Maintenance of key tree species

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A B S T R A C T

There is a widespread perception that certain dominant ('key') tree species are declining on conservation lands in New Zealand. This concern is usually based on observations suggesting undesirable shifts in the demographic processes regulating the distribution, size and viability of tree populations. Our project was initiated to define a process to understand and compare the vulnerability to population decline of key tree species at a range of scales and to set priorities for conservation management. We first consider in detail observations and possible causes of population decline of seven selected tree species, then consider more generally the critical stages in tree life cycles likely to affect population viability of indigenous species and, finally, suggest an approach to establishing priorities among tree species. Prioritising tree species should involve: showing there is reason for concern about the maintenance of a tree species in terms of a population imbalance; understanding the causes of any imbalances in the demographics of a tree species; determining the significance of maintaining a tree species within a context of its contribution to ecosystem functions; and showing that the trajectory of a tree species population can be changed to something judged more desirable. In all of these we assess the adequacy of knowledge, suggest research questions in need of answers, and consider the implications for management.

Keywords: Forest, tree species, vulnerability, risk assessment, monitoring, forest health, indicators.

1. Background

There is a widespread perception among indigenous forest managers, ecologists, and the wider public, that certain dominant ('key') tree species are declining in indigenous forests. In a general sense, this is not a new concern as numerous examples of extensive tree death can be listed from around New Zealand over the past century (e.g. Morgan 1908; Chavasse 1955; Holloway 1959; Stewart & Veblen 1982b; Rose et al. 1992). Usually this concern is based on observations suggesting undesirable shifts in the demographic processes regulating population size and viability, e.g.:

- Low numbers of mountain beech (*Nothofagus solandri* var. *cliffortioides*) seedlings in the Kaweka Range (Allen & Allan 1997).
- Extensive mortality of pahautea (*Libocedrus bidwillii*) trees at Hihitahi (Rogers 1997).

To assess the significance of such observations, a number of related questions should be asked, such as:

- Is pahautea regenerating in stands where trees are dying, or in other nearby stands at Hihitahi?
- Is recent mortality of pahautea a feature of most forests in the Hihitahi area, or certain areas of the country, or nationally? Are there some areas where there is compensatory regeneration of pahautea?
- Is the imbalance of mortality and regeneration of pahautea at an area or national scale of more concern than that for other tree species (e.g. mountain beech or Hall's totara (*Podocarpus hallii*)?

Addressing such a sequence of questions is essential in establishing whether there is a problem, the scale of any problem and, therefore, our ability to prioritise which species should be of most concern. This prioritisation is necessary because of the need to make informed management choices and focus research efforts.

The process of prioritising which species are of most concern should also take account of what is causing any undesirable shifts in the demographic processes regulating population size and viability. The difficulty of ascribing cause has bedeviled pathologists, ecologists, and forest managers for a long time (e.g. Chavasse 1955; Wardle 1966; Veblen & Stewart 1982a; Bellingham et al. 1999a). Too often a simplistic view is presented that does not stand further scrutiny, for example:

- In a simple sense it could be argued, as many authors have, that defoliation by possums (*Trichosurus vulpecula*) kills southern rata (*Metrosideros umbellata*) trees.
- However, not all southern rata trees that die are killed by possums. For example, most tree death in natural populations is the result of competitive thinning.
- The important question, then, becomes: 'what proportion of southern rata tree death is primarily caused by possums defoliating trees?'.

In a general sense, this last question is difficult to answer for at least two reasons. Firstly, the structure, composition and functioning of forest ecosystems is driven by a wide range of interacting factors (Table 1), some of

TABLE 1.   FACTORS COMMONLY INFLUENCING THE COMPOSITION OF
FORESTS. SOME OF THE VARIABLES COMMONLY MEASURED TO REPRESENT
THESE FACTORS, AS WELL AS SOME OF THE MECHANISMS THROUGH WHICH
THESE FACTORS MAY OPERATE, ARE GIVEN (MODIFIED FROM ALLEN 2000).

FACTORS	VARIABLES	EXAMPLE OF MECHANISM
Disturbance	Changes in biomass or number of trees	Individuals killed of one or more species
Herbivory	Level of defoliation, individual height growth	Reduced photosynthetic ability
Species effects	Litter quality	Modifies the abilities of seeds of other species to germinate and grow
Climate	Temperature, precipitation	Changes physiological processes
Soil	Texture, N availability, cation availability	Influences resources essential for growth and development
Dispersal	Seed dispersal, available regeneration niches	Seeds do not arrive at an otherwise suitable site
Time	Tree age, relative biomass	Species differential longevity

which are relatively easy to measure (e.g. rainfall), others we know little about (e.g. infrequent disturbance impacts); and finally, we must add chance. Additionally, because many of these factors are correlated with each other at any particular temporal or spatial scale, it is difficult to separate the influence of an individual factor and define causal relationships. The following example shows this limitation for spatial data. A study in south Westland evaluated tree mortality in three localities along a possum invasion front; it was only in the write-up stage of this study that the invasion front was also shown to coincide with a compositional gradient usually related to soil fertility (Stewart 1992). Because we know from elsewhere that mortality in such forests apparently relates to a soil fertility gradient, it was therefore difficult to partition the effects of a possum density gradient along the Westland invasion front from those driven by soil fertility. It cannot be over-emphasised that correlation is not cause—a cautious interpretation will always ask what other factors could be involved. Secondly, understanding the factors driving tree population demography is made difficult by the long time-scales involved. Demographic processes may reflect events that occurred over past centuries and millennia. Even with this complex background, appropriate management responses require the correct interpretation of what is driving tree population demographics.

This paper first considers in detail what is known about the vulnerability of selected tree species, then considers, more generally, the critical stages in tree life cycles, and suggests a way of establishing priorities among tree species. In all of these we assess the adequacy of knowledge, suggest research questions that are in need of answers, and consider the implications for management. Finally, we conclude with some recommendations for ongoing work required.

2. Objective

To define a process that can be used to understand and compare the vulnerability of key forest tree species populations and set priorities for conservation management.

3. Case studies of selected species

The following case studies consider what is known about the demographic processes of selected tree species. These species are considered in detail as a means of demonstrating the complexity of factors involved. The key demographic processes that affect population regulation are: flowering; pollination; seeding; dispersal; establishment; vegetative reproduction; competitive interactions; and mortality. These processes are influenced by the range of factors previously listed in Table 1. Species discussed in the following case studies were selected because they are of concern to forest managers in various parts of the country and because they encompass a broad range of the perceived problems. Often the data available about the selected species are from limited time frames and few sites which imposes serious constraints on the generalities and inferences that can be made.

3.1   KAMAHI (*Weinmannia racemosa*)

Although kamahi is considered to flower profusely in every year (Wardle 1966), quantitative time-series data have not so far been available to characterise between-year variability. Flowering occurs largely in the early summer, although flowers can be found on trees between November and May. Flowers contain nectar and are visited by insects, including bees, and birds—although we know little about how pollinators are being affected by introduced fauna. When available, kamahi flowers (and buds) can form an important component of possum diet (Nugent et al. 2000; H. Cochrane unpubl. data). Hamish Cochrane (unpubl. data) recorded kamahi flowers constituting 36% (dry weight) of possum diet in January for a northern South Island beech (*Nothofagus* spp.) forest, where kamahi is a minor component in the subcanopy. Elsewhere, the apparent attractiveness of flowers as a food source has been demonstrated by excursions outside their normal home range of possums in radio-tracking studies (Ward 1978). Such a response in feeding behaviour, in forests where kamahi is a minor forest component, may create situations where possums have the greatest impact on the proportion of flowers lost. Although the primary focus here is to consider factors significant to the life history of kamahi populations, it is worth pointing out that from a conservation

perspective altering the level of flowering may significantly affect ecosystem processes and indigenous fauna that feed on flowers. Flowers can be a high-quality food resource in what can be nutrient-poor systems (H. Cochrane unpubl. data). We are also uncertain of the level to which possum flower predation has a prehistory equivalent.

There are no published accounts of how kamahi seed production may be influenced by possums eating flowers. It appears some seeds are produced by trees in most years (see Section 4.2) and that seeds ripen and fall by early autumn. Seeds are small (about 0.1 mg) with basal and terminal tufts of hairs that assist with wind dispersal (Wardle 1966). There are no quantitative data available on seed dispersal—although establishment on formerly deforested sites suggests a considerable number of seeds may be transported some distance (> 100 m). Kamahi commonly establishes terrestrially in successional communities following fire, landslides and volcanic activity (e.g. Mark et al. 1964; Stewart & Veblen 1982a). There is circumstantial evidence that the typical successional replacement of kanuka by kamahi has not occurred in some parts of the central North Island due to browsing by deer (e.g. McKelvey 1955). In the Urewera National Park, kamahi does not now regenerate under some kanuka stands as it apparently did prior to colonisation by deer (Payton et al. 1984; Fig. 1). It is unclear how general this pattern is or whether it is still the case following 30 years of intensive deer control by commercial operators. Another instance where seedling counts show kamahi is apparently not regenerating, and where it might be expected, is in extensive forest dieback areas in the southern Ruahine Range (e.g. Batcheler 1983; Rogers & Leathwick 1997; Bellingham et al. 1999a). Rogers & Leathwick (1997) present a recent analysis of this canopy dieback in terms of spatial distribution and intensity. Bellingham et al. (1999a) suggest the lack of kamahi regeneration, on apparently suitable sites, is unlikely to be the consequence of current herbivore populations. These authors suggest that as kamahi regenerates in a wide range of sites, and that its seeds are dispersed over long distances by wind, it would be desirable to establish the apparent cause of this 'displacement dieback'.

In dense forest, much kamahi regeneration occurs on raised surfaces such as logs, tree trunks and tree fern trunks, particularly those of *Dicksonia squarrosa* (Wardle 1966). It is generally considered that tree ferns are unpalatable to introduced ungulates; however, there is a notable exception on Stewart Island where white-tailed deer (*Odocoileus virginianus*) have

Figure 1.   Development of a bush oat grass and hook grass sward under a 50-year-old kanuka stand in the Urewera National Park where normally kamahi regeneration is expected. (*Photograph*: John Barran).

been shown to influence tree fern population dynamics (Stewart & Burrows 1989). In that instance kamahi, at least, appears capable of regenerating terrestrially. The point is that there are complex interactions between herbivores, fern understories, and regeneration of tree species (like kamahi) which are little understood. Multi-stemmed trees are a feature for kamahi. These may include coalesced stems of numerous individuals establishing on raised surfaces, but the extent to which multiple stems is a consequence of vegetative propagation is unclear. In Westland's southern rata-kamahi forests, kamahi apparently regenerates intermittently in response to the formation of canopy gaps (Stewart & Veblen 1982a).

Synchronous mortality of canopy kamahi trees, along with other species, has been a prominent feature in several montane forest areas throughout New Zealand (e.g. Chavasse 1955; Batcheler 1983; Jane & Green 1986). It is therefore not surprising that it should emerge as a species of concern to conservation managers. With respect to the human-related causes of mortality, there is a large amount of circumstantial evidence linking the synchronous death of kamahi trees to browsing by possums as a primary factor. This evidence comes from diet and browse preference studies as well as studies demonstrating the coincidence of mortality with possum invasion (e.g. Mason 1958; Pracy 1962; Fitzgerald & Wardle 1979; Pekelharing & Reynolds 1983). Kamahi foliage is commonly the most important possum diet component (Nugent et al. 2000). In contrast, we are unaware of direct experimental evidence for possum browsing being the primary cause of tree death. It is also worth noting that possums now occur in many forests, with kamahi as a prominent species, without any stand-scale (or greater) kamahi death. In addition, Payton et al. (1984) and Beveridge & Franklin (in Wardle 1966) have evidence that stand-scale kamahi mortality occurred in central North Island forests apparently before possums were present. In some localities synchronous death of kamahi trees has been attributed to other factors, for example waterlogging and drought in the Kaimai Range (Jane & Green 1986). This cannot always be viewed in isolation, as Milligan (1974) considered that the susceptibility of woody species like kamahi to pathogen attack is compounded by stresses like drought. The native pinhole borer (*Platypus* sp.) beetles have been recorded from kamahi dieback stands in several locations (Payton 1989). Payton's (1989) experimental study that showed that the fungus *Sporothrix* sp. (associated with *Platypus* attack) can debilitate and kill otherwise healthy kamahi trees is the most conclusive evidence for a causal agent in the dieback of kamahi—although there are other possible primary causes. As the fungus impedes sapflow, inducing a wilt, and because *Platypus* population build-up is favoured by dry conditions, it is sometimes difficult to partition the impact of this pathogen from drought in natural tree populations.

Bellingham et al. (1999b) provided a robust analysis of whether, in general, kamahi mortality in New Zealand forests exceeds recruitment. Nine localities (each usually more than several thousand hectares) were selected throughout the country representing a range of environments and possum histories, and each had been sampled representatively by permanent plots. Tagged individuals were used to calculate average recruitment and mortality for each locality (for between 14 and 23 years). In eight of these localities, mortality of kamahi trees was less than, or approximately equal to, recruitment. Only at Pureora did

annual mortality (6.6%) far exceed annual recruitment (1.8%). This is a very high mortality rate and could have a similar consequence for kamahi to that observed in the Ruahine Range, although there is some recruitment at Pureora.

3.2 SOUTHERN RATA (*Metrosideros umbellata*)

Flowering of southern rata is considered to occur every summer, but the intensity of flowering varies markedly among years and among trees at any particular location (Wardle 1971). Quantitative data on factors predisposing flowering (and seeding) are not available, yet it has been suggested heavy flowering usually occurs in years following a dry summer. Flowering occurs between December and March, becoming later with increasing altitude. The colourful red flowers contain nectar and are pollinated by a range of animals, e.g. tui (*Prosthemadera novaeseelandiae*) and honey bees (*Apis mellifera*). As is the situation for kamahi, we know little of how native pollinators of southern rata are affected by introduced fauna. Airborne pollen is rarely transported beyond the canopy height of a tree (M. McGlone pers. comm.). This supports the importance of mobile pollinator assemblages, particularly in forests where southern rata trees grow as widely spaced individuals. Southern rata flowers are eaten by possums (Nugent et al. 2000) but, again, as for kamahi, the extent to which flower predation has a prehistory equivalent is not known.

Southern rata is massively variable in the amount of seed produced among years (see Section 4.2). The seeds of southern rata are small (c. 2.0 mm × 0.4 mm) and weigh less than 0.1 mg (Wardle 1971). The small seeds are shed from capsules that split open during winter and seeds are wind dispersed by early summer. In contrast to the pollen, seeds appear to be well dispersed (> 200 m) although they do not have special structures to aid in dispersal (Wardle 1991). Usually, in close proximity to forest containing southern rata, this species readily establishes terrestrially on landslide surfaces including those formed as rocky rubble or finer material (e.g. Wardle 1971; Stewart & Veblen 1982a). Many 'even-aged' stands containing southern rata in central Westland probably established after major Alpine Fault earthquakes (Wardle 1980; Wells et al. 1998). In an extensive southern rata dieback area in the Kokatahi Valley, Allen & Rose (1983) observed few southern rata seedlings present on recent landslide surfaces greater than 300 m from a seed source. As seedlings were more abundant on landslide surfaces near intact forest, these authors suggested that seed dispersal may be a more important factor controlling regeneration success than whether seed (flowers) were being produced. It is unclear how general this pattern is among forested areas experiencing southern rata dieback. Southern rata can also establish on surfaces exposed by glacial retreats in Westland, following fire and, at some locations, on sand dunes. Browsing by possums has been recorded on southern rata seedlings growing in the open conditions of these early successional communities.

There are several detailed studies of population dynamics of relatively intact stands of southern rata based on time-specific stand reconstructions. On relatively stable sites (often ridges) in central Westland, few southern rata seedlings were encountered because this species regenerates intermittently (Veblen & Stewart 1980; Stewart & Burrows 1989). Such intermittent

regeneration results in the development of mixed-age stands. Although some of these individuals establish terrestrially, a high proportion (> 70%) of seedlings can be found on raised surfaces such as logs, stumps, and upturned root plates (Wardle 1971; Stewart & Veblen 1982a). In some of these stands, southern rata trees have diameters in excess of 200 cm (Fig. 2A). This, in combination with their relatively slow diameter growth rates (1.9 mm/year, mean of 14 stem discs from three locations in Westland and calculated as diameter/age), indicates how long-lived some trees can be, and the apparent stability of some parts of the generally dynamic Westland landscape. Sometimes southern rata trees exhibit growth forms where they lean over until their trunks lie prostrate along the ground, from which they can reproduce vegetatively. This has been observed on granitic domes in Westland (e.g. Hohonu Range), on steep slopes near the upper altitudinal limit of southern rata, in the coastal forests on Stewart Island, and on the Auckland Islands (Wardle 1971; Veblen & Stewart 1980; Reif & Allen 1988). One possible explanation for this growth form is that the wood is so dense that large trees collapse on substrates unable to support the immense weight that develops. In other than conifer broadleaved-hardwood forests, southern rata can be locally abundant, for example on exposed rocky substrates (e.g. Omihi, north Canterbury) or stunted forest on infertile ridges (e.g. Coromandel Range). Quantitative information on the dynamics of these stands, often setting the distributional limits of this species, is not available.

Extensive dieback of southern rata trees in some conifer broadleaved-hardwood forests has been documented over the last century (e.g. Chavasse 1955; Pekelharing & Reynolds 1983; Rose et al. 1992). It is this type of dieback that has invoked most of the concern about this species over the last 50 years. An extreme example of southern rata dieback was recorded in a survey plot (54 m × 36 m) established at 700 m elevation in the Kokatahi Valley in 1983. At this time all 32 southern rata stems were dead (Fig. 2A). These included stems with a wide range of diameters, and Allen & Rose (1983) suggested that these are likely to be 'mixed-age' stands. No live trees, or saplings, of southern rata remained in

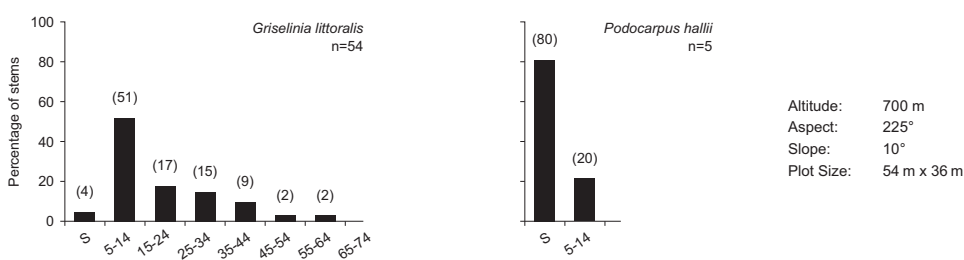**A. Dead Stems**
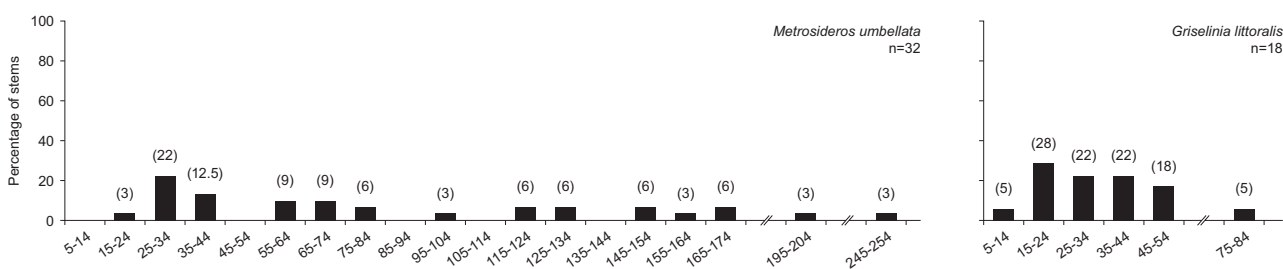
B. Live Stems

Figure 2. Percentage of dead (A) and live (B) stems for canopy tree species in diameter size classes for a 0.1944-m² plot at 700 m elevation in the Kokatahi Valley. Size classes used are S (Saplings) for stems with diameters < 5 cm and then stems in 10-cm-diameter classes.

this stand (Fig. 2B), and one etiolated seedling was the sole representative of the species on 180 m² of seedling plots measured on logs, tree fern trunks, and the forest floor over the 1944-m² plot area. Recent observations (P. Bellingham pers. comm.) in Kokatahi dieback stands suggest there may now be more southern rata regeneration than there was in the early 1980s. Notwithstanding this, because of the long-lived nature of southern rata, a return to the pre-dieback forest structure is at least a millennium away, assuming such a recovery is actually possible.

There has been a long debate as to what is the primary cause of synchronous dieback in southern rata. Defoliation by possum browsing has commonly been invoked as the cause. The clear exceptions are those areas where dieback pre-dates the establishment of possums or where possums have never been present. Coastal dieback is a prominent feature on islands where possums have never been present; for example, on Bench, Rose, Queen, and Enderby islands (Taylor 1971; Wardle 1971; Veblen & Stewart 1980). This coastal dieback is similar to that occurring in coastal areas where possums are present; for example, the south coast (Fiordland), the Catlins, and Stewart Island (Wardle 1971). The primary cause of this coastal dieback may be sea spray associated with storms, although fire may also be a factor on subantarctic islands. In some areas where possums are now present canopy dieback occurred before the build-up in animal numbers (e.g. Morgan 1908; Douglas in Holloway 1957). Even in areas where possums have been present, not all trees or stands appear susceptible.

Some examples include:

- Young, even-aged stands remain vigorous among dieback stands of larger trees (e.g. Chavasse 1955; Veblen & Stewart 1982a). Further, some researchers argue that the synchronous senescence of trees is an essential contributory factor to the mortality (e.g. Stewart & Veblen 1983). However, as Figure 2 suggests, it is unlikely that all dieback stands are even-aged.
- Plant community analyses have shown that a higher proportion of plots containing dead trees occur in vegetation on more fertile soils than on less fertile soils (Reif & Allen 1988). From this it has been hypothesised that forests on less fertile substrates may be a less desirable habitat for possums.

It may be expected that conclusive evidence for possums being the primary factor for dieback would come from direct observation of browse, levels of defoliation, and tree death. In reality, the widely collected evidence linking levels of foliage browse to possum control (possum density) is often weak—let alone being able to explicitly link browse to tree death. Even in the few instances where possum access to southern rata crowns has been stopped (by banding trees), over time the banded trees may show no recovery above that observed in non-banded trees (e.g. on Stewart Island, K. Pekelharing unpubl. data). Often the long-term observational records needed to detect differences in forests have not been maintained. Another constraint is that research usually focuses on those areas with a perceived possum problem—so the tree crowns may already be thinned. Payton (1988) has shown that in canopies opened up by possum browsing, exposed leaf bunches continue to deteriorate, even in the absence of further browse. The loss of large tree crowns leads to opening up of stands and continuing damage by wind, fungi, and insects (Payton 1988). Pathogens have always been considered a secondary factor in southern rata dieback (e.g. Hoy 1958), but this requires further evaluation.

Bellingham et al. (1999a) have suggested that time-specific surveys indicating excessive mortality of southern rata may be a consequence of this species' dead stem durability. Instead, these authors used permanent plots that representatively sampled Kokatahi forests to show (at least from the early 1970s) that rates, and directions, of southern rata population change depended on location in the forest mosaic—increasing in some and decreasing in others (Fig. 3). Over 23 years there has been a catchment-level decline in southern rata stem biomass of 17% (Fig. 3), which is not beyond the range seen in nearby beech forests (Harcombe et al. 1998). Certainly, southern rata has not yet been lost from the catchment and time-series data suggest the mortality is hardly synchronous.

1972$\bar{x}$ = 92.5 tonnes/ha
1979$\bar{x}$ = 94.4 tonnes/ha
1995$\bar{x}$ = 77.1 tonnes/ha
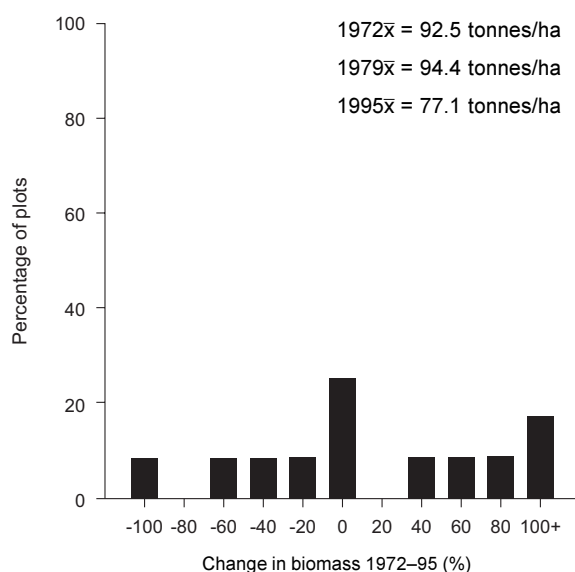
Figure 3.   Changes in stem biomass for southern rata in the Kokatahi Valley based on measurement in 1972 and 1995 of tagged individual tree stems on 22 permanent plots. Also given is the mean southern rata stem biomass for the three measurements of these plots (from Bellingham et al. 1999a).

3.3   NORTHERN RATA (*Metrosideros robusta*)

Northern rata is a conspicuous component of lowland-lower montane forest (< 800 m a.s.l.) throughout the North Island and in the South Island (Knightbridge & Ogden 1998) to about Blenheim in the east and the Taramakau River in the west (Wardle 1991). Trees of 425 cm diameter and at least 35 m tall have been recorded (Burstall & Sale 1984). Although found mostly on deep soils, northern rata is almost as well adapted as pohutukawa (*M. excelsa*) to rupestral (rocky) environments (Wardle 1991). In recruitment, it is a light-demander that contributes to the canopy or emergent tiers following establishment either as an epiphyte or terrestrially, the latter passing through a seral (successional) stage (Wardle 1991).

Flowering occurs from December to January and vegetative growth from January to March (Meads 1976). Twigs elongate 70–80 mm annually and leaves remain for 3–4 years. Leaves are shed throughout the year but with a summer peak. Partially browsed leaves are shed earlier than undamaged leaves. Northern rata has light, wind-dispersed seed, but low seed viability as indicated by an average 3% germination in growth cabinets (Knightbridge & Odgen 1998). It produces abundant aerial roots (Beddie 1953), as does pohutukawa, with which it hybridises. Adventitious roots have maximum descending growth of 1.2 mm/day in the field.

The decline in abundance and distribution of indigenous pollinators, such as lizards and nectivorous birds, may threaten the survival of the species in some places (Burns 1996), although introduced honey bees may have offset the loss of indigenous pollinators. Northern rata's high nectar output has important implications for ecosystem nutrient cycling as a food source for indigenous nectivorous bats, birds, and insects (McKessar & Sawyer 1999).

In established forest northern rata usually starts life as an epiphyte on podocarps such as rimu (*Dacrydium cupressinum*) or broad-leaved trees such as hinau (*Elaeocarpus dentatus*) or pukatea (*Laurelia novae-zelandiae*). Northern rata trees with solid trunks mostly signify terrestrial establishment, which is common on steeper or exposed sites, whereas hollow-trunked trees commenced life as epiphytes. In tree-fall-gap-disturbed forest the spatial and size-class pattern of northern rata would relate to host availability and dynamics. Sites with a history of exogenous disturbances will have size-class distributions determined either by terrestrial establishment or by the host dynamics and its own longevity. As with most other tree species that exploit catastrophic disturbance, its seed is wind-dispersed.

Knightbridge & Ogden (1998) found that northern rata preferred host trees > 50 cm in diameter. They found that puriri (*Vitex lucens*), dead trees, and the podocarps rimu, kahikatea (*Dacrycarpus dacryoides*), and miro (*Prumnopitys ferriginea*) were 'preferred' hosts at a range of northern North Island sites. Hall's totara and pukatea were 'preferred' at some sites but not at others. The tree ferns *Cyathea cunninghamii* and *C. smithii* and the nikau palm (*Rhopalostylis sapida*) also featured as hosts. Druce (1964) suggested that the podocarps, and especially rimu, are favoured hosts in Mt Egmont National Park. In all, 20 of 42 woody species acted as hosts to northern rata in northern North Island forests (Knightbridge & Ogden 1998). Despite dominating the basal area of some forests, kauri (*Agathis australis*) hardly featured as a host—possibly because the dry ridge sites favoured by kauri may hinder the descending root phase of rata establishment. Branch forks were the usual establishment sites for rata in the flaking-barked, usually emergent, rimu and miro. Overall, sites with accumulations of organic matter and/or horizontal surfaces were 'preferred' on a range of blister-barked, smooth-barked, or flaking-barked species, including rewarewa (*Knightia exselsa*), pukatea, taraire (*Beilschmiedia tarairi*), tawa (*Bielschmiedia tawa*), kohekohe (*Dysoxylum spectabile*), and puriri. The proportion of epiphytic rata increased with the time since the last disturbance and, overall, host size rather than species appears to be the most important factor limiting establishment. Knightbridge & Ogden (1998) concluded that as large trees tend to be old, there has simply been more time for northern rata to establish on them than on smaller trees. Alternatively, terrestrially-established populations seemed to be correlated with disturbance events at scales from tree-falls to catastrophically cleared gaps (Knightbridge & Ogden 1998). Emergent northern rata can therefore be described as a long-lived pioneer that requires gaps for successful regeneration but that can also regenerate as an epiphyte.

Fitzgerald (1976) showed that northern rata contributed 30% to the foliar diet of possums in lowland podocarp-broadleaved forest of Orongorongo Valley, with little monthly variation in its consumption. Mason (1958) noted that flower buds are eaten in winter and flowers in January, with some evidence that

flowers are preferred over leaves when available. Leaves of northern rata have low (5.5%) protein content and comparatively high fibre content. Atkinson (1992) confirmed Mead's (1976) observation that newly emergent leaves between January and March were generally not browsed until they are fully expanded and hardened. Other work suggests forage selection of northern rata by possums is based on leaf chemistry (Burns et al. 1998). Studies to identify antiherbivory compounds in the leaves of southern rata are underway (I. Payton pers. comm.).

Meads (1976), in the Orongorongo Valley, noted that heavy and sustained possum browse can kill trees in 3 years, after a total of 11 out of 50 monitored trees died in 5 years. Projecting forward, these figures raised the prospect of all study area rata dying by 1993 (Brockie 1992). Cowan et al. (1997) observed no further death of Mead's (1976) surviving study trees through to 1994, but additional trees had died close by. Campbell (1990) using the same 2.25-ha plot as Meads and Cowan et al., recorded 15% loss of northern rata basal area for stems > 10 cm dbh between 1969 and 1985. In another study, de Monchy (2000) recorded 26% death of 62 monitored trees between 1995 and 1999 in the Coromandel Range.

These studies suggest that certain trees are susceptible to possums and others may withstand their attacks in some forest types. Possums show highly variable preferences for individual trees. Meads (1976) found that tree size, shape, or form, whether growing epiphytically or terrestrially, was not correlated with browsing pressure. However, he concluded that in the Orongorongo study area with c. 10 trees/ha and c. 1 possum/tree and consistent annual cropping there is little chance for regeneration for the species. Cowan et al. (1997) suggested that browsed trees may be able to recover in periods of lower possum density as did Payton (1985) for southern rata. Increasing levels of defoliation corresponded to years of above-average possum density and to other stress factors such as drought. Efford (1991, and unpubl. data) showed that the density of possums fluctuated with no regular pattern, but that there were periods of below average density for more than 2–3 years that Meads (1976) suggested were the minimum required for recovery from browsing. Meads suggested that patchy feeding patterns resulted from differences in tree access, exposure, and nutrient quality. In agreement with Payton's (1988) observations for southern rata, Cowan et al (1997) noted more exposed northern rata were more heavily browsed and defoliated. This could reflect a site-determined possum preference, or an increased susceptibility to defoliation may result from damage from wind, insect browse, and disease. However, Atkinson (1992) found no relationship between exposure and severity of browsing on rata in Kapiti Island's comparatively young forests (generally < 100 years old). Atkinson (1992) suggested several reasons for the unpredictable distribution of browsed and unbrowsed individuals of the same tree species. Microsite differences in soil properties might affect the palatability of foliage; the total nutritional values of the foods available to an individual possum within its regular feeding range may influence what trees it chooses to browse; individual possums may have different taste preferences, or exhibit different behaviour responses to undefined social factors. It is also possible that foliage palatability changes following browsing (Payton 1983).

By comparing possum-trapped with untrapped blocks, Brockie (1992) showed that many rata and kamahi continued to die in blocks where trapping maintained possums at approximately half the density of the untrapped study area. Therefore, commercial trapping may slow, but not halt, forest degradation. Although Payton et al. (1997) recorded variable recovery of northern rata following possum culling at Waipoua, other studies (Atkinson 1992; Broome 1995b; de Monchy 2000) report substantial and rapid recovery. Possum eradication from Kapiti Island resulted in rapid recovery of the previously debilitated northern rata population there. The species can be highly resilient, as shown by its capacity to recover from severe defoliation levels (Campbell 1990).

Knightbridge & Ogden (1998) suggested that even-aged/sized terrestrial stands of northern rata may be less vulnerable to possum damage while in their natural thinning stage. They may become become more vulnerable to possums (and other forms of disturbance) once they reach maturity (see also Payton 1988 and Stewart & Rose 1988 for southern rata). By largely eliminating regeneration in epiphytic populations, possums may pose a threat to the long-term presence of this species (Knightbridge & Ogden 1998). Atkinson (1992) recorded heavy possum browse of terrestrially established saplings on one part of Kapiti Island.

Knightbridge & Odgen (1998) also found that insect browse of artificially established seedlings on tree hosts was greater than that of possums. Atkinson (1992) recorded 33% frequency of low-intensity browsing by insects, particularly stick insects, on Kapiti Island northern rata in 1975.

Emergent trees are not ideal candidates for ground-based scoring systems of foliar health such as the Foliar Browse Index method (Payton et al. 1999) because of their distant foliage and often multi-tiered architecture. Nevertheless, selection of this species as a browse indicator (Broome 1995a and 1995b; de Monchy 2000) reflects its association with many forest types across a varied environment, its palatability to possums, its response to possum browsing rather than to changes in other environmental factors, and its recovery potential when possum numbers are reduced so that its indicator function remains should possum numbers increase again (Atkinson 1992). As a component of possum browse pressure, high trunk use of northern rata reflects three factors: its foliage is highly preferred; its often high epiphytic loading can consist of preferred species; and its hollow trunks provide abundant roost sites (Meads 1976).

We have found no information from exclosure plot studies of the impact of ungulates on terrestrial seedlings and saplings.

There have been some observational reports of the widespread elimination of northern rata from the flanks of mountain ranges and lowland districts. The previously conspicuous northern rata component of podocarp-broadleaved forests of the southern Ruahine Range is extinct in most catchments and reduced to isolated individuals in the remainder (Rogers & Leathwick 1997). Elder (1957) indicated that northern rata was eliminated from the southern Ruahine Range early in the era of gross transformation of its forests. According to Druce (1971) it is nearly extinct in the Aorangi Range, southern Wairarapa. Overall, northern rata has gone through a large contraction in its lower North Island range (McKessar & Sawyer 1999). In the Orongorongo Valley, rata trees

of all sizes and on all sites have been dying since the 1930s (Brockie 1992). On most higher bluffs in the southern Rimutaka Forest Park no living rata trees remain (Brockie 1992).

Over recent decades, the spread of possums through Northland has been flagged by dieback of northern rata (Wardle 1991). However, Wardle (1991) reported that northern rata on the coastal ranges of west Nelson was generally healthy, although possums had been present for many years. This contrasts sharply with the North Island, where the theme is of substantial depletion of populations.

3.4 HINAU (*Elaeocarpus dentatus*)

From 1978 to 1984 hinau flowered yearly between November and January in the Orongorongo Valley (Cowan 1990). Although the flowers and flower buds of hinau are probably browsed by insects and birds, as they are a high nutrient source, this has not been quantified. In contrast, analyses of possum faeces show flower stamens and anthers were eaten from September to February, and flower buds from January to September (Cowan 1990). A possum removal experiment has shown that these animals depress the level of fruiting (Cowan & Waddington 1990). Although leaves are browsed, with a spring peak, their use is low relative to their availability (Fitzgerald 1976; Cowan & Waddington 1990). Cowan & Waddington (1990) favour the interpretation that fruiting is depressed because possums feed extensively on flower buds and flowers rather than browsing on leaves. The showy white flowers are probably insect pollinated, and the simple radially symmetrical flowers with exposed pollinating surfaces typify those for pollinating mechanisms that operate in an imprecise manner (Lloyd 1985). We are unaware of any detail on the pollinators involved, but it seems likely that such unspecialised flowers may be visited by a broad spectrum of insect pollinators. In summary, it would seem likely that if there is a demographically significant change in fruit production brought about by human-related impacts, it more likely operates through altering the number of flowers produced rather than pollination efficiency.

Although, as Lloyd (1985) has pointed out, we have little detailed knowledge on fruit production in the New Zealand flora, or their dispersal, and predation, partial data do exist for some sites for hinau. The fruit of hinau is a drupe, oval in shape, and about 1 to 2 cm long. We know the large fruits of hinau are consumed by kaka (*Nestor meridionalis*), brown kiwi (*Apteryx australis*), kereru, kokako (*Callaeas cinerea*), weka (*Gallirallus australis*) and, in the past, huia and, possibly, moa (e.g. Buller 1888; Leathwick et al. 1983; Clout & Hay 1989; Moorhouse 1997). In some instances, seeds within fruits are destroyed by birds that gnaw the fruit (e.g. kaka). In other birds (e.g. kiwi and the now extinct moa) seeds may be abraded in the gizzards but still remain viable, whereas in others (e.g. kereru, *Hemiphaga novaeseelandiae*) they pass through the bird intact (Clout & Hay 1989). A significant proportion of hinau nuts can be gnawed open by Norway rats (*Rattus norvegicus*)—although this is not necessarily just a recent pressure as Polynesian rats (kiore, *R. exulans*) have been present for > 500 years and feed in a similar way on many fruits (Brockie 1992). Because of the longevity of hinau trees (> 500 years), and their sparse

distribution, it will be a challenging task to determine, in the short term (decades), any impacts of seed predation on the viability of hinau populations. This viability would also need to be assessed in a spatial context because of changes in dispersability.

Details about the dynamics of hinau are uncommon in the literature in part because this species is sparse on the landscape and is therefore not adequately represented in data collected for more general purposes. Even though sparse, hinau can be frequently associated with certain other species, for example, in central Westland hill country, Reif & Allen (1988) have described this species as commonly co-occurring with rimu and kiekie (*Freycinetia baueriana*). We are not aware of any studies focusing on the population dynamics of hinau. Esler & Astridge (1974) noted that hinau was present in secondary successions following abandonment of pastures, or after fires, in the Waitakere Range. In this instance hinau saplings were present under a much taller kanuka (*Kunzea ericoides*) canopy. Certainly, our review of the literature did not indicate anywhere that it is a common species in secondary successions—and, therefore, in a position to markedly extend its range.

In relatively intact forest, Smale et al. (1997) considered hinau to be less shade tolerant than most of the dominant broadleaved hardwood species in central North Island forests. Seedlings usually establish terrestrially, and are abundant (Smale et al. 1997). In contrast to other broadleaved hardwoods in Tongariro National Park forests, the multi-aged population structure of hinau reflects the ability of this species to take advantage of frequent small canopy gaps (Lusk & Ogden 1992). By growing rapidly in these small treefall gaps the species can overtop competitors and reach the canopy. Hinau is usually ranked as having low palatability to introduced browsing animals and so concern has not focused on its regenerative ability. Diameter growth rate comparisons with other co-occurring conifer and hardwood trees suggest hinau can be a relatively rapidly growing species (Lusk & Ogden 1992). Although there are apparently some observations of synchronous hinau mortality in North Island forests—these appear to be localised and are not usually associated with possum browsing (e.g. Herbert 1986). Atkinson (1992) has associated hinau death on Kapiti Island with possums.

Hinau is not an abundant species at a stand scale; for example, at Pirongia and Pureora its average plot basal area (plot area 400 m^2) is less than 3 m^2/ha (Table 2). At Pirongia, basal area declined between 1979 and 1987, reflecting tree mortality higher than recruitment. When the time scale was extended for the same set of plots from 1979 to 1999, there was, instead, a small increase in average basal area and the mortality rates were only marginally higher than recruitment rates (Table 2). The higher mortality in the early time interval appears to be a consequence of relatively high mortality of small-diameter trees. At Pureora there has been a marginal increase in basal area with tree recruitment higher than mortality (Table 2). Hinau has increased in basal area and stem density between 1969 and 1994 on a 2.25-ha plot in the Orongorongo Valley (Bellingham et al. 1999a). Such evidence indicates that hinau is maintaining its representation in the canopy of these forests. Similar quantitative data were not available to examine demographic processes in forests where this species was less frequent or abundant.

TABLE 2. DEMOGRAPHIC PARAMETERS FOR HINAU AT PIRONGIA (15 PLOTS) AND PUREORA (28 PLOTS) IN THE NORTH ISLAND. THE PARAMETERS ARE CALCULATED FOR ALL TREES OF THIS SPECIES, OVER SPECIFIED TIME INTERVALS, FOR TREES > 25 mm AND >100 mm (P. DE MONCHY UNPUBL. DATA).

LOCALITY	PERIOD OF MEASUREMENT	TOTAL NUMBER OF STEMS		MEAN BASAL AREA (m²/ha)		RECRUITMENT (%/YEAR)	MORTALITY (%/YEAR)
		INITIAL	FINAL	INITIAL	FINAL		
Pirongia							
> 25 mm	1979–87	21	13	1.1	0.7	1.5	7.4
> 100 mm	1979–87	12	10	1.0	0.7	1.7	4.1
> 25 mm	1979–99	21	22	1.1	1.5	1.6	2.5
> 100 mm	1979–99	12	15	1.0	1.4	1.8	1.7
Pureora							
> 25 mm	1975–93	50	69	2.2	2.4	1.7	0.9
> 100 mm	1975–93	29	38	2.1	2.3	1.6	0.9

5.5 RED BEECH (*Nothofagus fusca*)

Red beech, like the other New Zealand beeches, is monoecious and spring flowering, with male flowers shedding pollen a few days before the female flowers are receptive (Ogden et al. 1996). Flowering varies from September to January depending on altitude, latitude and aspect, but generally coincides with leaf loss and renewed shoot growth. A hot, dry summer in the preceding season stimulates prolific flowering (Poole 1955) and this pattern usually occurs at intervals of 3 to 5 years. Such prolific flowering is generally (but not always) associated with abundant seeding in the same season (Wardle 1984). The amount of seed produced varies greatly from year to year and extremely heavy seeding years occur with a frequency of 3 to 11 years (Wardle 1984). This intermittent pattern of seed production has important conservation implications for the welfare of native bird populations because of the build-up of predators after seeding (see section 4.5).

Seed usually falls in March, April and May. Seeds are winged and, for the most part, are dispersed to distances of less than 100 m. About 85% fall at distances less than tree height. In rare instances, seed may be dispersed up to 25 km from isolated stands (Haase 1990). Germination is highly variable and normally greatest with a temperature of 22–26°C (day) and 18°C (night). Germination is improved by stratification, with an optimum period of 70 days (Ledgard & Cath 1983). Although immediate germination may occur, most seeds remain dormant and germinate the following spring (September to December). Following a mast year in 1990 in red-silver beech (*N. fusca-N. menziesii*) forest in north Westland, Stewart (1995) recorded populations of up to 2 500 000 seedlings/ha. Seedling mortality is initially very high and the surviving seedlings then comprise an 'advance growth' population (June & Ogden 1975).

Seedling survivorship is determined primarily by variation in the microsite conditions on which they establish (June & Ogden 1975). In general, seedling survivorship is highest on elevated microsites such as tip-up mounds, stumps, and fallen logs (Stewart & Rose 1990). In north Westland red-silver beech

forests, Stewart & Rose (1990) found that c. 50–75% of seedlings > 15 cm occurred on these elevated substrates, which made up only about one-third of available microsites in the forest understorey. Seedlings that do establish directly on the forest floor suffer high mortality if the litter layer dries in summer. Elevated substrates are even more crucial for seedling survival when a dense fern or shrub understorey is present. In red beech forests of the Ruahine Range in the central North Island, June & Ogden (1975) found that differential mortality progressively restricted seedlings to fallen logs. Seedlings in dense shade beneath the ground cover of ferns (*Dicksonia lanata*) were quickly eliminated (June & Ogden 1975).

Concern has been expressed about a perceived lack of red beech regeneration in some areas of New Zealand, especially where the previous forest canopy has collapsed (e.g. Ruahine Range). In many instances the lack of regeneration has been attributed to browsing by introduced animals such as red deer (*Cervus elaphus*). However, red beech is generally regarded as of moderate to low palatability (Wardle 1984). It is more likely that the lack of regeneration is due to other causes such as the absence of a readily available seed source, seed predation, or lack of suitable establishment sites (Wardle 1991). Rogers & Leathwick (1997) have suggested for the Ruahine Range that red beech regeneration is being smothered by unpalatable grasses and shrubs that have established after the removal of palatable species by deer. In some of the areas of concern it may be that our existing understanding of the regeneration ecology of red beech is inadequate to explain the scarcity of seedlings. In these instances further research on stand dynamics may be required.

Seedling growth rate is highly variable, depending on the environment. Under low light conditions suppressed red beech seedlings may add only 1 or 2 mm/year whereas under good light conditions and plentiful moisture height growth rates in excess of 50 cm/year are observed (Ogden et al. 1996). Seedling density influences height growth rate. Natural populations of seedlings, saplings and adult trees often have inverse-J-shaped size frequency distributions, which suggest self-thinning hierarchies. The importance of density influencing growth is evident; when thinning trials are carried out in these populations, marked increases in growth rate occur (e.g. Franklin 1976).

Recruitment to the canopy occurs when an opening in the canopy (a 'gap') is formed by disturbance. Various natural disturbances including wind, snowbreak, drought, and insect attack create canopy gaps. Red beech displays rapid height growth rate in response to these openings, capturing the canopy space before many other species can attain similar height. For example, in mixed red–silver beech forests, red beech can attain the canopy in as little as 100 years, rapidly out-competing the slower-growing silver beech (Stewart & Rose 1990; Runkle et al. 1997). The faster growth rate of red beech is related to differences in leaf structure and longevity. Its leaves are strictly annual and are renewed in the spring flush associated with leaf fall (Wardle 1984). In contrast, leaves of silver beech are retained for up to 3 years (and in extreme instances up to 5 years). The greater leaf longevity, slower growth of seedlings, and variable adult growth rates suggest that silver beech is more shade tolerant than red beech. Gap size has a significant effect on relative height growth rates, red beech having a clear advantage over other species such as silver beech in larger gaps (i.e. > 400 m², Stewart et al. 1991). The patterns of canopy recruitment are

more complex in red beech forests with a conifer and/or hardwood component and vary in relation to stand disturbance history and site fertility and drainage (Urlich 2000).

Red beech is relatively long-lived, typically reaching 400+ years and perhaps 500–600 years in extreme cases (Ogden et al. 1996; Stewart & Rose 1990). Mortality of seedlings and small stems is high, and declines with age until trees begin to become overmature (Wardle 1984). Mortality of the canopy can be relatively synchronous and occur over relatively large areas as a result of drought and insect attack. In the Maruia Valley, north Westland, spring droughts during the period 1974 to 1978 were followed by an outbreak of the scale insect *Inglisia fagi* and the subsequent death of many red beech trees in valley floor forests (Fig. 4; Hosking & Kershaw 1985). Maruia Valley red beech trees showed more than 60% foliage loss over 5000 ha in September 1978 and up to 75% of mature red beech were dead in February 1980 after an outbreak of pinhole borer beetles (*Platypus* sp.) in 1979 (Hosking & Kershaw 1985). This widespread canopy mortality released advanced-growth seedlings, resulting in the rapid recruitment of a new, relatively even-aged stand. Such even-aged stands are prone to synchronous mortality and many of the extensive areas of 'dieback' that are observed from time to time reflect synchronous establishment (Ogden 1988). Such widespread tree death may occur every 100 to 400 years (Ogden et al. 1996).

Other large-scale natural disturbances may also result in the development of even-aged stands. The Murchison earthquake (Magnitude 7.7) triggered hundreds of landslides within an area of 5000 km^2 of mixed species beech forests in north Westland in 1929 (Pearce & O'Loughlin 1985). The age structure of the beech forests showed an increase in red beech establishment after the earthquake, even on assumed stable landforms (Vittoz et al. 2001). Even-aged stands established on landforms most devastated by the earthquake such as alluvial fans and unstable sideslopes. Windstorms also flatten extensive areas of beech forest; an example is the 1981 event in the Waimakariri Catchment in inland Canterbury (Wardle 1984).

Figure 4. Areas of red beech mortality (lighter shading) in the Maruia Valley, north Westland, in 1980, about 5 years after the onset of a drought-related dieback event in the mid-1970s.

In between dieback events or in forests where extensive dieback is uncommon, mortality is less evident, occurring in trees of varying size and in single tree to several trees in patches. This pattern forms almost annually (Stewart et al. 1991). In mixed red–silver beech forests of the Maruia Valley, north Westland, gaps in the canopy are predominantly formed by the death of large red beech trees. Gaps may be formed by dead standing trees or by dead standing and live trees that are blown down or snapped. Gaps commonly occupy 4–15% of the land area and range in size from 25 to 525 m^2 (Stewart et al. 1991). A variety of biotic and abiotic disturbances may lead to the death of single trees or groups of trees. These include pinhole borer beetles, drought, windsnap, snowbreak, toppling by earthquakes, windthrow, co-opted windthrow, crushing by falling live or dead trees,

defoliating insects, and lightning strike. This results in highly variable annual mortality. For example, from as little as one to as much as 32 m³ of logs and snags > 20 cm dbh were formed annually over the period 1987 to 1998 in the Maruia forests (Stewart 1997). In one extreme case (1994) mortality contributed 147 m³/ha of logs and snags to the detrital pool. Large gaps tend to favour the regeneration of red beech whereas small gaps (generally < 400 m²) are more commonly captured by the more shade-tolerant silver beech or closed by lateral crown growth of surrounding canopy trees.

3.6 PAHAUTEA (*Libocedrus bidwillii*)

Pahautea (New Zealand cedar) is wind pollinated and male cones are produced in abundance from spring to early summer. As with *Pinus radiata*, pollen-laden male cones may be an attractive food for possums. Mature pahautea are believed to produce cones and seed annually (Hinds & Reid 1957; Rogers pers. obs.) but, like most tree species, wide yearly fluctuations in quantity and viability of seeds are likely. Male strobili have been noted on c. 15-year-old cultivated trees, but female cones were absent (Rogers 1987). Seed of pahautea is particularly small (2.5–3.0 mm long, wing 5.0–5.5 mm long), light (c. 1800–2500 fresh seed/g), and the vestigial wings suggest adaptation for limited wind dispersal (Rogers 1987 p. 142). No information exists on its seed dispersal properties or whether the two fertile seeds per cone are shed separately or within the cone. Information on seed dispersal distances can be inferred from juveniles in seral shrub-tussockland and their proximity to old-growth parent trees (Rogers 1987). A dense seed rain covers < 80 m, although outlier trees occur up to 400 m from the nearest seed source. Strong and turbulent winds within the predominantly mountain environment of pahautea enhance its capacity to colonise the patchy availability of windthrow and mass-movement scars required for population rejuvenation. Seed predation by rodents and possums is possible, but the presence of some juveniles in most demographic studies suggests that survival of seed in recent times has been sufficient, where disturbance permits, for stand rejuvenation. Life expectancy is estimated to exceed 1000 years on some sites (Rogers 1987). Dead trees may remain standing for up to two centuries (Clarkson & Clarkson 1983; Xiong pers. comm. 1995). Pahautea, unlike most other subalpine shrubs and trees, retains its dead leaves for some time (Wardle 1963a). The growth patterns of pahautea are typical of most New Zealand conifers. Seedlings, saplings and young trees are generally scarce; seedlings, once established grow consistently, though slowly, under a closed canopy, but respond rather weakly to increased light; and adult trees usually form a sparse overstorey instead of a closed canopy (Wardle 1963a). Individuals may spend a century in the seedling stage (< 1.4 m tall, Ogden & Stewart 1995; Norton 1983) based on 40 years to reach 50 cm in height (Stewart & Rose 1989) and up to 100 years to reach 1 m (Norton 1983). The radial increment growth rates of pahautea are comparatively low for a New Zealand conifer (e.g. Scott 1972; Dunwiddie 1979; Norton 1983; Rogers 1987; Stewart & Rose 1989), averaging 0.5–1.7 mm/year.

New Zealand Forest Service reports from the 1950s onwards contained accounts of unhealthy-looking stands of pahautea from Westland and the central

North Island but these did not lead to research into causal mechanisms of apparently widespread decline. Pahautea did feature in several tests of a hypothesis ascribing a perceived regeneration failure spanning several centuries in a number of conifers to historical climate change. Several studies in both main islands using size and age data (Wardle 1963b, 1978; Chapman 1972; Goldthorpe 1968; Clayton-Greene 1977; Child 1978; Veblen & Stewart 1982b; Norton 1983; Boase 1988; Stewart & Rose 1989; Ogden et al. 1991; and summarised in Ogden & Stewart 1995) were used to reconstruct its population dynamics. The regeneration of pahautea may be generalised into catastrophic and gap-phase modes. In most cases relatively even-aged stands were encountered and inferred to reflect the effects of past windthrow, mass movement, fire, and volcanic eruptions on disturbance-prone sites. In addition, smaller-scale gap-forming events, such as treefall, predominated on poorly drained sites, where site stress reduced the abundance and vigour of the young trees of most of the species in the small gaps (Veblen & Stewart 1982b). So, pahautea forms more or less even-aged stands covering up to several hectares corresponding to catastophic, disturbance-induced, site renewal events, and uneven-aged, treefall-gap-stimulated regeneration on poorly drained sites. Consequently, most montane forests containing pahautea comprise a mosaic of differently aged cohorts, in most of which recruitment will be absent pending the next catastrophic disturbance (Boase 1988). Continuous recruitment via shade-tolerant seedlings beneath a forest canopy is not reported for the species. Several studies reported a lack of regeneration in more or less even-aged stands in the last 200–300 years (e.g. Stewart & Rose 1989). This has been interpreted as reflecting a period without catastrophic disturbance, apparently operating over a wide scale.

Two recent studies from the central North Island have combined pollen studies from peat bogs with an analysis of stand dynamics along environmental gradients to understand the ebb and flow of pahautea abundance through time. Across an altitudinal gradient on Mt Hauhungatahi, Tongariro National Park, Horrocks & Ogden (2000) predicted greatest long-term persistence for the species 'in the centre of its niche'. Beyond the centre, expansion and retreat are more likely at its 'niche margins' in lowermost montane forests and on subalpine bogs where just single cohorts are likely. Rogers (1997) showed bimodal characteristics of stands along an altitudinal gradient in Moawhango Ecological District. Lower montane stands were even-aged in a marginally dry climate with the greatest exposure to volcanic-ash-shower rejuvenation of soils. At higher, more humid altitudes and further from the Tongariro volcanoes, upper montane stands were all-aged, with treefall gap turnover patterns. The latter climate may be interpreted as closest to the species' optimum environmental conditions (Rogers 1989) with the more marginal lower montane stands reliant on catastrophic disturbance events for long-term landscape persistence. Integrating pollen studies (Rogers & McGlone 1989) with an analysis of the boundary dynamics between pahautea and beech forest communities (Rogers 1989) suggests that pahautea has been gradually giving ground to the more aggressive beech species throughout the last 10 000 years. Temporary but unsustained increases in pahautea abundance at lower altitudes probably resulted from infrequent volcanic ash showers.

Circumstantial and direct evidence for possum defoliation of pahautea has recently emerged (Rogers 1997). Close inspection of branchlets has indicated that defoliation is confined to terminal buds and leaves, and seldom occurs on the more mature scale-leaves subtending the bud. However, defoliation symptoms in the form of hedging are difficult to detect from the ground for the following reasons. The scale-leaves and terminal buds are tiny and difficult to visually separate (Fig. 5); the tree's tall conical or stag-headed profile means

Figure 5. Removal of terminal buds of pahautea by possums has truncated many branchlets. Possums may favour the emergent terminal shoots or just the male pollen or female ovule cones, which appear around terminal shoots in early summer. Decapitated shoots eventually turn brown and die.

lowermost and often distant branches only are visible; and possums seem to select individual branches randomly (similar to their use of northern rata (Meads 1976)). Following decapitation, the remaining scale-leaves of branchlets turn brown, then grey and, as dead foliage is shed, classic dieback symptoms develop (Fig. 6). Life expectancy of the imbricate or scale-leaves is unknown. Consequently, the time for dieback symptoms to appear following defoliation is also unknown but is likely to be within 3–4 years.

Direct evidence for defoliation of pahautea comes from a 2-year browse-preference study of possums from Hihitahi Forest Sanctuary (Rogers 1997). Pahautea was the third most preferred species in this upland conifer forest behind wineberry (*Aristotelia serrata*) and Hall's totara. Seasonal preference indices for pahautea ranged from near neutral (food use equals availability) in early summer to not preferred in winter (Rogers 1997). The inference is that immature foliage during shoot extension in early summer, and/or pollen and ovule cones only, are moderately attractive food for possums, but with advancing maturity of leaves pahautea attractiveness rapidly declines. Where pahautea foliage appeared in possum stomachs it frequently formed the bulk of that night's feeding. At 10% of summer and 7.8% of overall diets, pahautea was an important food item for possums at Hihitahi.

Figure 6. A dead young pahautea showing dieback systems of dead foliage and limbs. Immature pahautea have conical architecture, mature and overmature trees become stag-headed. Despite direct evidence of possum defoliation of pahautea, there is no explicit evidence linking this to death of trees.

Possums have previously not been strongly implicated in the decline of pahautea (e.g. Batcheler 1983), although its foliage has appeared at low levels in other dietary studies of possums. Two factors may have contributed to possums not being implicated. Browse sign is mostly inconspicuous on lofty trees, and traditional sieving techniques in dietary studies lose the masticated fragments of terminal buds in the washing process. A revised laboratory procedure now overcomes this bias (Rogers 1997). Dieback progresses as the apparently random death of a sequence of individual branches (c.f. northern rata). Changes in crown foliar density result not so much from consumption of individual shoots but from the death of entire branches after removal of a proportion of their terminal buds. We have no information on what proportion of branchlets must be decapitated to lead to the death of the entire branch, but it appears to be much less than all. The assumption that decapitated branchlets and branches eventually die is based on visual evidence over 2 years of several populations of banded trees. Individual twigs have little or no capacity to resprout after decapitation from their woody portions and a very limited capacity from their green leaflet portion (Rogers 1997). In almost all monitored instances, bud removal initiated an irreversible decline of the subtended scale-leaves (G. Rogers unpubl. data), often from the youngest to the oldest leaves of the twig (Fig. 5). We suggest further study to fully understand this trait. However, there are no explicit links between levels of defoliation and tree death. No South Island studies have examined evidence for possum defoliation of pahautea.

Evidence of trunk use by possums remains for many years in the thick excorticating bark of pahautea (and Hall's totara) because claw and tooth marks penetrate multiple bark layers. For this reason, reductions in possum use of trunks may not be immediately apparent. Further, not all trunk use is direct evidence of possum access to crowns for roosts or fodder; rather, scratching and bark biting on trunk bases appears to be part of ground-based territorial behaviour.

We have found no references suggesting that deer or goats consume pahautea foliage. At this stage, therefore, absence of pahautea seedlings and saplings cannot be ascribed to removal by ungulates.

Synchronous mortality of canopy pahautea was a feature of montane forests of central Westland in the 1890s (Holloway 1957) and was also evident near Dunedin in the 1950s (Wardle & Mark 1956). Dead pahautea, along with co-occurring Hall's totara, has been a conspicuous feature of upland conifer forests in Mt Egmont National Park, Moawhango Ecological District, and Ruahine Range of the North Island (Rogers 1997; Rogers & Leathwick 1997). Historical and present-day aerial photographs were used to judge the degree of mortality and dieback over recent decades. An estimated 25% reduction in the total area of pahautea- and Hall's totara-dominated forest had occurred in the last 35 years in Mt Egmont National Park and another 50% showed light to moderate mortality. Approximately 75% of Hihitahi Forest Sanctuary in Moawhango Ecological District, central North Island, was classed as having moderate to severe dieback and stand collapse. The picture from the northwestern, western, and southern Ruahine Range again was of substantial proportions of synchronous mortality in a range of forest types with abundant pahautea; again, over and above that evident in the 1940s and early 1950s. Grant (1984) linked substantial dieback of

beech forests in the eastern Ruahine Range early in the 20th century to a severe drought in 1917. Another severe drought affected central North Island in 1947. It is, therefore, not yet possible to confidently apportion the large synchronous increase in death of pahautea (and associated Hall's totara) in recent decades to either natural causes (e.g. drought) or to possum browse. To resolve this, tree death could be dated by cross-dating dead tree increment cores against living trees.

Stand structure analysis across the altitudinal range of sites in Moawhango Ecological District revealed 43% of basal area and 52% of pahautea stems were dead-standing in mid-montane sites across all size-classes. In addition, no seedlings or saplings were recorded from 8.01 ha of plots in Hihitahi Forest Sanctuary nor any seen in extensive survey of the 2500-ha forest, bar those on the fire-modified margins (Rogers 1997). Although substantial proportions of decaying stems and stumps on the forest floor indicate some mortality in most size classes over perhaps one to two centuries (depending on decay rates), the proportions of dead-standing to live stems were much greater than to be expected from natural stand turnover or when compared to those in other studies (Norton 1983; Stewart & Rose 1989). However, in the highest altitude, uneven-aged stands of the Moawhango, the much smaller proportions of dead-standing stems were implicitly assigned to what would be expected from normal density-dependent thinning.

Coincidentally, pahautea stands with advanced mortality were those with previously abundant possum-preferred species, namely wineberry, Hall's totara, lacebark (*Hoheria* sp.), tree fuchsia (*Fuchsia excorticata*), mountain five-finger (*Pseudopanax colensoi*), and mountain ribbonwood (*Hoheria* sp.). These mid-montane stands also received the greater depths of airfall tephra (Rogers 1987). It is also possible that the high-altitude, uneven-aged stands occupied stable and, probably, lower-fertility soils and co-occurred with unpalatables such as pink pine (*Halocarpus biformis*), mountain toatoa (*Phyllocladus alpinus*), bush tussock (*Chionochloa conspicua*), and small-leaved *Coprosma*. In this, the Moawhango pahautea forests show parallels with patterns of possum modification in Westland rata-kamahi forests (Reif & Allen 1988).

Recent research in Westland has established that many pahautea stands along at least 375 km of the Alpine Fault are even-aged and established after earthquakes in 1717, c. 1630 and c. 1460 AD (Wells 1998; Wells et al 1998; Wells et al. 1999). The extensive even-aged nature of these, and other forests, further supports the notion that much of the widespread synchronous mortality observed in Westland may be the result of natural stand dynamic processes, as suggested by Veblen & Stewart (1982a), Stewart & Veblen (1982b), Stewart & Veblen (1983). In this interpretation, stands that established after major earthquakes are attaining maximum longevity and are dying together.

On Banks Peninsula, every adult tree of pahautea except one died between 1941 and 1961 (Wardle 1991). Wardle (1978) suggested that low rainfall between 1947 and 1949 may be implicated and Norton & Molloy (1986) suggested that drought and/or exposure to desiccating southerly winds could be involved.

It is, therefore, not surprising that pahautea should emerge as a species of concern to forest managers of central North Island, Canterbury, and Otago. This is as much from the recent evidence of its possum defoliation as from their

inability to measure foliar health improvements or detect regeneration following possum control. However, if we are applying a robust interpretation of turnover processes from forest age-structures, forest managers will find juveniles only where the regeneration model predicts—in a spatial and temporal pattern determined by the history of catastrophic disturbance events or in treefall gaps. Stands corresponding to the perceived margins of its niche may have little evidence of second or subsequent generations of trees replacing the catastrophically initiated stand. Possum control may currently be justified on evidence of defoliation and unthrifty trees, but should include regeneration where the turnover model would predict.

3.7 HALL'S TOTARA (*Podocarpus hallii*)

Hall's totara, like most of the other New Zealand podocarps, is dioecious (Allan 1961). Male catkins form on short stalks in late spring. The fruit, which ripens from about May onwards, is an ovoid nut seated on an enlarged, succulent red peduncle (Cockayne & Phillips Turner 1967). Seed dispersal is often via birds; bellbirds (*Anthornis melanura*) are efficient dispersers of Hall's totara seed (Wells 1972) and it is likely that other native bird species are as well (e.g. kereru). Surprisingly little is known about the reproductive biology of the species, particularly for seed dispersal and seedling germination and establishment.

The seedling demography of Hall's totara has only been studied in a peripheral way in that it is often a minor component of forests dominated by other species. The highest density of seedlings (< 1.4 m tall) recorded are for stands in central Westland and inland Canterbury which reach 7000–12 000 seedlings per ha (Stewart & Veblen 1982a). In contrast, in Ruahine Range forests, subjected to severe dieback, Rogers (1997) recorded only 80–100 seedlings per ha. In comparison with other species such as southern rata, only a small proportion of Hall's totara seedlings, saplings, and trees are found on elevated surfaces such as logs, stumps, and upturned root plates (Stewart & Veblen 1982a).

Hall's totara is obviously a long-lived tree (Enright & Ogden 1995), although longevity for the species is not well defined. Wells (1972) estimated maximum ages of 660–1290 years based on counting annual rings on single radii. These are likely to be overestimates because they were based on extrapolation from short-increment cores that did not reach the chronological centre of the tree. However, Hall's totara trees commonly live for several centuries and probably often in excess of 500 years; trees of 60–70 cm dbh have been aged at 500–600 years near Otira, central Westland (G. Stewart unpubl. data). Since the species may attain diameters in excess of 100 cm dbh, even greater longevity is possible. Hall's totara (and pahautea) can remain standing for decades after death, as illustrated by extant Hall's totara spars whose death dates to the 1886 eruption on Mt Tarawera (Clarkson & Clarkson 1983).

There has been spectacular mortality of Hall's totara in many forests in New Zealand over the last several decades. It is generally argued that possum browsing is the cause of mortality (Rose et al. 1992). For example, in the Copland Valley in South Westland from 1978 to 1992, 31–44% of Hall's totara

stems > 3 cm dbh died on permanent reference plots in areas inhabited by possums (Stewart 1992). This was about three times the mortality of southern rata, a species commonly believed to be more palatable to possums. On plots where possums were rare, only 4% of similar-sized Hall's totara trees died over the same period. The presence of Hall's totara foliage in possum faeces and studies of possum browse (Rogers 1997; Nugent et al. 2000) has suggested that possums may be the immediate cause of tree death. Rogers (1997) found that Hall's totara was the second most preferred species after wineberry in the possum diet at Hihitahi Sanctuary. Although Hall's totara may be a prominent component of possum diet at certain times of the year in some areas, the degree to which mortality can be attributed to possum browsing is difficult to determine. That is because we have no idea of what proportion of the individual tree's foliage is being removed and what this means in terms of overall tree vigour. At Waihaha in the central North Island, annual foliage production of Hall's totara was in excess of 200 kg/ha whereas possum use was < 20 kg/ha (Nugent et al. 2000). Attributing Hall's totara mortality solely to possum browse obscures the complex nature of the mortality.

Bellingham et al. (1999b) conducted an analysis of recruitment and mortality of Hall's totara at locations across New Zealand based on the remeasurement of tagged individual trees on permanent plots (for details see section on kamahi). In four out of six localities where Hall's totara occurred, mortality exceeded recruitment; the most extreme case being the Kokatahi Catchment in Westland where 3.1%/year mortality over 23 years contrasts with nil recruitment over the same period. In the other two instances, recruitment and mortality were approximately in balance (Waitutu) or recruitment exceeded mortality (Tararua). It would appear that in extreme cases such as the Kokatahi Catchment, Hall's totara will become locally extinct in the short term (Bellingham et al. 1999b).

The population dynamics of stands containing Hall's totara have been little studied. In central Westland, Stewart & Veblen (1982a) examined regeneration patterns in mid-elevation rata–kamahi forests that also contained the conifers Hall's totara and pahautea. All four canopy species regenerated intermittently after both large- and small-scale disturbances. Hall's totara frequently established on slip surfaces, along with southern rata and kamahi. In south Westland, Hall's totara established in relatively even-aged stands along with pahautea on surfaces formed by major Alpine Fault earthquakes that have occurred about every 200 to 300 years (Wells 1998). In inland Canterbury, immediately east of the Southern Alps, Hall's totara is a relatively common component of stands dominated by pahautea and appears to have regenerated along with that species after catastrophic disturbances such as landsliding (Veblen & Stewart 1982a). Hall's totara seedlings, saplings and small trees were often prevalent in small canopy gaps resulting from recent canopy breakdown (Stewart & Veblen 1982a). Similar patterns of catastrophic and 'gap-phase' regeneration have been noted for Hall's totara in the central North Island (Rogers 1997). It is clear that research is required on the population dynamics of stands containing Hall's totara, especially in areas of dieback. One of the few quantitative studies available is that of Stewart (1992) for the Copland Valley and it was principally established for the purposes of monitoring possum defoliation, not stand dynamics.

An interesting feature of Hall's totara mortality in many areas is that individuals of all sizes appear to be affected (unlike the dieback patterns in southern rata, for example, where primarily large canopy trees are affected). In the Copland Valley in South Westland, Hall's totara stems from 3 to c. 120 cm dbh died over a period of 13 years, with many dead stems < 40 cm dbh (Fig. 7; Stewart 1992). Interestingly, numerous saplings were recruited into the populations over this period (a five-fold increase), resulting in a shift from relatively even-sized, to inverse-J shaped population structures more indicative of all-aged stands. In the central North Island Rogers (1997) also documented dieback across a range of diameters but regeneration was more variable; it was abundant at some sites, and almost totally lacking at others.
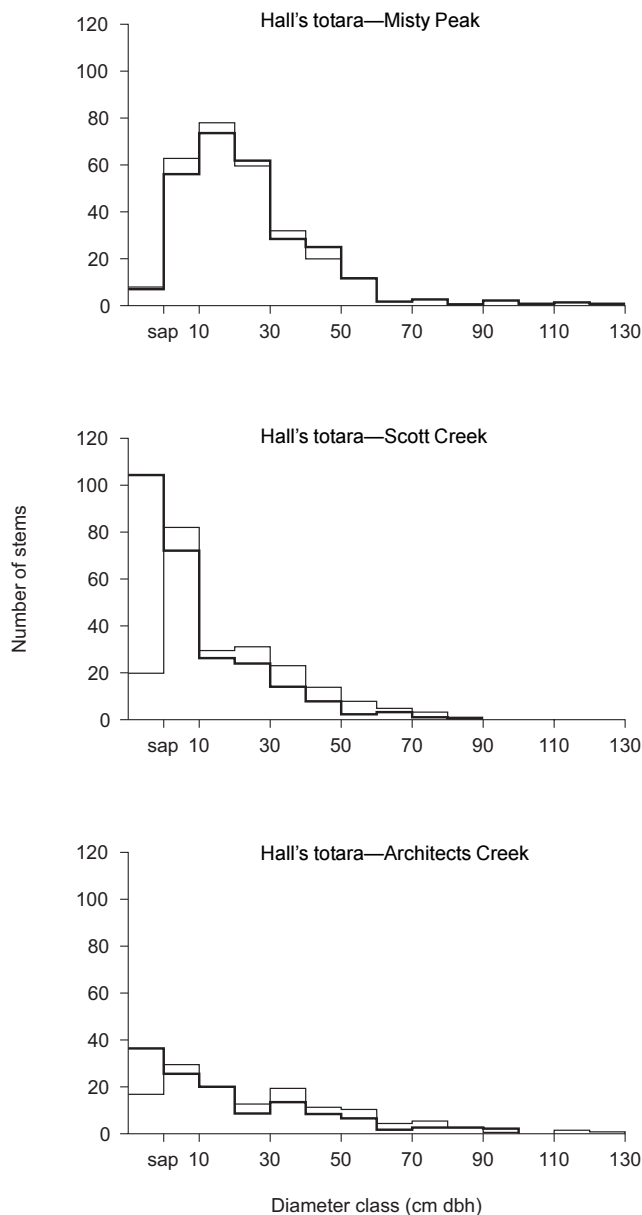

Figure 7.   Size-class frequency distributions for Hall's totara pooled from 15 permanent plots (20 m × 20 m) at Misty Peak (low possum numbers), Scott Creek (moderate to high possum numbers) and Architects Creek (post peak) in 1978/79 (thin line) and 1992 (thick line). All study sites were in south Westland.

4. Critical stages of life history in indigenous trees

Tree species vary in many aspects of their life history such as periodicity of flowering and seed production, requirements for seed germination and growth, and susceptibility to defoliation. And at different stages in their life history tree species may be more vulnerable to mortality as a result of natural processes or to the deleterious effects of predation and herbivory. In this section we examine the vulnerability of species at various stages in their life history.

4.1 FLOWERING AND POLLINATION

In late spring or early summer when flowers and flower buds are available, possums may move outside their normal range to browse them (Ward 1978; Nugent et al. 2000). In the Orongorongo Valley, flowers of four native plants: hinau, rewarewa, kawakawa (*Macropiper excelsum*) and nikau were consistently eaten (Cowan 1990). In other parts of New Zealand flowers of many other tree species are eaten by possums. These species include kamahi, towai (*Weinmannia silvicola*), northern and southern rata, five-finger (*Pseudopanax arboreus*), tree fuchsia, kanuka, mahoe (*Melicytus ramiflorus*), *Astelia* sp., kiekie, bush lawyer (*Rubus cissoides*), wineberry, pokaka (*Elaeocarpus hookerianus*), and tutu (*Coriaria* sp.) (Mason 1958; Gilmore 1967; Fitzgerald 1976; Nugent et al. 2000). Flowering could potentially be a very vulnerable stage in the life history of species that rely primarily on sexual reproduction. Species that can reproduce vegetatively are likely to be less vulnerable. For example, the flowers of southern rata are browsed by possums but the species can also reproduce vegetatively, unlike a species such as hinau that cannot do so.

4.2 SEED PRODUCTION—ASYNCHRONY ACROSS SPECIES

Because of the importance of disturbance to regeneration processes, the timing of seed production becomes a crucial factor in controlling which species establish on disturbed sites. Many indigenous tree species seed irregularly (see individual species sections for examples) and not necessarily synchronously across species. In forests where extensive dieback has occurred, this could potentially cause major shifts in species composition. In the Kokatahi Catchment in Westland, for example (see southern rata, Section 3.2), southern rata seedlings and saplings are rare or absent over many hectares, and Allen & Rose (1983) proposed that seed dispersal may have been the limiting factor for southern rata establishment. It is equally plausible that irregular seed production may have been a factor in this compositional shift. As mentioned previously, we have few data on seed production for species such as southern

rata and kamahi. The little data that is available (see Table 3) supports the notion that seed production is not synchronous across species. For example, southern rata seed production at both Aickens and Alexander in the Taramakau Catchment was very low in 1975 and 1976, years when both kamahi and *Quintinia* seeded prolifically. In fact, over the 5 years of record, the only year when rata seeded heavily was 1974. It follows that seed availability at the time of a disturbance may be a significant factor in determining which species colonise the site created. In this particular example kamahi and *Quintinia* have an advantage over southern rata as they produce abundant seed in most years.

TABLE 3.   MEAN NUMBERS OF SEED PER SEED TRAY THAT FELL AT AICKENS (7 TRAYS) AND ALEXANDER (5 TRAYS), TARAMAKAU CATCHMENT, FROM 1973 TO 1977 (G. STEWART, UNPUBL. DATA).

SITE	SPECIES	YEAR				
		1973	1974	1975	1976	1977
Aickens	Southern rata	162	9 760	69	74	nil
	kamahi	1 949	26 001	17 909	9 897	355
	Quintinia	21 079	7 683	7 772	16 261	1 834
Alexander	Southern rata	18	17 996	45	138	nil
	kamahi	516	15 156	3 339	2 686	595
	Quintinia	5 436	3 037	4 595	4 302	872

4.3   SEED PREDATION

Some 14% of indigenous plant species and 60% of the woody genera in New Zealand have succulent fruit, and they occur in all tiers of the forest from the understorey to the canopy (Wardle 1991). Large and medium-sized drupes are confined to forest trees, except for those of the liane *Ripogonum*. These species include many hardwood trees in genera such as *Hedycarya, Beilschmiedia, Carpodetus, Alectryon,* and *Elaeocarpus* (Lord 1999). Most of the tree species that possess fleshy fruits are susceptible to predation by possum browsing (Nugent et al. 2000b). Possums in the Orongorongo Valley ate the fleshy fruits of almost all species available with large numbers of fruits consumed (Cowan 1990). However, in a study in Westland podocarp-hardwood forest, although many species were eaten, only a few were highly sought after (Coleman et al. 1985). Possums may also eat large quantities of fruit of species whose foliage is rarely eaten including the podocarps rimu, kahikatea and matai (*Prumnopitys taxifolia*) and hardwoods hinau, marbleleaf (*Carpodetus serratus*) and pigeonwood (*Hedycarya arborea*) (Cowan 1990, Coleman et al. 1985). For large-seeded fruits such as miro and hinau, usually only the flesh is eaten and the seed remains viable. At certain times of the year (autumn) when fruit is available it can form the bulk of possum diet, and it has been argued that possums prefer fruit to foliage as it is of higher nutritional value (Nugent et al. 2000). Introduced birds and rodents may also be significant seed predators (Willson et al. 1990).

4.4   DISPERSAL

The importance of birds as dispersers of seeds of New Zealand plants cannot be underestimated. Of the c. 240 species of woody plants occurring in New Zealand mainland forests, about 70% have fleshy fruits suited to vertebrate dispersal (Clout & Hay 1989). Some may have evolved for dispersal by lizards, but the majority, especially those with orange, red and black fruits, are undoubtedly dispersed by birds. The extinction or decline of New Zealand native bird species in the past few hundred years has reduced the number of effective dispersers. This is particularly true for plants with large fruits (> 1 cm diameter) because kereru are now virtually the sole dispersers. *Beilschmiedia* spp., *Corynocarpus laevigatus,* puriri, and *Planchonella costata* also fall into this category (Clout & Hay 1989). Overall, kereru eat and disperse over 70 species of plants. The reduction in numbers of kereru and the extinction or decline of other important seed dispersers has definitely reduced seed dispersal (Clout & Hay 1989). Species that have become extinct (e.g. huia) are likely to have been important dispersers as well. Although the diet of huia is little known, Buller (1888) reported that they ate fruits of hinau, pigeonwood and *Coprosma* spp. The reduction in dispersal by native birds has, in a small way, been compensated by some exotic bird species such as blackbirds (*Turdus merulla*) and thrushes (*T. philomelas*). This reduction in the numbers of dispersers must be having an influence on successional processes in the forests, but has yet to be studied.

4.5   SEED PREDATION FOLLOWING DISPERSAL

The predation of seed after dispersal has been little studied in New Zealand forests. Seed predation by mice and rats is well documented for beech forests, especially following mast seed years (Ogden et al. 1996). The subsequent build-up of mustelids that feed on mice (especially stoats, *Mustela erminea*) has devastating effects on native bird populations. Although much beech seed is eaten by mice and rats, the enormity of seedfall in a mast year means that some seed survives and germinates, so seedlings are generally available to replace the canopy.

Seed predation of fleshy-fruited species also occurs following dispersal. Studies on offshore islands where mice and rats have been removed or excluded have shown a dramatic increase in seedling establishment of fleshy-fruited woody species (Allen et al. 1994; Campbell & Atkinson 1999). This means that fleshy-fruited species are potentially very vulnerable since their seeds are eaten at two stages, firstly by possums in the canopy, and then by mice and rats on the forest floor. Many of these same species are also highly palatable to deer, so seed that does escape possums and mice may germinate, but then be browsed by deer. In extreme cases, seedling mortality can be high.

For species that produce small, wind-dispersed seeds such as southern rata and kamahi, seed predation by possums, rats or mice, either on the tree or after dispersal, may not be a problem as the seeds are too small for these animals to get hold of. Small seeds may, however, br susceptible to insect predation (Sullivan et al. 1995).

4.6   SEEDLING ESTABLISHMENT

In some areas of forest an apparent lack of adequate seedlings to replace the existing canopy has been noted; for example, in the mountain beech forests of the Kaweka Range (Allen & Allan 1997) and in the central North Island mixed conifer forests (Rogers 1997). In some instances, such as in the dieback forests of the Kaweka Range, deer browsing appears to limit seedling growth. In others, such as in the central North Island forests, it has been hypothesised that grass and shrub species that have replaced the dying forest canopy preclude the establishment of seedlings (Rogers 1997). Whilst the latter has yet to be researched, grass or turf swards have been noted as increasing in the Kaweka Range and in other areas of forest dieback such as the coastal forests of Stewart Island. Research is required to ascertain the degree to which these 'displacement diebacks' are impeding the re-establishment of the original tree species.

Many tree species in New Zealand have specific requirements for seedling establishment. In many cases elevated sites such as upturned root plates, stumps and logs are favoured as they are above dense competing understorey vegetation and retain moisture better than the forest floor. On the other hand, in very wet forests elevated sites tend to be drier, and many species establish on them to avoid standing water. In extreme cases, introduced animals can alter the abundance of seedling microsites. For example, in the coastal forests of Stewart Island many tree species (including southern rata and kamahi) establish on the trunks of the tree fern *Dicksonia squarrosa* (Veblen & Stewart 1980). Once established, they produce roots that grow down the tree fern trunk to the forest floor and, eventually, the growing tree coalesces around the tree fern trunk. Introduced white-tailed deer have markedly reduced the abundance of palatable tree and shrub species on Stewart Island (Stewart & Burrows 1989). These deer also browse tree ferns and have considerably reduced their numbers, therefore reducing the availability of establishment sites for seedlings of species such as southern rata and kamahi.

4.7   CANOPY DEFOLIATION

Many tree and shrub species are vulnerable to defoliation by natural physical and biological causes, and also to the depredations of introduced possums. Defoliation by salt-laden storms was the likely cause of coastal dieback in the mixed forests on the east coast of Stewart Island and outlying islands in the 1970s (Veblen & Stewart 1980). Defoliation by several native insects such as *Neomycta* and *Inglisia* is a feature of periodic natural dieback events in beech forests (Wardle 1984). But perhaps the most widely perceived defoliation, especially in mixed conifer–broadleaved hardwood forests, is by the introduced brushtail possum. In native forests possums eat a wide variety of foods, with 53 species eaten in the Orongorongo Valley (Mason 1958) and about 100 species in central Westland and central North Island (Coleman et al. 1985; Nugent et al. 1997). Typically, however, only a few species form the bulk of the diet, and in mixed hardwood and podocarp-hardwood forests the foliage of tree species usually dominates possum diet. Several of the most important dietary components are dominant canopy species such as kamahi, which is universally

eaten (Nugent et al. 2000). Northern rata, southern rata and pohutukawa are the other high-profile species eaten by possums. Conifers and beeches are generally not eaten, with the exception of Hall's totara and pahautea. Other important foliage foods are predominantly shrub hardwood species such as wineberry, tree fuchsia, mahoe, pate (*Schefflera digitata*), and several *Pseudopanax* species.

4.8 STAGE OF STAND DEVELOPMENT

If stands establish synchronously after major disturbances, they are often relatively even-aged. Once these stands reach maturity and begin to senesce they lose vigour, predisposing them to mortality. This regeneration cycle is well documented for mountain beech where stands rarely attain more than 200 years before a dieback episode commences (Wardle & Allen 1983). It has been long observed that many stands in the mixed southern rata-kamahi forests of Westland appear to be even-aged, perhaps due to their establishment after landsliding caused by Alpine Fault earthquakes (Holloway 1957; Wardle 1977; Stewart & Veblen 1982b). Recent research (Wells 1998; Wells et al 1998; Wells et al. 1999) has established that these stands are indeed even-aged and widespread throughout Westland. Not only are many of the hillslope rata-kamahi forests even-aged but so too are the podocarp forests on the floodplains (Duncan 1993). Furthermore, these stands established after earthquakes along at least 375 km of the Alpine Fault in 1717, c. 1630 and c. 1460 AD. It has been suggested that these stands are more predisposed to possum browsing and that browsing by possums may simply make the mortality more coincident that it might have been otherwise (Veblen & Stewart 1982a, Stewart & Rose 1988). Several authors have observed that young stands appear healthy and little browsed by possums (Veblen & Stewart 1982a; Leutert 1988).

4.9 MODIFICATIONS TO DISTURBANCE REGIMES AND SUCCESSIONAL DEVELOPMENT

Patterns of successional development can be severely modified by changes in the species composition of the understorey resulting from browsing by introduced animals such as deer. There is a wealth of published material on these changes for a range of forest types in New Zealand.

Successional development can also be modified by seed predation. In New Zealand's coastal forests, kiore have substantially reduced recruitment of *Pittosporum crassifolium, Planchonella costata, Streblus banksii* and *Nestegis apetala* by eating the seed (Campbell & Atkinson 1999). Seed consumption and/or depressed recruitment has been demonstrated for nikau, puriri, and *Pisonia brunoniana*. The successional changes that are occurring in our forests due to seed predation have not been studied and such studies are urgently required.

When large tracts of forest are fragmented into smaller patches by human activity such as farming, isolated stands or fragments are formed. The

Department of Conservation is responsible for the management of many of these fragments. Many of them are going through major shifts in species composition and some are undergoing dieback (Willems 1999). This is partly due to invasion by exotic plant species but is also due to altered disturbance regimes. On Banks Peninsula, for example, several isolated fragments of once extensive podocarp-hardwood forest occur as reserves on alluvial surfaces on the valley floors. These are typical of numerous small reserves throughout the country (e.g. Smale & Gardner 1999; Whaley et al. 1997). Prior to European settlement the podocarp-hardwood forests on alluvial surfaces on Banks Peninsula (and in many places in New Zealand) would have been subjected to periodic flooding and stand rejuvenation, especially for species such as kahikatea and matai. Following settlement, forest clearing and conversion to pasture, these small forest remnants have been isolated and their disturbance regimes drastically altered. Channelling of rivers has halted flooding, the very disturbance required for stand rejuvenation. The species composition of these isolated fragments is now changing dramatically with the old podocarp element dying, a lack of podocarp regeneration, and a shift to hardwood dominance (Willems 1999). Furthermore, the changes to the surrounding physical environment makes these isolated stands more susceptible to other impacts such as drought and frost (Atkinson & Greenwood 1972; Ogden 1976). Management of these areas poses a real challenge, particularly in understanding the compositional shifts set in motion by land clearance a century or more ago.

5. Establishing priorities among species

A particular challenge for managers is establishing priorities for conservation management at a range of scales (nationally, regionally, etc.). There has always been a rather large subjective element in how this prioritisation is applied to tree species and forests. Sometimes decisions have been based upon apparently excessive mortality, or lack of recruitment, on an unspecified proportion of the landscape. There remains considerable room for conservation managers to become more systematic about the collection of comparable data that may be used robustly over time to underpin conservation management decisions.

The current approach to defining which tree species are of most concern because of undesirable shifts in the demographic processes that regulate their population size and viability is rudimentary. In many instances it is based upon the visual impact in a particular area, or parts of an area—of, for example, canopy dieback. One argument says that this is all that is required because this evidence is enough to sway the necessary political influences. Much of the early expenditure on introduced animal control (1930–1950s) was based upon such evidence. Today, we are left with no way of judging whether that expenditure achieved its goal—although some commentators are prepared to speculate that it was ineffective (Caughley 1983). In recent decades several more quantitative

approaches have been applied to assessing the viability of tree populations; for example:

- Canopy tree mortality has been assessed both aerially (e.g. Rose et al. 1992; Rogers 1997) and from ground-based measurements (e.g. Allen & Rose 1983).
- The analysis of tree population size structures, sometimes with complementary tree age data, has been used to infer tree demographic processes (e.g. Stewart & Veblen 1982a).
- Various methods have been used for assessing canopy condition of live trees (e.g. Wardle et al. 1971; Meads 1976; Payton et al. 1999)—with the assumption that this can indicate negative impacts on tree populations.

Although such methods have increased our understanding of the factors controlling tree population structure, they carry with them certain deficiencies:

- They inadequately capture demographic processes. As Bellingham et al. (1999a) have re-iterated, point-in-time mortality assessments based on dead standing trees fail to capture differential decomposition rates of dead trees among species.
- The level to which defoliation and demographic processes (such as mortality) are linked has not been carefully tested.
- The issue of assessing population size, and viability, at defined spatial and temporal scales has received little attention, but is a critical component to establishing priorities.

It is surprising that our ability to objectively assess the widespread perception that certain tree species are declining on conservation lands is obscured by a lack of systematically collected quantitative data on tree demographics that can be used to consider the issue at a range of scales (but see Bellingham et al. 1999a). We are unaware of an alternative to a robustly designed demographic approach for assessing vulnerability—one that operates at a range of spatial and temporal scales.

If a way of prioritising a response to concerns about tree species is developed, the process should involve five components. It must:

- Show effectively that there is reason for concern about the maintenance of a tree species in terms of population imbalances.
- Understand the causes of any imbalances in the demographics of a tree species.
- Determine the significance of maintaining a tree species within a context of its contribution to ecosystem dynamics.
- Show that the trajectory of a tree species population can be changed to something more desirable.
- Compare the vulnerability of tree species.

To address these components comprehensively, for a range of tree species, is a large task, but it does provide a framework for prioritising species and assessing the completeness of our knowledge base. We address the five components in the following subsections, with emphasis on the seven species previously considered in detail.

5.1 USING DEMOGRAPHIC PARAMETERS TO SHOW THAT THERE IS REASON FOR CONCERN ABOUT THE MAINTENANCE OF A TREE SPECIES

It would be rather difficult to monitor a full range of population processes at a wide range of sites—Bellingham et al. (1999b) settled on the solution of using the imbalance of mortality and recruitment of individual trees of a species (at certain scales) as an index. These authors presented such analyses from standard permanent plots (Allen 1993) throughout New Zealand for selected species. A representative sample population is selected using fixed-area permanently marked plots and demographic parameters estimated from this sample based on tagged individuals. Using a logarithmic model, a mortality rate can be calculated for each plot, or across all plots, as an annual percentage of the initial stems (McCune & Cottam 1985; Sheil et al. 1995). A recruitment rate (above a minimum size) as an annual percentage to a similar logarithmic model can also be calculated (Bellingham et al. 1999a). These values are calculated as rates (percentage per unit time) because this allows comparisons among data having different time intervals between remeasurement. The baseline for a population imbalance would be that there are differences in average mortality and recruitment rates. This method is applicable at any scale, although with different sampling intensities. The pervasive importance of disturbance means that there is no reason to necessarily expect mortality and recruitment to be in balance at local scales, or even at large spatial scales. However, where imbalances occur at large spatial scales, the size and viability of a tree species' population is most at question. Quantitatively demonstrating such an imbalance is an effective way of showing that there is reason for concern about the maintenance of a tree species. Relatively high mortality over large areas, and little or no recruitment, would give the most reason for concern. Whether mortality is high, or recruitment is low, will also give some indication of mechanisms that may be responsible—although establishing the reasons for an imbalance may not necessarily be part of monitoring demographic parameters. Some considerations of sampling design—extent, intensity, frequency—for assessing tree species are considered elsewhere (Bellingham et al. 1999a; Allen 2000).

Although the approach outlined for establishing changes in the size and viability of tree populations is simple, there are several methodological challenges:
- The demographic approach outlined is based on selecting a representative sample—at whatever scale analyses are undertaken. It is quite easy to inflate mortality rates by selecting stands on a small part of the landscape where trees are moribund—and where management may wish to focus its efforts. Other sampling design issues include the intensity required to robustly estimate population parameters, which is intimately related to the period of observation (see Table 2). There is a need for further research in this area (Bellingham et al. 1999b).
- The sampling universe needs to recognise that recruitment may occur on sites beyond a species' historical distribution and also that historical distributions may have contracted because of 'displacement diebacks'. Distributional adjustments, at a range of scales, may be significant from a range of perspectives, including the maintenance of genetic diversity within species.

Range extensions can be captured when sampling takes place beyond the distributional range of species. It is also important to track the nature of range contractions over a range of spatial scales. If an area is representatively sampled, then the proportion of sample areas (plots) occupied can be used as an index of range, and contagion among plots from which a species is lost as an index of 'displacement diebacks'.

- A critical decision in calculating recruitment rates is to decide upon the minimum size for inclusion. The standard plots (20 m × 20 m) tag all tree stems greater than 25 mm diameter at 1.4 m height (Allen 1993). Below this size the fate of individuals is not measured and therefore cannot be used to estimate demographic parameters. Bellingham et al. (1999a) used a minimum diameter size of 100 mm for two reasons: for comparability with the international literature; and because it was believed that all stems were reliably tagged above this size in the range of data sets used. A consequence of using a larger minimum size limit is that there could be a considerable time lag in detecting recruitment limitation—and, hence, how responsive the index is in the short term. This would be of most concern for species where recruitment limitation coincides with high mortality rates—dramatically reducing the time until extinction. There is the opportunity to assess the trade-offs between the advantages of following the fate of smaller individuals versus the time involved in the field—for a range of species and types of forest.

- Vegetative reproduction (e.g. from root sprouts by *Quintinia acutifolia* or layering from collapsed trunks by southern rata) creates difficulties in deciding upon what is an individual. How to treat southern rata in coastal Stewart Island forests where the sprawling stems take root in a number of places requires consideration in established protocols.

- There are practical difficulties in recording the fate of individuals. For example, southern rata often establishes epiphytically well beyond the reach of field workers. What field workers are most likely to have access to is aerial roots. Even when trunks of this species are within the reach of field workers, they may be fused so tightly with the host that it is impossible to measure their dimensions. There is a need to incorporate specific considerations of some of these problematic species in standardised field manuals such as those produced by Allen (1992, 1993). This problem can be common in complex forests where species establish on raised surfaces.

To recover some composure after outlining a set of current limitations, Bellingham et al. (1999a) demonstrated the utility of this approach. In their analysis of the status of four canopy species (silver beech, mountain beech, Hall's totara, and kamahi) from throughout New Zealand's indigenous forests, they found that Hall's totara was clearly the species of most concern. This poor outlook was most pronounced in some central Westland catchments where Hall's totara exhibited high mortality and no recruitment. In these same areas other species of concern, e.g. southern rata, had lower mortality rates and some recruitment when averaged over a catchment (Fig. 8). Such analyses cannot be undertaken over extensive areas for many tree species because systematically collected data are not available.

In contrast, some data exist that representatively sample particular localities. We now consider an analysis of data from one of these locations (Pureora) to demonstrate the approach at a smaller spatial scale. The results in Table 4 are based upon the remeasurement of 28 plots over an 18-year period (1975-93). The
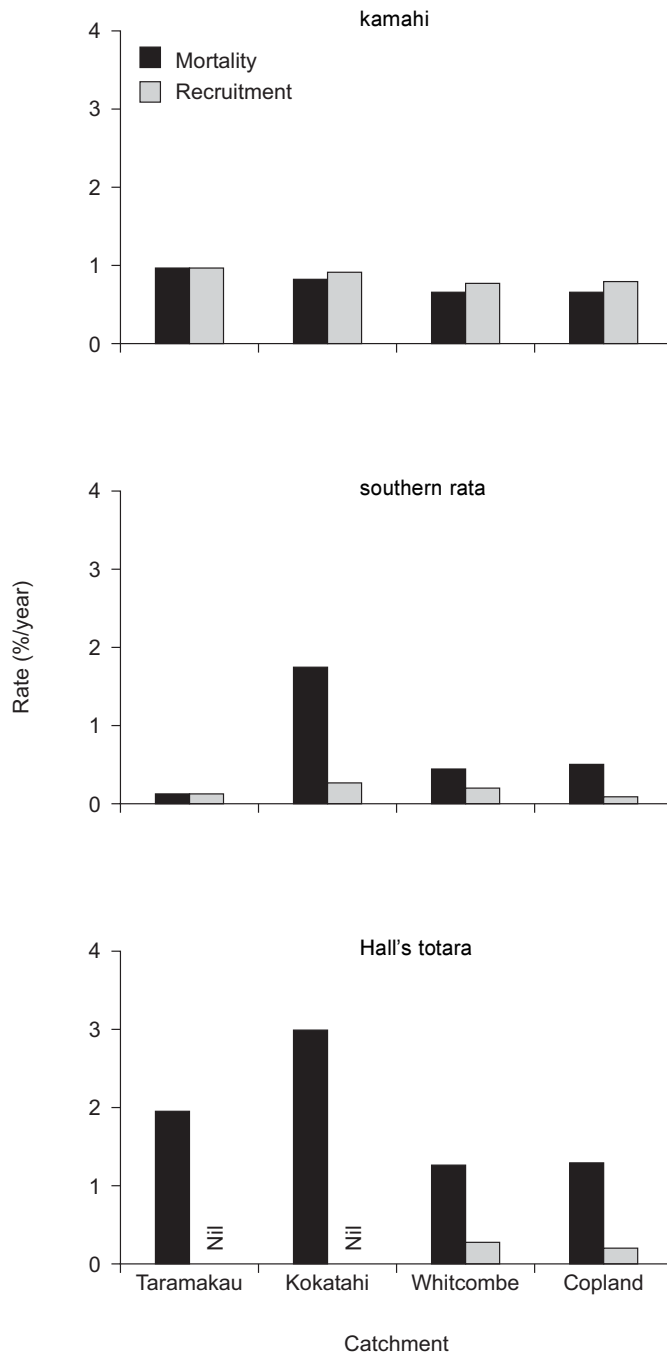
Figure 8. Annual mortality and recruitment rates of stems over 100 mm diameter at 1.4 m height for three tree species in permanent plots in high-altitude forests in four Westland catchments (P. Bellingham unpubl. data).

species presented were the more common ones on this set of plots. There was quite a large group of species (e.g. tawa, rimu, pigeonwood and, importantly, Hall's totara) that increased in numbers because recruitment exceeded mortality. Not all of these increased in basal area (e.g. rimu, matai), indicating that large individuals of these species were being lost from the population. A few species were declining in numbers (e.g. five-finger, pate, kamahi), although the increasing basal area for kamahi suggested that for this species it was a consequence of self-thinning (Table 4). Because this dataset documents the trajectories of a diverse North Island forest, it is very useful; and it is important that these plots are remeasured in the not too distant future. There is a noted deficiency of such data from forests, and particularly within many of the more diverse species mixtures found in the northern part of North Island.

TABLE 4. DEMOGRAPHIC PARAMETERS FOR PUREORA TREES AND SUBCANOPY TREES AND SHRUBS. BASED ON 28 PLOTS FROM 1975 TO 1993. STEMS LESS THAN 25 mm IN DIAMETER HAVE BEEN EXCLUDED.

SPECIES	NUMBER OF STEMS ON 28 PLOTS		MEAN BASAL AREA (m²/ha)		RECRUITMENT (%/YEAR)	MORTALITY (%/YEAR)
	1975	1993	1975	1993		
Beilschmiedia tawa (tawa)	272	603	13.9	14.9	2.4	0.2
Dacrydium cupressinum (rimu)	11	62	3.8	2.9	3.3	0.1
Melicytus ramiflorus (mahoe)	168	200	2.9	3.6	1.5	1.0
Weinmannia racemosa (kamahi)	147	94	2.7	2.9	1.2	3.8
Prumnopitys taxifolia (matai)	13	32	3.4	3.1	2.7	0.3
Elaeocarpus dentatus (hinau)	50	69	2.2	2.4	1.7	0.9
Quintinia serrata	93	79	2.1	2.0	0.5	1.4
Hedycarya arborea (pigeonwood)	120	258	1.1	1.9	2.4	0.4
Laurelia novaezelandiae (pukatea)	32	78	1.0	0.6	2.6	0.3
Knightia excelsa (rewarewa)	11	50	0.9	0.7	3.2	0.3
Pseudowintera colorata	174	313	0.7	1.0	2.3	0.9
Pseudopanax arboreus (five-finger)	19	11	0.5	0.1	1.4	4.7
Fuchsia excorticata	23	13	0.4	0.4	0.2	3.2
Prumnopitys ferruginea (miro)	27	72	0.4	0.7	2.7	0.1
Griselinia littoralis	24	36	0.3	0.5	2.2	1.4
Pseudopanax crassifolius	31	48	0.3	0.4	2.1	1.1
Nestegis cunninghamii	12	15	0.3	0.1	2.0	2.0
Aristotelia serrata	21	100	0.2	0.3	3.3	1.0
Myrsine salicina	15	14	0.2	0.2	1.0	1.6
Elaeocarpus hookerianus (pokaka)	3	11	0.2	0.2	3.0	0.0
Carpodetus serratus	15	20	0.1	0.2	1.4	0.3
Podocarpus hallii (Hall's totara)	12	27	0.1	0.3	2.5	0.6
Schefflera digitata (pate)	22	14	0.1	0.2	1.2	3.8
Neomyrtus pedunculata	18	40	0.1	0.1	2.6	0.7
Geniostoma rupestre	19	47	0.1	0.1	2.7	0.8

5.2 UNDERSTANDING THE CAUSES OF ANY IMBALANCES IN THE DEMOGRAPHICS OF A TREE SPECIES

There is a long history of attempts to explain undesirable shifts in the demographics of tree species, but too often the results have lacked clear interpretation. In the absence of clear understanding of processes, it will always be necessary for managers to make decisions based on imperfect knowledge. However, an ongoing improvement in the identification of specific causes of shifts in tree demographics is clearly required. The following subsections indicate how improvements could be made.

5.2.1 Measure the correct parameters in the most appropriate way

The first component to understanding causal factors is to measure demographic parameters in an appropriate way. Some data currently collected does not focus on parameters necessary for tree demographics. For example, variation in Foliar Browse Index data (see Payton et al. 1999) in relation to defoliation has not, so far, been linked to survival of canopy trees. This link may not be that strong, as in some locations (e.g. Fox Glacier in the 1950s) kamahi has previously died back, generating considerable concern, but recovered by sprouting epicormic

shoots (e.g. Allen & Rose 1983). Although it may be argued that defoliation provides an early warning of possum impacts, the link to tree mortality is too tenuous for it to provide the only basis for management decisions. The estimation of robust demographic parameters requires a long-term commitment to monitoring—a commitment that has usually been lacking. With long-lived trees, observations over decades may be necessary, depending on sample size, to estimate tree mortality rates. There has also been a strong tendency for species to be studied at locations where there is already concern about their continued existence. For example, studies on possum impacts have often focused on whether, with possum reduction, there is recovery of already defoliated trees—and any consequences for mortality. Compensatory growth may not occur where defoliation has increased the stress within a tree's canopy (Payton 1988). Mechanisms such as lack of compensatory growth will make it difficult to show consistent gains from animal control. A similar explanation has been used to answer why the anticipated regeneration of canopy tree species following a reduction in deer numbers is difficult to demonstrate (Allen 2000).

As indicated earlier in this report, a clear interpretation of the drivers of undesirable changes in forest dynamics has bedevilled forest ecologists and managers alike. In a general sense there are three approaches to identifying which factors in Table 1 influence tree population dynamics at a particular location. All have their advantages and disadvantages (many of the examples previously discussed in the text support one or more of the three following approaches):

Point-in-time studies that infer temporal dynamics from spatial variation in tree populations, as well as interpreting this variation in relation to a range of other factors. Although spatial pattern analysis is often the easiest and quickest option to pursue, the major difficulty with this approach is in partitioning out just what proportion of spatial variation in tree populations is actually related to temporal dynamics, rather than to other factors. Even when a comprehensive suite of other factors are included in the analyses, it still remains difficult to ascribe cause, because some spatial variation in tree populations can co-vary with other factors and not all important factors may be quantified. Point-in-time studies are usually appropriate in the early stages of study.

Temporal studies that measure dynamics over time and interpret these changes in relation to a suite of factors. Because the temporal changes are measured rather than inferred, this approach provides a clearer means of understanding causal factors. It is interesting to note that, at least so far, sites with strong temporal data have not been given a high priority in the selection of 'mainland islands'. This is surprising, given the difficulty in monitoring temporal changes for a wide range of population processes. For example, to answer whether flower and seed predation is significant to population viability for a suite of tree species and, if so, under which conditions, would be a major research task. Certainly this relationship requires further research to assess its significance.

Experimental studies that impose treatments at a range of scales and document temporal dynamics. Superficially this may seem the most attractive option because the time dimension is explicitly measured and there is

some control over the factor(s) being investigated. In reality, large-scale experimental manipulations often fail to show that initial conditions are equal between treatment areas before manipulations are initiated, and also often suffer from pseudoreplication. Some past examples include trials associated with deer poisoning on Stewart Island and poisoning of possums in Westland National Park. Where manipulations are less extensive there are potential problems with boundary effects.

No matter what approach is used, a careful interpretation will always ask: 'what other factors may have changed to confound the results?' Some authors have argued that in New Zealand we too often turn to the impacts of introduced animals to explain patterns (e.g. Veblen & Stewart 1982a). In most instances it is possible to suggest other factors that may have changed, and the point to make is that for all the approaches outlined it is the context that is important.

By context, we mean documenting as full a range of factors as possible to explain the uniqueness of each part of the landscape—at whatever scale. It implies that generalised patterns will be inadequate for explaining structural and compositional variation among parts of the landscape because, for example, variation in chance occurrences and history matter at this scale. Both spatial and temporal components need to be considered. For example, looking for relationships between deer density, averaged over a large area, and plant recruitment on a specific set of sites will obscure the strength of any relationships because deer differentially use the landscape. How deer differentially use the landscape, in turn, depends on the type of hunting pressure. Relating the amount of foliage on trees to variation in possum density over time needs to take account of other factors that drive the amount of foliage produced, for example, annual climatic variation. But the context is more complex than this (see Table 1); it involves understanding historical factors, such as past disturbance, it involves spatial location of individuals that can influence dispersal of propagules, and competitive interactions. There may be legacies from past inputs of litter, which may have been of a particular quality and mix, on below-ground processes. The implication is that much of the information required to provide context must be collected at that specific site. The accuracy of predictions about ecosystem responses, and the precision of these predictions, require a more complete treatment and integration of factors listed in Table 1 than has previously been made—this is the basis of the concept of ecosystem management.

5.2.2 Develop an encompassing framework for the demographics of tree species

Clearly, with an increased understanding of more and more specific processes that occur in forest ecosystems, and which provide the context for forest demographics, there will be an added requirement for ways of integrating this process-based knowledge. Eventually, this will provide a predictive ability under an increasingly wider range of conditions. A conceptual framework that can incorporate the full range of demographic processes, within a context of the full range of factors influencing these processes, is an intellectually challenging, but necessary, requirement. A range of forest dynamics models have been proposed that do this to varying degrees. Population matrix models can be used to assess demographic consequences of, for example, herbivory

(West 1995; Menges 2000). These models use relatively simple data and can be used to detect which parts of the life cycle have pronounced consequences for maintenance of a population. However, these population matrix models fail to capture the spatial variability in processes, do not integrate the factors driving change, or the interactions between these (Bierzychudek 1999). Canopy gap models have also been widely used (e.g. JABOWA), but these also do not explicitly include spatial processes, such as seed dispersal. Recently, Landcare Research and the Department of Conservation have initiated a project using the model SORTIE. This is a process-based, spatially explicit model that provides a framework for integrating the influences of competition, disturbance, herbivory and nutrient cycling on the population dynamics of forests and a range of ecosystem properties (Pacala et al. 1996; Fig. 9). A defining feature of the model is its firm grounding on empirical data. Use of such a model will allow three interlinked drivers of ecosystem structure and function to be investigated simultaneously: (1) vegetation regeneration, dispersal and establishment processes, (2) key ecosystem processes including decomposition, microbial activity and light interception, and (3) the impact of introduced vertebrates on community and ecosystem properties. The major links to be explored, and how a SORTIE modelling approach will integrate research on these linkages is shown in Figure 9.
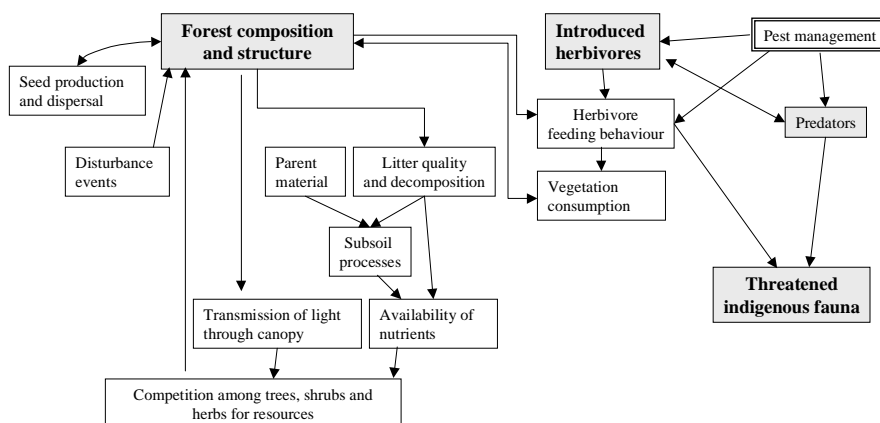
Figure 9. A schematic representation of the links between forest community dynamics, decomposition and subsoil processes, and the interactive dynamics of introduced vertebrates and their management. SORTIE provides the framework for making these linkages in a process-based, predictive model (not all possible linkages between boxes are shown).

Initially, it is proposed to achieve this advance in forest ecosystem modelling by working within a forest ecosystem that stretches along a clearly defined soil fertility gradient, and the Waitutu marine terraces (Southland) have been identified as a unique system for conducting such work. The model will be expanded progressively to be predictive in a range of forests, and for a broader range of interactions.

5.3 DETERMINING THE SIGNIFICANCE OF MAINTAINING A TREE SPECIES WITHIN A CONTEXT OF ITS CONTRIBUTION TO ECOSYSTEM DYNAMICS

Although demographic processes can be used to assess the vulnerability of a species, the level of concern we have about the loss of a species from an area of forest should also be related to its significance to that ecosystem. We should be

particularly concerned where a common and widespread structural dominant is being lost that has important consequences for the functioning of forested ecosystems. As physiognomic dominants, trees have a major impact on the structure, composition and functioning of forest ecosystems.

There has been a long debate in New Zealand about the significance of forests to erosion rates and regulation of catchment sediment and water yield (McKelvey 1995). Erosion rates in New Zealand mountainlands are high by world standards and have been related to underlying climatic and tectonic factors (see review by O'Loughlin & Owens 1987). This view led to a questioning by some of the effectiveness of policies that assumed forest management could influence processes such as erosion (e.g. Kirkland 1983; Caughley 1983). One area this debate focused on was those parts of the southern Ruahine Range where there had been severe dieback of northern rata, kamahi, and fuchsia (*Fuchsia excorticata*) over wide areas. Mosley (1978) questioned whether this deterioration in tree cover had influenced erosion, whereas other researchers took a clear stance that it did (Batcheler 1983). Subsequent comparative studies elsewhere have shown that in the short term (decades) forest cover can have a very marked influence on maintaining lower erosion rates (O'Loughlin & Pearce 1976; O'Loughlin & Zhang 1986; Whitehouse 1988; McGlone 1989). In 1988, Cyclone Bola released 400–900 mm of rainfall over a 500 000 ha area of the East Coast of the North Island during a 3-day period. Immediately after the storm, landslide density increased by $51/km^2$ on pasture lands compared with an increase of only $2-3/km^2$ in lands covered in native forest (Phillips et al.1989). This strongly implies that forest cover reduced the occurrence of landsliding after Cyclone Bola by 96%. Thus, against the long-term backdrop of geologic processes, forest cover clearly has a major influence by reducing erosion rates on a contemporary timescale relevant to society. McKelvey (1995) summarised the significance of forests over shorter time spans (decades and centuries). They can lessen erosion significantly in some localities and afford a measure of protection to downstream values. Certainly, where the retention of forest cover over extensive areas is at stake, there is room to further our understanding of the benefits arising from retaining an intact forest cover, and how this varies geographically. Such benefits are given little emphasis in New Zealand today, but widely underpin the rationale for forest management elsewhere.

There is a wider acceptance that trees protect the soils in which they root and the habitats of associated indigenous biota (McKelvey 1995). Recent research has shown that the effects of trees on soils are more complex than previously thought; for example, plant material enters the decomposer subsystem as litter where its breakdown is partially controlled by substrate quality (Wardle et al. 1997; Wardle et al. 1998). The foliage of different tree species varies considerably in the properties that influence decomposition. Broad-leaved hardwoods with thin leaves like fuchsia and *Aristotelia serrata* have high nitrogen and are readily decomposed whereas small, thick leaves like those of southern rata and Hall's totara are generally low in nutrients and thus decompose slowly. In a more general sense, any changes in litter type and composition will have flow-on effects for how forest ecosystems function. These flow-on effects drive the vigour of forests and successional change. Slower decomposition can be linked to increased carbon accumulation in soils, lower fertility and, as a consequence, slower-growing plants and considerable

compositional change. Plants that store nitrogen in secondary metabolites found in leaves will not be readily decomposed and nitrogen will be unavailable and accumulate in soils. Knowledge of soil dynamics can be used to better understand what is happening in those parts of Westland where there has been complete loss of southern rata and Hall's totara from the forest canopy, and where there is little or no regeneration of these species (Allen & Rose 1983). Allen & Rose (1983) suggested regeneration limitation was a consequence of the lack of seed input to large dieback areas. However, there are alternative explanations. In Hawaii, it has been shown that certain litter types can inhibit *Metrosideros* seed germination (Walker & Vitousek 1991). Using this information, David Wardle and Peter Bellingham are studying the implications of altering litter quality and mix on the establishment and growth of southern rata seedlings in Westland forests.

Changes in patterns of regeneration as a consequence of browsing in forest understoreys can also lead to changes in of litter inputs to the soils (Wardle et al. 2001). These authors have shown that the associated impacts of browsing on plant communities also affect most groups of litter-dwelling mesofauna and macrofauna as well as soil carbon and nitrogen storage. The end result could well be far-reaching consequences for forests both at the community and ecosystem level (Wardle et al. 2001). Also, it is possible that we should not expect vegetation to return to some former state with a reduction in browse pressure. Many of the plant species for which compositional changes were quantified in the Wardle et al. (2001) study were sub-canopy trees and shrubs. Until the results of such studies are available for specific species, or groups of species with like traits, it will remain rather speculative as to what the ecosystem consequences are of changing litter inputs through loss or gain of specific species and, also, whether loss of canopy trees has greater consequences than loss of sub-canopy species.

There can be feed-backs between how trees die and recruitment processes. For example, the microtopography induced by upturned root plates has consequences for which species find suitable sites for regeneration. In south Westland podocarp-hardwood forests, miro (*Prumnopitys* sp.) requires elevated sites for successful regeneration, whereas kahikatea (*Dacrycarpus* sp.) is successful on the ground surface (Duncan 1989). Glenn Stewart has unpublished data suggesting certain tree species are more successful at regenerating on the logs of certain other species. The analyses of logs as habitats for maintaining biodiversity are still very rudimentary—as the few analyses of decomposer trophic food-web structures usually focus on litter breakdown in soils rather than coarse material like logs. Logs on the forest floor can serve as habitat for a diverse range of saprobic fungi, the composition of which varies markedly with the stage of log decay (Allen et al. 2000). The specific physical properties of dead standing trees can also influence the suitability of these habitats for use by bats (Sedgeley & O'Donnell 1999). Logs also have many other functions in forests; for example, they perform as a nutrient store, particularly of cyclable cations (Stewart & Allen 1998). Clearly, any changes in the rates, and nature, of tree mortality will have many consequences for forest ecosystems through altering the functional roles of woody debris.

The focus of this discussion so far has been on the functional roles of detrital inputs; however, the role of live trees and their importance to dependent organisms has received much more attention from researchers (Wardle 1991; Ogden et al. 1996). Parasitic plants have clear associations with specific tree species; there are, for example, several mistletoe species, preferentially browsed by possums, that occur widely on *Nothofagus* species. Turnover in beech tree populations has not, so far, been considered as an important factor regulating mistletoe or wood rose (*Dactylanthus taylori*) abundance. However, the dynamics of tree species could have important consequences for dependent biota. Flower feeders (kereru), seed feeders (invertebrates), leaf feeders, cambium feeders, and root feeders may depend on certain tree species at certain times for food sources. Loss of particular species could thus affect the survival of some dependant animals. The loss of individual tree species will also influence forest compositional development through altering the mix of competitive interactions (light tolerance) and life-history attributes (e.g. longevity) between tree species in an area of forest. Other species-specific contributions to ecosystem function include the nature and level of biomass accumulation as well as the composition of epiphytes.

5.4 SHOWING THAT THE POPULATION TRAJECTORY OF A TREE SPECIES CAN BE CHANGED TO SOMETHING CONSIDERED MORE DESIRABLE

There are a range of human-related disturbances to forests, some of which have localised effects and others that are pervasive (e.g. CO_2 in the earth's atmosphere). Taking a pragmatic approach, we must ask: 'what are the range of threats that can be managed?' This question is made more complex because the separation of human-related disturbance events from those considered 'natural' is becoming increasingly difficult. For example, the level to which storm events are a consequence of human-induced atmospheric changes is unclear. The significance of this point is that it makes it difficult for forest management that attempts to maintain 'natural' communities. Increasingly, forest managers will need to consider a range of options that allow maintenance of tree species populations in ways that are becoming more distant from the notion of 'naturalness'.

5.4.1 The traditional option of minimising introduced animal impacts

The management response to undesirable shifts in the demography of tree species has traditionally been based on the premise that these shifts are often brought about by the impacts of introduced animals. It has long been debated, and this report is an extension of that debate, that the situation is more complex than this (e.g. Chavasse 1955; Wardle 1971). However, the management response has been to reduce animal numbers and thereby encourage regeneration or reduce tree mortality. After 50 years of this management response, the evidence that this leads to a positive outcome for canopy tree species is rather weak indeed. Bellingham et al. (1999a) argue that, based on

measured mortality rates of trees in a range of Westland forests, that extensive (and at the time judged successful) possum control campaigns have not markedly influenced tree mortality patterns. With sustained efforts in geographically restricted areas, such as mainland islands, it is possible that more consistent benefits of introduced animal control could be demonstrated, particularly with improved technologies. However, these benefits may be difficult to show for several reasons:

- In the past, expensive control efforts have been sustained over time periods considered long by today's standards.
- Introduced animals may not be the principal factor causing undesirable shifts in tree demography.
- Introduced animals may be the principal factor but, as discussed previously, their impacts are not necessarily reversible, at least in the short term.
- Introduced animals may be the principal factor causing change, but that this would only become apparent when their impact is investigated within the context of other factors. For example, we would only expect to show an impact on recruitment when forest structure would allow a regenerative response and when propagules are available.

5.4.2   Is there a need for more direct management?

There are options other than animal control available for mitigating negative trends in the viability of tree species populations that involve more direct forms of management. In some instances, where particular species are threatened, managers can implement more interventionist forms of management. For birds, this can involve translocation of populations and supplementing of diets. Currently there is considerable interest in maintaining and restoring indigenous biodiversity on private lands. Because seed sources (and dispersers?) have been lost for some species, planting of nursery-raised seedlings provides a viable means of overcoming recruitment limitation. This leads to the question of whether managers should be artificially establishing tree species on conservation lands; for example, in those areas where there has been extensive 'displacement diebacks'. Some of the issues are:

- As this synchronous dieback event disappears into the past it will likely be more difficult to determine the primary factor responsible.
- There are no seedlings of some of the former dominant tree species present in the dieback area, and reducing herbivores will then not allow a recovery as the seed sources have gone.
- What happens as such events are repeated on conservation lands, and an increasing proportion of the lands show dramatic change with little restorative capacity?

Should managers artificially re-establish northern rata in those parts of the Southern Ruahines where it has disappeared? If this is desirable, then what are the appropriate planting strategies? The ability of some species to regenerate may also require specific disturbance events. Past regeneration of pahautea in the central North Island has often been associated with historical fire. Would managers entertain using fire to establish a cohort of trees of this species? This decision may be less problematic where it is clear that human activity has altered background disturbance regimes. For example, the development of hydro-electricity schemes on many of New Zealand's major rivers will have altered flooding patterns. Therefore, it is possible that tree species that would

have regenerated following such events—kahikatea, for example—may now not successfully regenerate. The pressure for direct forms of management will only increase if ecological research shows that this is required to maintain forested ecosystems. Without this, all we may do is continue to further document the decline of certain tree species in some locations.

5.5 COMPARING THE VULNERABILITY OF TREE SPECIES

5.5.1 Vulnerability of tree species

Any vulnerability scoring system must take into account the following four points:

1. The distribution of the species
- If species have a restricted distribution, then they would potentially be more vulnerable than species that are widely distributed and/or only affected over part of their range. In addition, species that have a restricted distribution and are also locally rare would be particularly vulnerable.
- If we apply this to our seven selected species, those with the more limited distributions (Hall's totara, northern rata, hinau, and pahautea) would be the most vulnerable to mortality, followed by the widely distributed southern rata, kamahi, and red beech.

2. Vulnerability of species at different stages of their life history
Species are vulnerable at critical stages in their life history. Species that are vulnerable to browsing and predation at several stages in their life history may be more vulnerable than those that are susceptible at only a single stage. For example, hinau flowers are browsed by possums, which prevents pollination and seed set. Seeds are eaten by possums on the tree and seeds that fall to the forest floor are eaten by mice and rats. In contrast, red beech is vulnerable only at the post-dispersal seed predation and establishment stages and so may be less vulnerable than hinau. Any assessment should be modified by an appreciation of variable longevity. Hinau, for example, although very vulnerable at several stages in its life history, is quite long-lived (and the foliage is not browsed by possums). Therefore, individuals will remain in a tree population for a long time, even when regeneration is limited.

3. The causes of mortality
- As we have already discussed, it is extremely difficult in many (most?) situations to separate natural from human-induced mortality and to ascribe cause. This, in many instances, is due to lack of knowledge. However, if several factors are implicated in the mortality of a species, then that species is likely to be more vulnerable. On this basis Hall's totara, pahautea, southern rata, and kamahi would be ranked as the most vulnerable since their foliage is browsed by possums, and all undergo relatively synchronous mortality of disturbance-initiated even-aged stands.
- If natural factors can be readily identified as the cause of mortality then the species would be ranked less vulnerable. For example, red beech mortality caused by drought and insects.

4. The significance of species loss to ecosystem processes

- The loss of the dominant species in an ecosystem can have the greatest impact since those that contribute the largest biomass are often drivers of ecosystem processes. If species that are suffering mortality clearly play a role in key ecosystem processes, they would be scored as more vulnerable. This is an area where very little knowledge is presently available.

- The loss of any species results in a change in successional processes, particularly if the species is a canopy dominant. If canopy dominants are lost, major shifts in species composition can result in 'displacement diebacks'.
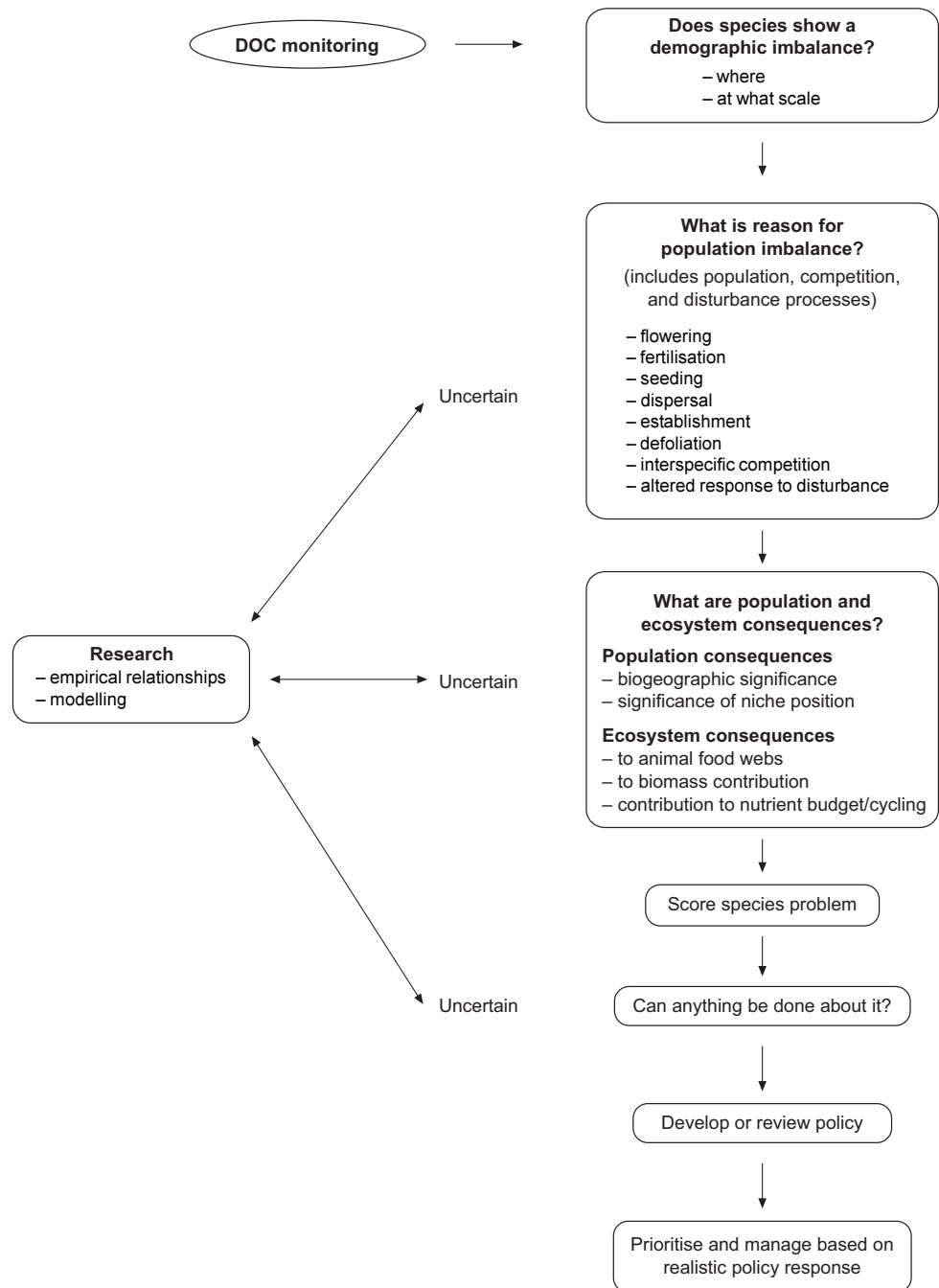
Clearly, there are limitations on this approach. For example, not all factors should carry an equal weighting—and we know little of how to apply weightings. But what such a structured approach does is forces us to consider the full range of relevant population processes and what may be driving these processes.

5.5.2   A systematic approach to scoring species

We propose a generalised framework for assessing the vulnerability, importance of, and research needs for management of key tree species. A diagrammatic representation of this framework is shown in Figure 10. The tree population information necessary to assess demographic imbalances at a range of scales, and locations, would come from efforts to monitor the status of forests—and include a broader range of attributes than just tree population information (e.g. see Coomes et al. 2002). Ideally, this information would be from permanent plots representatively sampling indigenous forests. Where there is an undesirable trajectory for a tree species population, this contributes to a ranking of species in terms of priority for management action. If the reasons for the undesirable trajectory, i.e. declining population, are unclear, as is currently often the case, there is a research requirement that should focus on the factors driving the suite of population processes (Fig. 10). It is worth commenting that increasing populations of certain species, for example unpalatable plants, may also be viewed as an undesirable trajectory. Part of assessing the significance of changes in the abundance and distribution of a species involves evaluating its contribution to how the ecosystem functions. Any uncertainty about ecosystem consequences also flags a requirement for further research to appropriately rank species. Even when population trends are known, and the causes and consequences understood, any assessment of management priority still requires knowledge of viable management strategies. Whether anything can be done about undesirable changes also has implications for the formulation of policy (Fig. 10).

Our generalised framework for assessing vulnerability of tree species accounts for how indicators are measured, interrelated, and understood, when assessing priorities among species. In our framework, we do not, however, consider that human-related impacts provide the only reasons for concern by conservation managers. We also stress the need for more proximate measures of impacts; for example, we consider pest abundance as an inadequate measure of pest impacts. In this report we have only outlined an approach to scoring tree species, and because data are scarce, implementation of this process remains subjective and/or intuitive at this stage. We must use quantitative data where we can, but it will be some time before these data are broad enough to capture the complexity involved.

Figure 10. Generalised framework for assessing the vulnerability, importance of, and research needs for management of key tree species.

```
   ( DOC monitoring ) ──────▶   ┌─────────────────────────────┐
                                │  Does species show a        │
                                │  demographic imbalance?     │
                                │     – where                 │
                                │     – at what scale         │
                                └─────────────────────────────┘
                                              │
                                              ▼
                                ┌─────────────────────────────┐
                                │   What is reason for        │
                                │   population imbalance?      │
                                │  (includes population, competition, │
                                │    and disturbance processes) │
                                │   – flowering               │
              Uncertain         │   – fertilisation           │
                  ▲             │   – seeding                 │
                   ╲            │   – dispersal               │
                    ╲           │   – establishment           │
                     ╲          │   – defoliation             │
                      ╲         │   – interspecific competition │
  ┌──────────────────┐ ╲        │   – altered response to disturbance │
  │   Research        │◀───── Uncertain  └─────────────────────────────┘
  │ – empirical relationships │                    │
  │ – modelling       │                            ▼
  └──────────────────┘         ┌─────────────────────────────┐
                      ╱         │  What are population and    │
                     ╱         │  ecosystem consequences?    │
                    ╱          │  Population consequences    │
                   ▼           │  – biogeographic significance │
              Uncertain        │  – significance of niche position │
                               │  Ecosystem consequences     │
                               │  – to animal food webs      │
                               │  – to biomass contribution  │
                               │  – contribution to nutrient budget/cycling │
                               └─────────────────────────────┘
                                              │
                                              ▼
                                ( Score species problem )
                                              │
                                              ▼
                                ( Can anything be done about it? )
                                              │
                                              ▼
                                ( Develop or review policy )
                                              │
                                              ▼
                                ┌─────────────────────────────┐
                                │ Prioritise and manage based on │
                                │ realistic policy response   │
                                └─────────────────────────────┘
```

This report focuses on the maintenance of tree species and in this way may appear at odds with initiatives aimed towards the implementation of an ecosystem-based management. Clearly, our framework calls for an understanding of the full range of consequences to indigenous forest ecosystems of changes in tree species dominance, and an evaluation of the full range of factors driving these changes. This is consistent with the view that ecosystem management should be driven by specific goals—in this instance that of maintaining structural dominants—based on our best understanding of the ecological interactions and processes necessary to sustain ecosystem composition, structure and function (Christensen et al. 1996).

6. Recommendations

Forest managers and researchers need to:

1. Collect data on tree species populations that are standardised and comparable across a range of spatial and temporal scales. This would provide a more comprehensive basis for the process of establishing which species are most vulnerable. We propose that demographic parameters (recruitment and mortality rates of individuals) should be used, at least in part, to assess this vulnerability.

2. Recognise that past interpretations of threats to indigenous tree species populations have been too simplistic and have hindered effective forest management. For example, while certain vegetation attributes, such as the level of defoliation of a species or the number of its seedlings, may be related to introduced browsing animal numbers, such relationships may not establish causal links and also may be deficient in representing the significance to maintaining tree populations.

3. Evaluate the goals they set for conservation achievement and the range of actions considered by managers. Increasingly, research results question the ability of forest ecosystems to always adjust to some desired state following a simple management action like controlling introduced animals.

4. Support further research on what we consider the most critical issues related to the maintenance of key tree species, including:
   - Detailed investigations of factors controlling the life history, vigour, and demographics of selected species (e.g. Hall's totara).
   - Better understanding the processes resulting in some of the more extensive and common displacement diebacks that have occurred, with particular emphasis on controls on regeneration of formerly dominant species and restorative strategies (e.g. Southern Ruahine Range).
   - Determining the consequences of predation and dispersal modification in some of the large-fruited tree species. Emphasis should be on short-lived species, which should show the impacts on population viability and distribution in the least time.

7. Acknowledgements

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