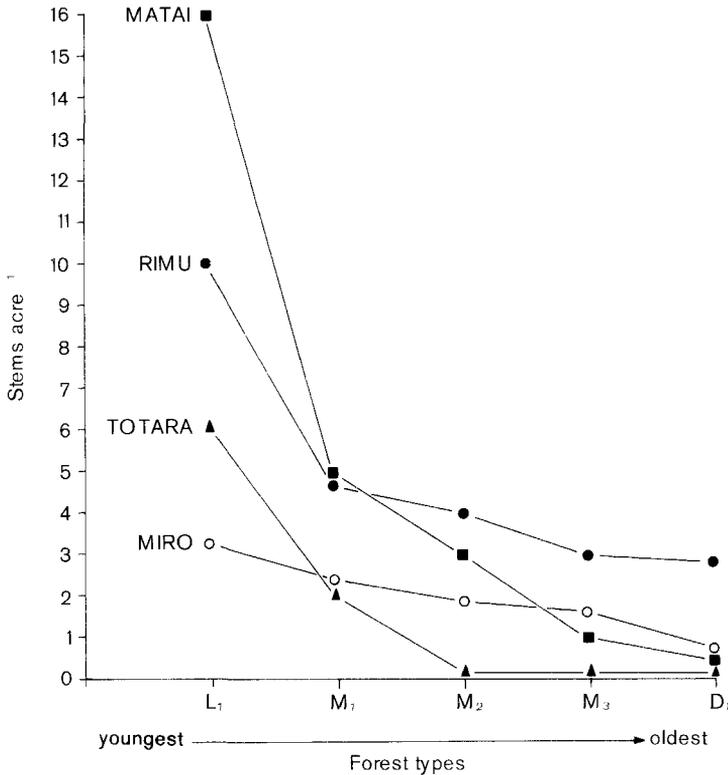


Fig. 6 Proportions of different podocarp species in different forest types arranged in a supposed successional sequence following the Taupo eruption c. A.D. 186. Redrawn from data in McKelvey (1963).

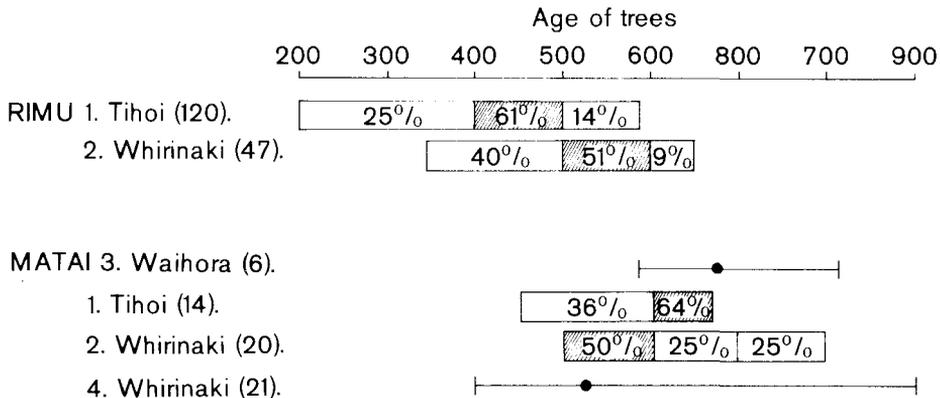


Fig. 7 Age structures of rimu and matai in some central North Island dense podocarp forests, excluding 'young' (< 30 cm dbh) and 'old' (rotten) trees. Ages were obtained from complete cross-sections in all cases. Redrawn from Katz (1980) with additional data provided by the Forest Research Institute, Rotorua (based on field counts of cut stumps) and from Bellingham (1982). Data sources: 1. Herbert (1980); 2. Katz (1980); 3. Bellingham (1982); 4. New Zealand Forest Service, Forest Research Institute, Rotorua (personal communication). Bar length indicates the range of the sample and the spot shows the mean age. Figures in brackets are sample size. Percentages of populations in different age classes also shown. Note that at both Whirinaki and West Taupo (Waihora, Tihoi) the matai population is generally older than the rimu population in the same stand. The age difference between the two species populations appears to be considerably greater in the West Taupo forests. June (1982, 1983) has described rimu populations in north Westland with individuals ranging from < 100 to > 1000 years of age.

information on the frequency of gap formation and probability of gap 'capture' by different species, both of which require age-specific survivorship data which are not available. One of the advantages of the modelling approach, especially that involving application of quantitative demographic models such as transition matrices, is that it directs attention to the hidden assumptions inherent in non-quantitative generalisations (Ogden 1983b).

Thus I suggest that the different seed dispersal characteristics of the species adapt them to different spatial scales and patterns of disturbance, while specific longevities are related to different temporal frequencies of disturbances of particular magnitudes. The life-expectancy of canopy dominant individuals of matai, rimu, or totara may be in excess of 800 years (Bellingham 1982, June 1982) so that, as with kauri, they can retain possession of individual sites until stochastic disturbance allows abundant if localised regeneration somewhere on the landscape. The time spans involved may encompass secular climatic shifts which themselves influence the disturbance regime in any century or millenium. The post-glacial replacement of matai by rimu on the Central Plateau described from pollen analysis by McGlone & Topping (1977) parallels that suggested on the basis of modern spatial patterns in the post-Taupo eruption forests by McKelvey (1963). Thus, while the plant demographer may restrain his science to the study of birth rates and death rates in the existing forest, further understanding of such long-lived species growing in mixed communities requires studies in a variety of disciplines on a Holocene time scale.

#### **The dilemma of survival in a heterogeneous environment — the case of red beech (*Nothofagus fusca*)**

The two extremes of the r-K continuum represent suites of selective forces favouring rapid colonisation of disturbed areas on the one hand, and population maintenance *in situ* on the other. The former is associated with the production of large quantities of small, easily dispersed seeds and light demanding seedlings, whereas the latter is associated with fewer larger seeds giving rise to more shade persistent seedlings. The extremes present a dilemma to which a variety of compromises are possible, variously fitting species to disturbance regimes with different spatial and temporal frequencies. Dispersal, allowing the capture of new areas, would seem to have evolutionary advantages, but massive seed production is energetically costly, and moreover most of the seeds inevitably fall in the shade beneath the parent tree. The opposed selective

pressures implied may be at the root of mast seeding behaviour and seedling physiologies which allow persistence in the shade and rapid growth in the open. These characteristics are found in many New Zealand tree genera, and their demographic consequences are embodied in the cohort model already discussed. Red beech illustrates the dilemma.

During a mast year of red beech several thousand seeds are shed per m<sup>2</sup>. The possibilities for long-distance dispersal of seeds, at least in quantity, may be enhanced in such years. Subsequently the forest floor is covered with seedlings at densities of up to several hundred per m<sup>2</sup>. The seedlings are shade persistent but require light for active growth and the majority, falling beneath ferns or other low cover, are rapidly eliminated. However, those seeds blown to recent areas of wind-thrown or land-slips have much higher survivorships and may form dense seedling stands. Within the forest, seed germinating in light gaps and/or on mossy logs raised above the ground layer also show increased survivorship. Once established in such situations individuals may grow slowly for decades, constituting an 'advance growth' seedling pool analogous to the 'seed bank' of herbaceous communities. June & Ogden (1975) have shown that mast seeding occurring at intervals of less than ten years, coupled with the measured survival rates, appears capable of maintaining the favourable log microsites permanently stocked with 'advanced growth' seedlings. Fallen logs may be available for colonisation for 200 years (June 1974) but only those in canopy gaps receive relative light intensities high enough (c. 35% of open sites) for rapid growth by established red beech seedlings. Thus recruitment from safe sites on the forest floor to maturity in the canopy requires the coincidence of two temporally shifting mosaics — rotting logs and canopy gaps — which are related to the disturbance regime.

Periodic mast seeding allows periodic colonisation of adjacent disturbed areas. The seedling pool, on the other hand, provides a juvenile population perennially ready for recruitment to gaps in an otherwise intact forest canopy. However, the relatively light demanding nature of the recruitment phase dictates the patchy distribution of red beech seedlings, rendering the species susceptible to competition with more shade tolerant species, such as silver beech (*N. menziesii*), able to maintain a more ubiquitous presence on the forest floor. We can envisage a red beech monoculture developing after local disturbance in terms of the cohort model described earlier. Succeeding cohorts become less synchronised and progressively lose sites to other species, until large scale disturbance provides the stochastic opportunity to reinstate the monoculture.

### Regeneration strategies in *Nothofagus*

John Wardle's (1970a, b) work on *Nothofagus solandri* is the most comprehensive population-orientated study of any indigenous tree, while the demographic data he has recently compiled for all the beech species in New Zealand (J. Wardle 1984) provide insights into their regeneration strategies.

Within the 'fusca' group seed weights can be ranked from smallest to largest: mountain (*N. solandri* var. *cliffortioides*) < black (*N. solandri* var. *solandri*) < red (*N. fusca*) < hard (*N. truncata*). Silver beech (*N. menziesii*) is intermediate. This ranking constitutes a first approximation to their relative positions on the r-K continuum. A contrast may be drawn between the large seeded, long-lived red and hard beech, occurring in relatively stable communities, and the smaller seeded *solandri* beeches, especially mountain beech, with a wide ecological niche and a relatively short life cycle (c. 300 years).

Mountain-beech often occurs in montane forests with silver beech, and the relative proportions of the two species then appear to be mediated largely by the frequency of disturbance. Silver beech probably has more regular seed production than mountain beech, and its seedlings are more shade tolerant. Moreover, it is longer lived, and pure stands can achieve higher basal areas than mountain beech (J. Wardle 1984). These characteristics ensure its eventual dominance in undisturbed mixtures. Demonstration of the dynamic relationship between this pair of species emphasises the value of a demographic or evolutionary approach to natural communities — attempts to explain distribution patterns in terms of site requirements alone are piecemeal and lack the predictive power of a unified conceptual approach based on life-cycles.

### CONCLUDING COMMENTS

I have endeavoured to introduce the subject of plant demography by pointing out that its basic laws, approaches, and concepts are applicable not simply to experimental monocultures of herbaceous species, but also to the tree species populations comprising the complex stratified forests of New Zealand. Competitive hierarchies and thinning processes are as much a feature of kauri rickers as they are of dense annual weed populations. The temporal and spatial context within which we view such processes is, of course, vastly different, and the forest population ecologist must be cognisant of advances in Holocene palynology and palaeoclimatology if the subject is to be seen in a realistic perspective.

Since the classic paper by Holloway (1954) 'the regeneration gap' has been a persistent theme in forest ecology in New Zealand. I have emphasised my belief that the conceptual model on which the interpretation of the regeneration gaps has rested has been inappropriate for the New Zealand forests. A "gap-phase or 'mosaic' generation model seems more in keeping with the evidence for widespread forest disturbance, and would predict regeneration gaps localised in time and space. I have presented a diagrammatic cohort model which implies that depleting waves of regeneration following localised disturbance are a feature of the long-lived canopy gymnosperms, and possibly other species also. The time scales involved are prodigious, and allow stochastic events to intervene to complicate our interpretations.

An approach involving the comparative concept of 'strategy', while liable to arm-chair theorizing, may give insights. Attempts to apply rather rigorous demographic models, based perhaps on inappropriate assumptions, will nevertheless force the investigator to appreciate our ignorance of quite 'simple' demographic parameters (such as age-specific life-expectancies). There is a lot of work to be done, and I have stressed those areas in which I think useful contributions can be made most readily. New Zealand appears well placed to contribute to a more general understanding of the roles of small scale and large scale disturbance in forest, and the consequent interaction between seed and seedling regeneration patterns and adult tree longevity. Detailed and long-term population orientated studies of individual species seems to me to be the best approach.

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### REFERENCES

- Ahmed, M. 1984: Ecological and dendrochronological studies on *Agathis australis* Salisb. (Kauri). Unpublished Ph.D. thesis, University of Auckland, New Zealand.

- Allan, M. 1977: Darwin and his flowers. The key to natural selection. London, Faber and Faber.
- Barden, L. S. 1980: Tree replacement in a cove hardwood forest of the southern Appalachians. *Oikos* 35 : 16–19.
- Bathgate, J. L. 1981: Holloway's climatic change hypothesis. Unpublished Ph.D. thesis, University of Canterbury, New Zealand.
- Bellingham, P. 1982: Some ecological aspects of Matai (*Podocarpus spicatus* R. Br. ex Mirbel) in West Taupo indigenous forests. Unpublished B. For. Sc. dissertation, University of Canterbury, New Zealand.
- Beveridge, A. E. 1964: Dispersal and destruction of seed in central North Island podocarp forests. *Proceedings of the New Zealand Ecological Society* 11 : 48–55.
- 1973: Regeneration of podocarps in a Central North Island forest. *New Zealand journal of forestry* 18 : 23–35.
- 1977: Notes on the silviculture of kauri. In: Chavasse, C. G. R. ed. *New Zealand Institute of Foresters (Inc.) forestry handbook*. Rotorua, New Zealand Institute of Foresters. Pp. 125–130.
- 1983: Regeneration of podocarp forests and maintenance of productivity. In: Thompson, K.; Hodder, A. P. H.; Edmonds, A. S. ed. *Lowland forests in New Zealand*. University of Waikato, Hamilton, New Zealand. Pp. 93–112.
- Bierzuchudek, P. 1982: The demography of Jack-in-the-pulpit, a forest perennial that changes sex. *Ecological monographs* 52 : 335–351.
- Burgess, R. E. 1984: The life history strategy of *Carex pumila* Thunb. (Cyperaceae) a rhizomatous perennial pioneer species on the sand plains of the dune system of coastal Manawatu. Unpublished Ph.D. thesis, Massey University, Palmerston North, New Zealand.
- Burke, W. D. 1974: Regeneration of podocarps on Mt Tarawera, Rotorua. *New Zealand journal of botany* 12 : 9–26.
- Burns, B. R.; Ogden, J. 1985: The demography of the temperate mangrove (*Avicennia marina* (Forsk.) Vierh.) at its southern limit in New Zealand. *Australian journal of ecology* 10 : (in press).
- Cameron, R. J. 1955: Mosaic or cyclical regeneration in North Island podocarp forests. *New Zealand journal of forestry* 7 : 55–67.
- 1960: Natural regeneration of podocarps in the forests of the Whirinaki river valley. *New Zealand journal of forestry* 8 : 337–354.
- Clayton-Greene, K. A. 1975: Vegetation of the Kimihia Block in the Taupiri Range, North Island, New Zealand. *New Zealand journal of botany* 13 : 61–72.
- 1977: Structure and origin of *Libocedrus bidwillii* stands in the Waikato district, New Zealand. *New Zealand journal of botany* 15 : 19–28.
- Clements, F. E. 1916: *Plant succession: An analysis of the development of vegetation*. Washington, Carnegie Institution.
- Cockayne, L. 1928: *Vegetation of New Zealand*. ed. 2. Leipzig, Engelmann.
- Cody, M. L. 1966: A general theory of clutch size. *Evolution: N. Y.* 20 : 174–184.
- Connor, H. E. 1966: Breeding systems in New Zealand grasses. VII. Periodic flowering of snow tussock, *Chionochloa rigida*. *New Zealand journal of botany* 4 : 392–397.
- Conway, M. J. 1949: Beetle damage to Beech forest. *New Zealand journal of forestry* 6 : 67–68.
- Darwin, C. 1859: *The origin of species* ed. 6, popular impression, 1920. London, John Murray.
- Daubenmire, R. 1968: *Plant communities: A textbook of synecology*. New York, Harper & Row.
- Dick, R. D. 1956: Sixty years after a mountain beech forest fire. *New Zealand journal of forestry* 7 : 104–108.
- Dugdale, J. S. 1965: Damaging insects in beech and possible control measures. In: Beech forestry in New Zealand Vol. 2. New Zealand Forest Service, *Forest Research Institute Symposium* 5 : 72–78.
- Dunwiddie, P. W. 1979: Dendrochronological studies of indigenous New Zealand trees. *New Zealand journal of botany* 17 : 251–266.
- Ecroyd, C. E. 1982: Biological flora of New Zealand, 8, *Agathis australis* (D. Don) Lindl. (Araucariaceae) Kauri. *New Zealand journal of botany* 20 : 17–36.
- Elder, N. L. 1965: Vegetation of the Ruahine Range. *Transactions of the Royal Society of New Zealand. (Botany)* 3 : 13–66.
- Enright, N. J. 1978: The ecology and population dynamics of *Araucaria* in Papua New Guinea. Ph.D. thesis. Australian National University, Canberra, Australia.
- 1982: Does *Araucaria hunsteinii* compete with its neighbours? *Australian journal of ecology* 7(1) : 97–99.
- Enright, N. J.; Ogden, J. 1979: Applications of transition matrix models in forest dynamics: *Araucaria* in Papua New Guinea and *Nothofagus* in New Zealand. *Australian journal of ecology* 4 : 3–23.
- Esler, A. E.; Astridge, S. J. 1974: Tea tree (*Leptospermum*) communities of the Waitakere Range, Auckland, New Zealand. *New Zealand journal of botany* 12 : 485–501.
- Forcier, L. K. 1975: Reproductive strategies and the occurrence of climax tree species. *Science* 189 : 808–810.
- Foster, F. W. 1931: A stand of beech regeneration of known age. *New Zealand journal of forestry* 3 : 39–40.
- Fox, J. F. 1977: Alternation and co-existence of tree species. *American naturalist* 111 : 69–89.
- Franklin, D. A. 1968: Biological flora of New Zealand, 3, *Dacrydium cupressinum* Lamb. (Podocarpaceae) Rimu. *New Zealand journal of botany* 6 : 493–513.
- Grant, P. J. 1984: Drought effects on high-altitude forests, Ruahine Range, North Island, New Zealand. *New Zealand journal of botany* 22 : 15–27.
- Grime, J. P. 1979: *Plant strategies and vegetation processes*. Chichester, John Wiley and Sons.

- Halle, F.; Oldeman, R. A. A.; Tomlinson, P. B. 1978: Tropical trees and forests: an architectural analysis. Berlin, Springer.
- Harper, J. L. 1967: A Darwinian approach to plant ecology. *Journal of ecology* 55: 247-270.
- 1977: Population biology of plants. London, Academic Press.
- Harper, J. L.; Ogden, J. 1970: The reproductive strategy of higher plants. 1. The concept of strategy with special reference to *Senecio vulgaris* L. *Journal of ecology* 58: 681-698.
- Harper, J. L.; White, J. 1974: The demography of plants. *Annual review of ecology and systematics* 5: 419-463.
- Herbert, J. 1976: Raising seedlings from seed contained in forest duff. New Zealand Forest Service, Forest Research Institute. *Production Forestry Division Indigenous Silviculture report No. 15* (Unpublished) Pp. 12.
- Herbert, J. 1980: Structure and growth of dense podocarp forest at Tihoi, Central North Island, and the impact of selective logging. *New Zealand journal of forestry* 25: 44-57.
- Holloway, J. T. 1954: Forests and climates in the South Island of New Zealand. *Transactions of the Royal Society of New Zealand* 82: 329-410.
- Horn, H. S. (1975): Markovian properties of forest succession. In: Cody, M. L.; Diamond, J. M. ed. *Ecology and the evolution of communities*. Cambridge, Massachusetts and London, Belknap Press. Pp. 196-211.
- 1981: Some causes of variety in patterns of secondary succession. In: West, D. C.; Shugart, H. H.; Botkin, D. B. ed. *Forest succession: concepts and application*. Pp. 25-35.
- Hutchinson, C. E. 1965: The ecological theater and the evolutionary play. New Haven, Yale University Press.
- James, I. L.; Franklin, D. A. 1978: Recruitment, growth and survival of rimu seedlings in selectively logged terrace rimu forest. *New Zealand journal of forestry science* 8: 207-212.
- Jane, G. T.; Green, T. G. A. 1983: Episodic forest mortality in the Kaimai Ranges, North Island, New Zealand. *New Zealand journal of botany* 21: 21-31.
- Jones, E. W. 1945: The structure and reproduction of the virgin forest of the North Temperate Zone. *New phytologist* 44: 130-148.
- June, S. R. 1974: The germination, growth, and survival of red beech (*Nothofagus fusca*) seedlings in relation to forest regeneration. Unpublished M.Sc. thesis, Massey University, Palmerston North, New Zealand.
- 1982: Ecological studies in the indigenous forests of north Westland, New Zealand. Unpublished Ph.D. thesis, University of Canterbury, New Zealand.
- 1983: Rimu regeneration in a north Westland podocarp-hardwood forest (résumé). *New Zealand journal of ecology* 6: 144-145.
- June, S. R.; Ogden, J. 1975: Studies on the vegetation of Mount Colenso, New Zealand. 4. An assessment of the processes of canopy maintenance and regeneration strategy in a red beech (*Nothofagus fusca*) forest. *New Zealand journal of ecology* 1: 7-15.
- Katz, A. 1980: Structure and growth of dense podocarp forest in Whirinaki. N.Z. Forest Service. Forest Research Institute, *Indigenous forest management report No. 25*. (Unpublished). 12 Pp.
- Kirkland, A. 1961: Preliminary notes on seeding and seedlings in red and hard beech forests of north Westland and silvicultural implications. *New Zealand journal of forestry* 3: 482-497.
- Leslie, P. H. 1945: On the use of matrices in certain population mathematics. *Biometrika* 35: 183-212.
- Lloyd, R. C. 1960: Growth study of regenerated kauri and podocarps in Russell Forest. *New Zealand journal of forestry* 8: 355-361.
- 1971: Quantitative linear sampling of indigenous forest. New Zealand Forest Service, Forest Research Institute. *Indigenous silviculture report No. 7* (Unpublished).
- MacArthur, R. H.; Wilson, E. D. 1967: The theory of island biogeography. Princeton, New Jersey, Princeton University Press.
- Makepeace, W. A. 1980: Ecological studies of *Hieracium pilosella* and *H. praealtum*. Unpublished Ph.D. thesis, University of Canterbury, New Zealand.
- Mark, A. F. 1968: Factors controlling irregular flowering in four alpine species of *Chionochloa*. *Proceedings of the New Zealand Ecological Society* 15: 55-60.
- 1970: Floral initiation and development in New Zealand alpine plants. *New Zealand journal of botany* 8: 67-75.
- Mark, A. F.; Scott, G. A. M.; Sanderson, F. R.; James, P. W. 1964: Forest succession of landslides above lake Thomson, Fiordland. *New Zealand journal of botany* 2: 60-89.
- Mason, R. 1950: Notes on regrowth in part of the Tararua following the 1936 storm. *Bulletin of the Wellington Botanical Society* 22: 11-12.
- McGlone, M. S. 1983: Polynesian deforestation of New Zealand: a preliminary synthesis. *Archaeology in Oceania* 18: 11-25.
- McGlone, M. S.; Topping, W. M. 1977: Aranuiian (post-glacial) pollen diagrams from the Tongariro region, North Island, New Zealand. *New Zealand journal of botany* 15: 749-760.
- McKelvey, P. J. 1963: The synecology of the West Taupo indigenous forest. *New Zealand Forest Service bulletin No. 14*. Wellington, Government Printer.
- McNaughton, S. J. 1975: r- and K- selection in *Typha*. *American naturalist* 109: 251-261.
- McQueen, D. R. 1951: Succession after forest fires in the southern Tararua mountains. *Bulletin of the Wellington Botanical Society* 24: 10-19.
- Mead, D. J.; Dijkstra, H. G. S. 1983: Stand structure in terrace rimu forests of south Westland and its implications for management. (Abstract) Pacific Science Association 15th Congress. *Programme abstracts and Congress information*. 1: 163.

- Micheau, B. 1984: Biological control of Scotch Thistle (*Cirsium vulgare*). Unpublished M. Phil. thesis. University of Auckland, New Zealand.
- Milligan, R. H. 1974: Insects damaging beech (*Nothofagus*) forests. *Proceedings of the New Zealand Ecological Society* 21: 32–40.
- Mirams, R. V. 1957: Aspects of the natural regeneration of the kauri (*Agathis australis* Salisb.). *Transaction of the Royal Society of New Zealand* 84: 661–680.
- Molloy, B. P. J. 1969: Evidence for post-glacial climatic changes in New Zealand. *Journal of hydrology (N.Z.)* 8: 56–67.
- Molloy, B. P. J.; Burrows, C. J.; Cox, J. E.; Johnston, J. A.; Wardle, P. 1963: Distribution of subfossil forest remains eastern South Island, New Zealand. *New Zealand journal of botany* 1: 68–77.
- Morton, J.; Ogden, J.; Hughes, T.; MacDonald, I. 1984: To save a forest — Whirinaki. Auckland, David Bateman Ltd.
- Myers, S. C. 1984: Studies in the ecology of *Beilschmiedia tarairi* (A. Cunn.) Benth. et Hook. f. ex. Kirk. Unpublished M.Sc. thesis, University of Auckland, Auckland, New Zealand.
- Norton, D. A. 1983a: Population dynamics of subalpine *Libocedrus bidwillii* forests in the Cropp River Valley, Westland, New Zealand. *New Zealand journal of botany* 21: 127–134.
- 1983b: Modern New Zealand tree-ring chronologies 1. *Nothofagus solandri*. *Tree-ring bulletin* 43: 1–18.
- 1983c: Modern New Zealand tree-ring chronologies 2. *Nothofagus menziesii*. *Tree-ring bulletin* 43: 39–49.
- 1984: Phenological growth characteristics of *Nothofagus solandri* trees at three altitudes in the Craigieburn Range, New Zealand. *New Zealand journal of botany* 22: 413–424.
- Ogden, J. 1970: Plant populations structure and productivity. *Proceedings of the New Zealand Ecological Society* 17: 1–9.
- 1971: Studies on the vegetation of Mount Colenso, New Zealand. 2. The population dynamics of red beech. *Proceedings of the New Zealand Ecological Society* 18: 66–75.
- 1980: Dendrochronology and dendroecology — an introduction. (résumé). *New Zealand journal of ecology* 3: 154–156.
- 1983a: The scientific reserves of Auckland University II. Quantitative vegetation studies. *Tane* 29: 163–180.
- 1983b: Community matrix model predictions of future forest composition at Russell State Forest. *New Zealand journal of ecology* 6: 71–77.
- 1985: Past, present and future: studies on the population dynamics of some long-lived trees. In: White, J. ed. *Studies in plant demography*: John L. Harper Festschrift. Academic Press. *In press*.
- Ogden, J.; West, C. J. 1981: Annual rings in *Beilschmiedia tawa* (Lauraceae). *New Zealand journal of botany* 19: 397–400.
- Pickett, T. A.; White, P. S. ed. (In press): Natural disturbance: an evolutionary perspective. New York, Academic Press.
- Preest, D. S. 1963: A note on the dispersal characteristics of the seed of the New Zealand podocarps and beeches and their biological significance. In: Gressitt, L. S. ed. *Pacific Basin Biogeography Tenth Pacific Science congress*, Honolulu, Hawaii, 1961. Bishop Museum Press. Pp. 415–424.
- Rawlings, G. B. 1953: Insect epidemics on forest trees in New Zealand. *New Zealand journal of forestry* 6: 405–412.
- Reid, J. S. 1948: Regeneration of indigenous forest after blowdown. *New Zealand journal of forestry* 5: 436–437.
- Robbins, R. G. 1958: Direct effect of the 1855 earthquake on the vegetation of the Orongorongo Valley, Wellington. *Transactions of the Royal Society of New Zealand* 85: 205–212.
- 1962: The podocarp-broadleaf forests of New Zealand. *Transactions of the Royal Society of New Zealand (Botany)* 1: 33–75.
- Shaw, W. B. 1982: The impact of tropical cyclone Bernie on the forests of the Urewera National Park, North Island, New Zealand. (Résumé). *New Zealand journal of ecology* 6: 155–156.
- Shinozaki, K.; Yoda, K.; Hozumi, K.; Kira, T. 1964: A quantitative analysis of plant form — the pipe model theory. I. Basic analyses. II. Further evidence of the theory and its application in forest ecology. *Japanese journal of ecology* 14: 97–105, 133–139.
- Silvertown, J. W. 1980: The evolutionary ecology of mast seeding in trees. *Botanical journal of the Linnean Society* 14: 235–250.
- 1982: Introduction to plant population ecology. London and New York, Longman.
- Smale, M. C.; Kimberley, M. O. 1983: Regeneration patterns in *Beilschmiedia tawa* dominant forest at Rotoehu. *New Zealand journal of forestry science* 13: 58–71.
- Solbrig, O. T. ed. 1980: Demography and evolution in plant populations. *Botanical monographs* 15. Oxford, Blackwell Scientific Publications.
- Solbrig, O. T.; Simpson, B. B. 1974: Components of regulation of a population of dandelions in Michigan. *Journal of ecology* 62: 473–486.
- 1977: A garden experiment on competition between biotypes of the common dandelion (*Taraxacum officinale*). *Journal of ecology* 65: 427–430.
- Stearns, S. C. 1976: Life history tactics: a review of the ideas. *Quarterly reviews of biology* 51: 3–47.
- Stearns, S. C. 1977: The evolution of life history traits. *Annual review of ecology and systematics* 8: 145–171.
- Stephens, G. R.; Waggoner, P. E. 1970: The forests anticipated from 40 years of natural transitions in mixed hardwoods. *Bulletin of the Connecticut Agricultural Experimental Station, New Haven*, 707: 1–58.

- Stewart, G. H.; Veblen, T. T. 1982: Regeneration patterns in southern rata (*Metrosideros umbellata*) - kamahi (*Weinmannia racemosa*) forest in central Westland, New Zealand. *New Zealand journal of botany* 20: 55-72.
- Tansley, A. G. 1935: The use and abuse of vegetational concepts and terms. *Ecology* 16: 284-307.
- Thomson, A. P. 1936: The recovery of an indigenous forest after windthrow. *New Zealand journal of forestry* 4: 33-36.
- Trenbath, B. R. 1974: Biomass productivity of mixtures. *Advances in agronomy* 26: 177-210.
- Ure, J. 1970: The Tararua — a dual purpose North Island forest. *New Zealand journal of forestry* 15: 189-195.
- Usher, M. B. 1973: Biological conservation and management. London, Chapman and Hall.
- Veblen, T. T.; Schlegel, F. M.; Escobar, B. R. 1980: Structure and dynamics of old-growth *Nothofagus* forests in the Valdivian Andes, Chile. *Journal of ecology* 68: 1-31.
- Veblen, T. T.; Stewart, G. H. 1982: On the conifer regeneration gap in New Zealand: The dynamics of *Libocedrus bidwillii* stands on South Island. *Journal of ecology* 70: 413-436.
- Wardle, G. M. 1984: Observations on the structure and dynamics of kauri (*Agathis australis*) forest. Unpublished M.Sc. thesis, University of Auckland, New Zealand.
- Wardle, J. A. 1984: The New Zealand Beeches. Ecology, utilisation and management. New Zealand Forest Service.
- 1970a: The ecology of *Nothofagus solandri*. 3. Regeneration. *New Zealand journal of botany* 8: 571-608.
- 1970b: The ecology of *Nothofagus solandri*. 4. Growth, and general discussion to parts 1 to 4. *New Zealand journal of botany* 8: 609-646.
- Wardle, P. 1963a: The regeneration gap of New Zealand gymnosperms. *New Zealand journal of botany* 1: 301-315.
- 1963b: Growth habits of New Zealand subalpine shrubs and trees. *New Zealand journal of botany* 1: 18-47.
- Werner, P. A.; Caswell, H. 1977: Population growth rates and age versus stage distribution models for teasel (*Dipsacus sylvestris* Huds.) *Ecology* 58: 1103-1111.
- White, J. 1979: The plant as a metapopulation. *Annual review of ecology and systematics* 10: 109-145.
- 1980: Demographic factors in populations of plants. In: Solbrig, O. T. ed. *Demography and evolution in plant populations. Botanical monographs* 15: Oxford, Blackwells Scientific Publications.
- White, P. S. 1979: Pattern, process, and natural disturbance in vegetation. *The botanical review* 45: 229-299.
- Whitmore, T. C. 1975: Tropical rain forests of the far east. Oxford, Clarendon Press.
- 1984: Gap size and species richness in tropical rain forests. *Biotropica* 16: 239.
- Yoda, K.; Kira, T.; Ogawa, H.; Hozumi, K. 1963: Intraspecific competition among higher plants. XI. Self-thinning in over-crowded pure stands under cultivated and natural conditions. *Journal of biology of Osaka City University* 14: 107-129.