Predicting native plant succession through woody weeds in New Zealand

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Abstract

It is widely known that gorse (*Ulex europaeus*) eventually disappears from many areas in New Zealand where native forest is regenerating, but what about the numerous other woody weed species that dominate large areas of the landscape in New Zealand? Are any of them similarly susceptible to competition from native plants in the long term? Very little successional information has been published to date for most of these other species, so the answer to this question remains largely unknown. The aim of this work in progress is to begin to explore options for making general predictions about when and where native succession is likely to replace woody weeds. This information could allow weed managers to achieve conservation goals at significantly reduced cost. We searched the literature for studies about native succession through woody weeds and surveyed Department of Conservation weed managers to discover their understanding, beliefs and behaviour around this issue. We summarise the weed and site attributes that are likely to have the most influence over successional outcomes, and propose a number of options for predicting those outcomes. In general, quantitative data on native plant succession through woody weeds in New Zealand are scarce. For a handful of species it has been shown that native succession will replace the weed population under certain environmental conditions, but it is not known whether this will also occur with most other weed species. Despite these uncertainties, weed managers do make decisions about the likelihood of weeds being replaced by native succession. This study is the initial stage of a research project that will endeavour to reduce uncertainty and allow better decision-making around which woody weed species do and do not require active control in New Zealand.

Keywords: invasive species, native regeneration, weed management, weed persistence, invasion ecology, successional outcomes

1.   Introduction

Predicting the persistence of woody weed species is a crucial, yet little studied, area of invasive plant management. In a world where plant invasions are ever-increasing and, commonly, resources to manage those invasions are decreasing, the ability to determine which species do **not** need to be actively controlled is increasingly valuable. The growing literature on invasion ecology means that we now have some information about the range of effects invaders can have in the short to medium term (years to several decades), but what will happen in the very long term (50 years plus)? Might these invaders eventually give way to native succession and disappear without any active control? Little attention has been paid to the longer-term implications of weed invasion, particularly with respect to the persistence of the weed.

Succession is defined as a change in species composition within an ecosystem over time, although definitions differ in whether or not directionality is included (i.e. changes in species composition occur in a particular order) and whether succession follows a disturbance (Platt & Connell 2003). The particular sequence of species may not be predictable, but there can still be general directionality in the progression of vegetation structure and species composition. Pickett et al. (1987a) proposed a mechanistic succession framework that defined the general causes of succession as site availability, differential species availability and differential species performance. Under this scheme, site availability is determined by disturbance, while species availability is determined by propagule persistence and dispersal. Differential species performance depends on resource availability, ecophysiology, life history strategy, stochastic environmental stress, competition, allelopathy, and herbivory and predation (Pickett et al. 1987a). Historical contingencies may also play a major role in determining successional outcomes (Chase 2003; Motzkin et al. 2003). For example, the identity of early-successional species, whether native or exotic, can influence subsequent successional trajectories (Jones et al. 2004; Sullivan et al. 2007). Environmental conditions present during early succession can also affect which species establish, and in which successional order.

Other interactions that can affect succession include facilitation, inhibition and tolerance (Connell & Slatyer 1977; Pickett et al. 1987b). Facilitation and inhibition can occur simultaneously during succession, and appear to be major influences on subsequent vegetation composition (Pickett et al. 1987b; Bellingham et al. 2001). Rodriguez (2006) suggested that the facilitation of native species by invasive species is most likely to occur when the invasive species provides a limiting resource, increases habitat complexity, functionally replaces a native species, or ameliorates predation or competition.

If weed eradication can be achieved at an early stage of invasion using conventional control methods, this is often the most cost-effective option—even if future impacts of the weed are unknown (Harris & Timmins 2009). However, in many (most?) cases, by the time a weed has become conspicuous at a site, it has also become difficult to eradicate. Even when eradication can be achieved at a particular site, ongoing surveillance is often required in order to prevent reinvasion from other propagule sources in the wider landscape. A recent review of weed eradication programmes carried out by New Zealand's Department of Conservation (DOC) concluded that only 4 (out of a total of 90) had successfully eradicated the target weed species, and all of those were infestations of less than 1 ha (Howell 2012). When weed eradication is going to be expensive or difficult (or even impossible, as is often the case), native succession could be a feasible option for 'controlling' the weed, particularly if the weed is not compromising biodiversity values at the site and further spread of the weed is not a threat.

The aim of this project was to begin to explore options for making general predictions about when and where native succession is likely to replace woody weeds. We reviewed existing literature on the succession of native plants through weeds, both within New Zealand and

internationally, to determine whether we can predict the probability of native succession using weed attributes (e.g. habit, life strategy, functional traits, environmental tolerances) and site attributes (e.g. habitat type, community composition, disturbance regime). We also surveyed weed managers from DOC to identify whether they are already making weed control decisions in the field based on their understanding of native succession. We end by identifying significant gaps in our knowledge of succession of native plants through weeds, and recommend areas for future research.

This is the first stage of a broader research project that proposes to provide general guidelines about where, when and how woody weeds get replaced by regenerating native plant species on conservation land. Managers will be able to use this information to predict which woody weed species are likely to die out naturally in their area and which are likely to persist if they are not actively managed. Weed control resources could then be prioritised more effectively and spent only on weed species that require active management. This could result in weed managers achieving greater biodiversity gain for the amount of dollars/effort spent. Additional benefits of this 'minimal intervention' approach include reduced herbicide use, reduced disturbance and reduced risk of re-invasion by the same or different weed species. The potential risk of this approach is that valued early successional native species may be lost to a site if they are unable to establish in the presence of the dominant woody weed, particularly if the weed has a long-lived seed bank and is able to re-establish in newly-disturbed areas.

2. Methods

We conducted a literature search using Google Scholar, searching for the terms succession, weed, native, regeneration, recruitment, restoration, nurse plant, facilitation, life history traits and spontaneous succession. We also searched New Zealand university library catalogues for unpublished theses on this topic. We checked the contents pages of key journals (*Restoration Ecology, Biological Invasions,* and *New Zealand Journal of Ecology*) for relevant articles and found additional studies in the reference lists of previously located articles or theses.

We emailed DOC weed staff to find out where, when and why weed managers are already making the decision to not control weeds on the basis that natives will eventually outcompete them. Weed staff were asked the following questions:

1. What weed species do you currently leave for native succession to 'control'?
2. In what sort of habitat?
3. What sort of native vegetation do you expect will eventually take over?
4. What information/observations/evidence do you use to make your decision?

3. Weed attributes

Noble and Slatyer (1980) defined the 'vital attributes' for a plant species' role in succession as:

1. The plant's method of arrival or persistence at a particular site
2. Its ability to establish and grow there
3. The time it requires to reach critical life stages (reproductive maturity, lifespan, and propagule persistence)

The attributes of plant species that decrease their likelihood of replacement by other species include the ability to survive for long periods in a resting state, phenotypic plasticity (the ability to change phenotypic traits in response to changes in the environment) and inhibition of the establishment of other species (Platt & Connell 2003). Weed attributes considered to have an important influence on their potential for replacement by natives are summarised in Table 1 and discussed below.

3.1 Dispersal mode

The dispersal mode of a weed species can influence invasion and thus succession opportunities. Fleshy-fruited weed species can attract seed dispersers that travel over long distances to find a profitable food source (Neilan et al. 2006). Because New Zealand's native woody vegetation is predominantly fleshy-fruited (70% of trees and 49% shrubs) (Burrows 1994), fleshy-fruited weeds may facilitate succession of natives in forest and shrubland habitats by attracting birds bearing native seeds (Neilan et al. 2006). However, in habitats where the native vegetation is predominantly dry-fruited, fleshy-fruited plants may have an advantage that leads to an increase in invasion by fleshy-fruited weeds (Neilan et al. 2006). Additionally, the attraction of seed-bearing birds may also alter the successional trajectory from dry-seeded native species, such as kānuka (*Kunzea erecoides*), to fleshy-fruited species, native or exotic. There is also the risk that native and non-native frugivores may disperse fleshy-fruited weed species to other areas (Neilan et al. 2006).

3.2 Persistence

The persistent stage in a plant's lifecycle is usually the seed or spore. Seeds can form a soil seed bank, sometimes remaining dormant for many decades. Some weed species can form large, persistent seed banks (D'Antonio & Meyerson 2002). For example, in an undisturbed Hawaiian forest, exotic species formed 67% of the soil seed bank, but less than 12% of the aboveground cover and less than 5% of the seed rain (Drake 1998). Similarly, exotic species in a New Zealand study were disproportionately represented in the seed bank relative to their abundance in the seed rain (45% and 27% of seeds, respectively) (Ferguson & Drake 1999). Seeds of some weed species, e.g. gorse (*Ulex europaeus*) and broom (*Cytisus scoparius*), can persist in the soil for many decades (Wardle 1991). A persistent seed bank does not necessarily alter the chance of a weed being replaced by natives, but will influence its continued dominance of newly-disturbed sites in the area. Serotinous plants such as *Hakea* spp. form a canopy seed bank from which seeds are released after fire (Wardle 1991). Clonal growth can also enable a species to survive for long periods in a resting state, resprouting after disturbance (Platt & Connell 2003).

Table 1. Attributes of weeds that affect the likelihood of their natural replacement by natives.

ATTRIBUTE	TYPES	DESCRIPTION/IMPLICATIONS	REFERENCES
Dispersal mode	• Animal (internal or external) • Human • Wind • Water • Ballistic • Gravity	• Likelihood of ongoing seed input from other sites • Potential as food source for seed dispersers	Neilan et al. 2006
Persistence	• Dormancy • Resprouting	• Presence of seed bank • Persistence of adult in dormant state • Resprouting post-disturbance	Platt & Connell 2003
Time to reach critical life stages	• Time to reproductive maturity • Lifespan	• Shade-tolerant species are less likely to be replaced by native succession • Persistence of adults	Noble & Slatyer 1980
Phenotypic plasticity	• Yes • no	• Plasticity in plant traits increases competitive ability	Platt & Connell 2003
Environmental tolerances	• Shade • Moisture • Nutrient availability • Temperature	• Shade-tolerant species are less likely to be replaced by native succession	Fenner & Thompson 2005
Life form	• Tree • Shrub • Herb • Grass • Vine • Sedge/rush • Ferns & allies	Ability to: • Pre-empt space • Provide shelter • Block light • Provide perching sites for seed-dispersing birds	Grime 1977; Neilan et al. 2006; Platt & Connell 2003
Biotic interactions	• Facilitation • Inhibition	• Enhanced invasibility of propagules • Increased resource availability • Amelioration of environmental stresses • Structural or competitive dominance • Increased mortality of natives (e.g. facilitate fire)	Pickett et al. 1987b; Platt & Connell 2003; Rodriguez 2006

3.3 Time to reach critical life stages

The time taken to reach reproductive maturity and a plant species' lifespan can also have important effects on persistence at a site (Noble & Slatyer 1980). Weed longevity is likely to have the strongest influence on the length of time it takes for native species to replace the weed, rather than the successional outcome itself. On the other hand, if regeneration of the weed happens only occasionally, then being long-lived may increase the chance that another generation will have established by the time the original adults die. Weed species that reproduce quickly may be able to establish seedlings prior to natives colonising.

3.4 Phenotypic plasticity

Phenotypic plasticity can be defined as the ability of an organism to change phenotypic traits (e.g. morphology, physiology, phenology) in response to changes in the environment (e.g. climate, light environment). Phenotypic plasticity in weed species can result in increased competitive ability and prevent the subsequent establishment of natives (Platt & Connell 2003). The invasive dune grass marram (*Ammophila arenaria*) colonises newly formed sand dunes. It is thought to persist on stabilised dunes because of plastic changes in growth traits that enable it to inhibit colonisation by other species (Gray 1985). Marram's broad habitat use may also be the result of enemy release (Van der Putten et al. 1989).

3.5 Environmental tolerances

The key environmental factors that limit seedling establishment are light, moisture, and nutrient availability (Fenner & Thompson 2005). Environmental tolerances can affect whether a weed species persists at a site or is replaced by natives. For example, the exotic tree *Spathodea campanulata* is an excellent coloniser of abandoned pastures in Costa Rica, but it is shade intolerant and does not recruit in the forest understorey (Aide et al. 2000). After 30–40 years, *S. campanulata* dies out and is replaced by natives. In contrast, the exotic large-seeded *Syzygium jambos* has shade-tolerant seedlings that occur in their highest densities in old growth forests (Aide et al. 2000). Adult *S. jambos* form a dense canopy, resulting in low light levels in the understorey, restricting the establishment of more light-demanding native species (Aide et al. 2000). Natives that are shade-intolerant and require disturbance to establish may be competing directly with early-successional exotic species.

Differences in light availability beneath exotic and native canopies may influence successional trajectories. For example, the biomass of exotic buddleia (*Buddleja davidii*) had no effect on diversity of either native or exotic species in a New Zealand flood plain (Bellingham et al. 2005). In contrast, exotic plant diversity decreased with increasing native *Coriaria arborea* biomass, which was thought to be due to low light levels (three times lower than under buddleia) (Bellingham et al. 2005).

Both gorse and broom need full light to grow well and cannot regenerate significantly under their own canopy or that of other species (Wilson 1994). Native woody species are often shade tolerant and can regenerate under gorse and broom when not grazed by mammals (Wilson 1994). The shade tolerance of all of the 328 weed species recognised by DOC has been assessed (intolerant, tolerant, medium or aquatic), and recorded (K.M., unpubl. data). However, this assessment was done for adult plants only, because seedling shade tolerance is rarely known. Seed size could be an important predictor of the seedling shade tolerance of a weed species, as these traits are often correlated (Fenner & Thompson 2005). Large seed size is advantageous for seedling survival in a wide range of stressful environments, including deep shade (Fenner & Thompson 2005).

Light availability is also an important factor in native forest regeneration under forestry plantations (Brockerhoff et al. 2003; Lemenih et al. 2004). In a study of pine (*Pinus* spp.) plantations in New Zealand, the proportion of native species increased with increasing stand age and canopy closure, while exotic species decreased (Brockerhoff et al. 2003). When same-age pine

plantations planted at high and low densities were compared, the higher-stocked stands (where light levels are presumably lower) had lower overall understorey cover but a higher proportion of native species (Brockerhoff et al. 2003).

3.6 Life form

At each stage of succession, the major components of plant biomass are usually the species with the largest life forms (Grime 1977). Plants achieve dominance either through high resource uptake (competitive dominance) or the ability to sustain low rates of growth under limiting conditions for long periods (Grime 1977). Dominance depends on a positive feedback between the dominance mechanism and the deleterious effects large plants have on the fitness of smaller neighbours (usually shading, litter production, and depletion of nutrients and water in the soil) (Grime 1977). Thus, if all else is equal, trees are more likely to replace smaller life forms such as shrubs and herbs. Conversely, in non-woody vegetation types, weed tree species are unlikely to be replaced by the native herbaceous vegetation. Because weed species tend to be competitively dominant (by definition), native species may only achieve dominance through slow growth under low light levels, enabling eventual weed suppression.

3.7 Biotic interactions

Facilitation occurs when early successional species modify the physical environment, enabling colonisation by later species. Facilitation can occur by several mechanisms, including enhanced dispersal and/or establishment of propagules, increased resource availability, and amelioration of environmental stresses (Pickett et al. 1987b; Bellingham et al. 2001; Neilan et al. 2006).

In some instances, weed species can facilitate the establishment of native species by providing structural complexity or shade and shelter for seedlings. Neilan et al. (2006) found that the invasive weed camphor laurel (*Cinnamomum camphora*) is facilitating the recruitment of native rainforest plants in abandoned farmland in Queensland, Australia. Unlike many native trees, camphor laurel can successfully establish in pasture (Neilan et al. 2006). Once established, it forms a moderately dense canopy cover and litter layer, creating shade and other physical conditions that suppress the growth of pasture and herbaceous weeds, but which are suitable for establishment of rainforest plants (Neilan et al. 2006). Similarly, elder (*Sambucus nigra*) can facilitate the establishment of native vegetation in New Zealand by providing perching sites and fleshy fruits that attract seed-dispersing birds (Voyce 1998). Several examples of nitrogen-fixing invasive plant species facilitating native plant succession have been documented (e.g. Quinos et al. 1998), including in New Zealand (McQueen et al. 2006). Invasive species can, of course, also facilitate other invasive species (see, for example, Vitousek & Walker 1989; Carino & Daehler 2002; Jordan et al. 2008).

The effects of facilitation often increase as stress intensifies (Gómez-Aparicio et al. 2004). In a Mediterranean climate with summer drought, nurse shrubs increased survival and growth of seedlings compared with open sites (Gómez-Aparicio et al. 2004). The key facilitation mechanism appeared to be increased moisture availability beneath nurse shrubs; there was a greater facilitative effect at low compared with high elevations, on sunny compared with shady sites, and in the two dry years rather than in the one wet year (Gómez-Aparicio et al. 2004).

Inhibition occurs when early species dominate structurally or competitively so that other species cannot establish (Pickett et al. 1987b). Inhibition may occur through competition for nutrients and light, and the presence of chemical inhibitors (Pickett et al. 1987b). Establishment inhibition can occur when weeds pre-empt available space in an ecosystem, e.g. large trees in a forest (Platt & Connell 2003). Plant life form could therefore be an important predictor of replaceability in a given weed species. Establishment limitation can also occur when weeds increase the mortality of native species (Platt & Connell 2003). For example, weed species that facilitate fire can suppress the recruitment of less fire-tolerant but more shade-tolerant native species (Platt & Connell 2003).

4. Site attributes

Site attributes that are considered to have an important influence on the potential for succession of natives through weeds are summarised in Table 2 and discussed below.

4.1 Native seed availability

The availability of native seed sources is a critical factor influencing the succession of native species in weedy communities (Suding et al. 2004). In the absence of local native seed sources at a site, natural regeneration will depend on dispersal of seeds from nearby sites (Neilan et al. 2006). The site attributes that are important for attracting animal seed dispersers include the availability of perches, the structural complexity of the vegetation, and the presence of food sources, especially fruit, as an attractant (Wunderle 1997; Neilan et al. 2006). Sites with these attributes will be more attractive to animal dispersers, and therefore have higher levels of native seed deposition and subsequent recruitment (Wunderle 1997). For example, on Mana Island, seed rain density at forested sites was much higher than in grassland (3742 and 7.7 seeds per m^2, respectively) (Ferguson & Drake 1999). The fruits of many exotic species are largely ignored by most endemic birds, although they are eaten by native silvereyes (*Zosterops lateralis*) and introduced birds, especially blackbirds (*Turdus merula*) (Williams & Karl 1996).

The efficacy of animal seed dispersal to a site can be limited by the distance from a native seed source, and the presence and movement of animal dispersers in a landscape (Wunderle 1997; Neilan et al. 2006). Knowledge of how frugivorous birds use weedy communities is important

Table 2.   Site attributes affecting the likelihood of natural replacement of weeds by natives.

ATTRIBUTE	DESCRIPTION	IMPLICATIONS	REFERENCES
Native seed availability	• Presence of or distance to native vegetation in surrounding landscape	• Affects ability of natives to recolonise site by dispersal	Suding et al. 2004; Neilan et al. 2006
Seed bank composition	• Proportion and identity of native and weed seeds in soil seed bank	• Influences likelihood of native recruitment after disturbance	D'Antonio & Meyerson 2002; Suding et al. 2004
Vegetation composition	• Weediness • Identities of other weeds • Natives • Vegetation structure	• Potential for succession by other weed species • Presence of natives as local seed source • Perching sites for seed deposition by birds	Suding et al. 2004
Disturbance regime	• Type and frequency of disturbance (e.g. fire, wind throw, landslide, earthquake, flood, volcanic eruption)	• Increased nutrient availability after disturbance favours weeds and affects the likelihood of weed recolonisation of the site from soil seed bank	D'Antonio & Meyerson 2002; Suding et al. 2004
Trophic interactions	• Presence of herbivorous mammals • Presence of frugivorous birds	• Seed predation and herbivory may limit recruitment of natives • Movement of seed dispersers from native remnants to regeneration sites can provide seeds	Suding et al. 2004; Neilan et al. 2006
Habitat type	• Land Environments of New Zealand (LENZ) habitat types and predicted vegetation	• Determines vegetation structure and environmental conditions that affect type of natives that will recolonise	Leathwick et al. 2003

for understanding the potential for replacement of weeds by natives at a site (Neilan et al. 2006). Some international studies have found that structural complexity on its own can be insufficient to attract frugivorous birds across extensively cleared landscapes (Neilan et al. 2006). However, New Zealand avian frugivores, including kererū (*Hemiphaga novaeseelandiae*) and tūī (*Prosthemadera novaeseelandiae*), regularly fly between forest remnants separated by tens of kilometres. In a study near Nelson, the frequency of the presence of seed-dispersing birds was similar in native kānuka and introduced gorse (Williams & Karl 2002). Silvereyes (*Zosterops lateralis*) were more common in gorse than kānuka, while bellbirds (*Anthornis melanura*) were ten times more frequent in kānuka than gorse (Williams & Karl 2002).

4.3 Vegetation composition

Vegetation composition can have important effects on succession. Factors including the number and identity of weeds present, and the presence of natives are all potentially important. In New Zealand plantation pine forests, it is the age of the stand and other site factors that are important determinants of the establishment of native plants (Brockerhoff et al. 2003). However, differences in the identity of exotic plantation species have been found to affect the regeneration of natives in other countries (Fimbel & Fimbel 1996; Lemenih & Teketay 2005).

4.2 Disturbance regime

The disturbance regime at a site will also influence successional pathways. Disturbance includes fire, flood, wind throw, extreme climatic events and disease or pest outbreaks (Noble & Slatyer 1980). Disturbance type, intensity, frequency and spatial extent may all affect the course of succession (Pickett et al. 1987a).

The vegetation composition at a site after disturbance is somewhat predictable from the composition of the pre-disturbance seed bank (D'Antonio & Meyerson 2002). Disturbance at an invaded site tends to facilitate reinvasion by weeds because of a decline in the native seed bank in the absence of native seed input (Suding et al. 2004) and the propensity of some weeds to form large persistent seed banks (D'Antonio & Meyerson 2002). For example, gorse forms a persistent soil seed bank from which it will re-establish after fire (Wardle 1991) but which, if left undisturbed, will be replaced by native succession to forest (Wilson 1994).

Pine (*Pinus radiata*) seedlings establish when fires release seed from cones, but an increase in pine depends on sufficiently long intervals between fires for seedlings to reach reproductive maturity (Wardle 1991: 539). In New Zealand, exotic pioneer species often dominate following disturbance of plantation forests by harvesting or thinning, especially in heavily modified areas (Brockerhoff et al. 2003). Mammalian browsing is another form of disturbance that can inhibit the regeneration of native plants beneath weeds (Wilson 1994).

Some habitats are particularly prone to disturbance, which may decrease the likelihood of weed replacement by native vegetation. For example, in New Zealand, buddleia can survive burial by at least 0.5 m of alluvium by producing adventitious roots and shoots on buried stems (Smale 1990). Accordingly, where flooding is sufficiently frequent and severe, buddleia may persist indefinitely and native forest may never develop (Smale 1990). However, in the absence of disturbance, native forest is predicted to replace buddleia in streambeds as it collapses with old age (Smale 1990).

4.4 Habitat type

Habitat conditions (including climate and soil fertility) in combination with other site attributes can have a significant influence on successional processes. For example, regeneration of natives through broom and gorse appears to be maximised under conditions of high and reliable rainfall, fertile soils, abundant local seed sources and seed-dispersing birds, and minimisation of mammalian browsing (Wilson 1994).

The potential native vegetation type will have a large influence on the probability of native succession through weeds. In frequently disturbed lowland riverbeds, weeds generally dominate all successional stages (Wardle 1991: 364 & 372), although natives can establish beneath the canopy of exotic species such as willows (*Salix* spp.) (Pratt 1999). In the absence of disturbance, natives may eventually replace shade-intolerant exotic species such as willows. At higher altitudes, native species usually dominate succession in areas suitable for woody vegetation, which contrasts with what occurs in the lowlands (Wardle 1991: 547). Whether native species can replace seral weeds where the original vegetation was shrubby or herbaceous seems more difficult to predict (Wardle 1991: 557).

Geographic location influences regeneration of natives through exotic pine plantations (Brockerhoff et al. 2003). In dry areas of New Zealand, pine forests have little undergrowth (Wardle 1991: 547). For example, pine stands in Canterbury have less understorey cover and lower species richness than plantations on the West Coast, Bay of Plenty or central North Island, probably due to frequent drought conditions and a scarcity of native seed sources in the Canterbury Plains (Brockerhoff et al. 2003), but also because establishment and growth of natives is slow under dry conditions. Pine seedlings may also be able to compete with natives in these drier areas when the canopy is opened (Wardle 1991: 547). Successional outcomes are more difficult to predict when the pace of change is very slow.

The Land Environments of New Zealand (LENZ) classification (Leathwick et al. 2003) may be a useful tool for grouping sites when assessing whether weed replacement by natives is likely. The LENZ classification uses 15 environmental (climate, landform and soil) variables to group sites on a hierarchical basis (Leathwick et al. 2003). The variables were selected on the basis of high correlations with common New Zealand tree species distributions and a strong functional relevance to tree physiology (Leathwick et al. 2003). The LENZ classification groups sites by four levels that have an increasing degree of detail, with 20 environments in the top level of the hierarchy (Level I). Each of the Level I environments contains one or more Level II groups, while Level IV contains 800 groups. Level I may be the most practical group for the purposes of assessing the probability of natives replacing weeds at a given site. There are 20 environments that make up the Level I classification group, occurring in sequence from northern, lowland environments with warm temperatures and high solar radiation to the permanent snow and ice at high elevation in the Southern Alps/Kā Tiritiri o te Moana of the South Island (Leathwick et al. 2003). These 20 environments can be grouped in five clusters having similar climate, slope, drainage, soil type, and elevation (Leathwick et al. 2003).

5. Potential restoration outcomes

The identity of early successional species can influence subsequent vegetation succession (Connell & Slatyer 1977; Sullivan et al. 2007). For example, native forest successional trajectories differ through introduced gorse and native kānuka (Sullivan et al. 2007). In sites around Wellington and Nelson, species richness was often lower under gorse than kānuka, and there were fewer small-leaved shrubs and orchids (Sullivan et al. 2007).

In subtropical Australia, species richness and abundance of rainforest recruits under exotic camphor laurel was comparable with restoration plantings (Neilan et al. 2006). However, the long-term course of succession was uncertain, as camphor laurel is long-lived and natives have to compete with shade-tolerant exotics (e.g. privet, *Ligustrum* spp.) that dominate the recruitment cohort. In a study of natural forest regeneration of abandoned pastures in Costa Rica, forest structure (stem density, basal area, biomass and number of species) recovered in around 40 years (Aide et al. 2000). However, the species composition of regenerated forests was markedly different from that of old-growth sites (Aide et al. 2000).

6. New Zealand studies

Williams (2011) summarised existing information on the succession of native plants through weeds in New Zealand, and found that there were very few published data on this topic. Of the 36 species of non-native woody plants that occur at a landscape scale (defined as patches of greater than 80% cover and that exceed 0.25 ha in size) in New Zealand, only 14 were described in the literature as being replaced by native species. Most of these studies described succession under a limited set of environmental conditions, and none considered where or why exotic species are not replaced by natives. Here, we expand on the species that have been most thoroughly studied in New Zealand: gorse, broom, and conifer species (mostly *Pinus radiata*). These studies give some insight into the mechanisms that drive native succession through these weed species.

6.1 Gorse

The dominant early successional species in New Zealand, kānuka and mānuka (*Leptospermum scoparium*), have now been largely replaced by gorse (Sullivan et al. 2007). If disturbance such as fire or clearing of gorse is prevented, and a native seed source is available, native broadleaved species can dominate in around 30 years (Sullivan et al. 2007). Wardle (1991) noted that dense gorse stands collapse with age and are subsequently invaded by native plants. In Wellington, Druce (1957) found that gorse was vigorous in 10-year-old scrub, senile in 34-year-old scrub and dead in 40-year-old scrub, where it had been replaced by native trees. In Williams & Karl's (2002) study near Nelson, native seedling survival was higher in gorse stands than in kānuka, probably because of openings in the canopy and the lower density of hares (*Lepus europaeus*) and rabbits (*Oryctolagus cuniculus*). However, where seed sources of native forest species are remote, the environment is marginal for forest or grazing eliminates tree seedlings, seral species such as gorse can form self-perpetuating stands (Wardle 1991).

In a study near Dunedin, the establishment of native woody species was greater under taller, lower-density gorse with shallow litter, and where areas of bare soil or bryophytes were available (Lee et al. 1986). Native species failed to establish in 60% of gorse plots younger than 25 years, possibly because of the coarse-textured, deep and dry gorse litter and slower rates of both gorse

litter decomposition and native plant growth in the cooler climate (Lee et al. 1986). However, native woody species occurred in six of the seven plots that contained gorse older than 25 years. Lee et al. (1986) predicted that native species would establish during gorse senescence when gorse density is reduced and when gorse litter is disturbed. Because native species are longer-lived and grow taller than gorse, the replacement of gorse by native vegetation on an undisturbed site was predicted to take no more than 50–60 years (Lee et al. 1986). However, as discussed earlier, native species composition can differ between gorse stands and stands of early successional natives such as kānuka (Sullivan et al. 2007).

Ogle-Mannering (1995) completed a PhD thesis on gorse succession near Dunedin, the main findings of which are summarised below. Results from growth chamber experiments supported the hypothesis that deep gorse litter inhibits native establishment. Native seedling emergence decreased with increasing gorse litter depth. There was a significant interaction between litter depth and moisture, with decreased emergence under moist conditions with deep litter compared with emergence under moist conditions on the surface. The ability to emerge beneath deep litter was apparently related to seed size, with large-seeded species having greater emergence under litter than small-seeded species. Seed size appears to be related to light requirements for germination: small-seeded species failed to germinate in the dark, while large-seeded species did germinate.

By measuring seedling growth in pots outdoors, Ogle-Mannering (1995) also found that gorse growth rates were inhibited at low light levels. At 70% of full light, gorse relative growth rates (RGR) were significantly higher than all other species trialled—māhoe (*Melicytus ramiflorus*), putaputāwētā (*Carpodetus serratus*), karamu (*Coprosma robusta*), kāpuka (*Griselinea littoralis*), and tarata (*Pittosporum eugenioides*)—except kānuka. Gorse RGR declined significantly between 70% and 11% light, while differences in RGR at these two lights levels were insignificant in other species. At 2% light, the relative growth rate of gorse was significantly lower than that of tarata and māhoe. Gorse also had a significantly higher photosynthetic rate than other species at high light levels, although at low levels there was no significant difference between gorse and all other species.

Ogle-Mannering (1995) also conducted vegetation surveys and measured environmental variables in study plots at a site near Dunedin. For plots with greater than 70% gorse in the canopy, there was a significant positive correlation between light levels and age. Not surprisingly, gorse seedling survival was higher in clearings than under gorse and no gorse seedlings survived under native forest. Seedling composition varied depending on gorse age, soil moisture, and litter depth. Ordination results grouped plots into two groups:

1. Young gorse with dry soil and shallow litter, which had mostly exotic herbs and grasses
2. Older plots with moister soils and deeper litter, which had mostly native woody seedlings.

Results of a seedling transplant experiment showed that fencing increased the survival of all species in clearings (but not under gorse or native forest) by preventing rabbit herbivory (Ogle-Mannering 1995). Fencing increased survival of all species except māhoe under gorse. For most native species, RGR was highest under gorse, while the RGR of gorse was highest in clearings. Ogle-Mannering (1995) concluded that lifespan and stature help explain the replacement of gorse by natives; gorse lives for around 30 years and reaches a maximum height of 5 m, while kānuka can live for more than 70 years and reach 16 m in height.

Much of the evidence for replacement of gorse by native vegetation is anecdotal or qualitative, but there are also some quantitative data demonstrating that gorse can be overtopped by natives. For example, Sullivan et al. (2007) reported a mean maximum native vegetation height of 4 m in old gorse stands in Wellington. It may be possible to resurvey plots observed in previous studies (e.g. Lee et al. 1986) to determine whether gorse has been replaced by natives since the original survey.

6.2 Broom

Native species appear to successfully regenerate beneath broom at some sites if left undisturbed by fire (Wilson 1994). Browsing by introduced mammals seems to have variable effects on broom regeneration, with grazing by sheep and cattle inhibiting its regeneration (Williams 1983), and the presence of other introduced mammals inhibiting native regeneration (Wilson 1994). In a study on the Port Hills, Canterbury, succession of natives through broom occurred following an intermediate stage of exotic elder (*Sambucus nigra*) (Williams 1983).

In another study on the Port Hills, broom recruitment decreased over time in the absence of fire under all four treatments tested: annual removal of bracken (*Pteridium esculentum*), annual removal of broom, annual removal of bracken and broom, and no removal (Partridge 1992). In contrast to Williams (1983), however, Partridge (1992) found no recruitment of native woody species under broom, although the study was limited to a single 9 × 9 m plot. Partridge (1992) suggested that the only way native forest could establish at the study site was through amelioration of drought conditions in summer, potentially facilitated by elder establishment.

Williams (1983) suggested that broom is a more effective nurse plant than gorse because broom has a shorter lifespan, produces more readily decomposable litter, and allows more light to reach seedlings beneath its canopy. The twiggy crowns of broom are probably a more attractive perching site for frugivores than the spiny thorns of gorse (Williams 1983). Furthermore, kererū (one of the main seed dispersers in New Zealand) feed on the leaves, buds and flowers of broom, but not on gorse (McEwen 1978), although other native seed-dispersing birds are found in gorse (Williams & Karl 2002).

At some sites, native species are not regenerating beneath broom (e.g. Aratiaita, Waikato), even where broom stands are senescing and collapsing and despite the proximity of a native seed source (Smale et al. 2001). This could be due to seed and/or seedling predation by rats (*Rattus* spp.) or possums (*Trichosurus vulpecula*) (Wilson et al. 2003).

In broom-dominated vegetation in Tongariro National Park, Trass (2000) found that establishment and survival of native woody vegetation beneath broom was limited by both seed supply and the availability of suitable sites. Native seed and seedling density decreased with increasing distance to native forest. Seed rain species richness was highest in native forest, decreased under broom and was lowest in rank grass. Birds deposited much higher quantities of seeds in native forest (436 and 1028 seeds per m² at two sites over a nine-month period) than under broom (83/m²) or exotic grass (15/m²). Seed rain density and species richness also increased with increasing maximum vegetation height across all vegetation types, although this may have been due to a decrease in vegetation height from forest to broom and grass.

Trass (2000) also conducted a seed addition experiment to determine whether establishment of woody natives was limited by seed supply and/or availability of suitable sites. Seeds of *Griselinia littoralis*, *Coprosma taylorii*, and *Pittosporum tenuifolium* var. *colensoi* were added to native forest, broom and grass plots. Seed addition treatments were combined with clearing (all ground cover, litter, and roots removed from plots) and caging (large mammals excluded) treatments. Habitat type had the greatest effect on the survival of all three species. Seedling establishment and survival was greatest in native forest, low under broom, and extremely poor under exotic grass. Seed addition increased *Griselinia littoralis* seedling establishment and survival under broom, but had no effect for *Coprosma taylorii* or *Pittosporum tenuifolium* (very few seedlings of this species established in any habitat). Clearing of ground cover and litter increased *Coprosma taylorii* seedling establishment beneath broom but decreased seedling survival, while caging increased survival. However, clearing also increased the establishment of broom, which may dominate native seedlings. Survival of transplanted *Griselinia littoralis* seedlings was greatest under native forest (85–100%) and poor under broom (0–70%) and exotic grass (0–25%).

Light availability was the most important factor explaining seedling performance, with significantly higher native seedling establishment and survival at low light levels (Trass 2000). Light availability differed significantly among habitats and was much lower in native forest than under broom or exotic grass.

Scientists at Landcare Research and DOC are currently investigating whether weeds facilitate native tree and shrub establishment in New Zealand dryland environments (Walker et al. 2009). As part of this project, scientists have been monitoring plots in north Canterbury where a range of native plant species were planted into broom stands in 2002/03. Despite conditions at the site being harsh (dry, with extreme temperatures), survival of natives has been high to date, which indicates that broom can facilitate native plant establishment (Larry Burrows, Landcare Research, Lincoln, pers. comm. 2012). Whether the natives will eventually replace the broom remains to be seen. This is part of a Landcare Research programme aimed at improving understanding of dryland woody species ecology (present distributions, succession pathways and rates, traits, and factors that control and limit their spread). This knowledge will be used to develop and test low-input methods for facilitating native woody succession in the field.

6.3   *Pinus radiata* and other conifers

Diverse native vegetation often develops under pine (*Pinus radiata*) plantations (Wardle 1991; Brockerhoff et al. 2003), although pines may persist for centuries if they are left unharvested (Wardle 1991: 157). Some pines have lifespans of several centuries and there are generally enough pine seedlings to ensure at least scattered second-generation pine trees (Wardle 1991). Brockerhoff et al. (2003) studied the vegetation of 5-, 16- and 27-year-old *P. radiata* plantations in four areas of New Zealand (Bay of Plenty, Volcanic Plateau, Westland, and Canterbury Plains). Both richness and cover of exotic species decreased with time, while native species richness and cover was greatest in oldest stands (Brockerhoff et al. 2003). Changes in vegetation composition over time were correlated with canopy closure as the pine stands aged, which influenced light availability (Brockerhoff et al. 2003).

Similar temporal changes in understorey vegetation have been reported for other *P. radiata* plantations (Allen et al. 1995, cited in Brockerhoff et al. 2003; Ogden et al. 1997). In a study of *P. radiata* plantations in the central North Island, Ogden et al. (1997) found that exotic shrubs dominated the understorey in stands less than 20 years old. In older stands, light-demanding native shrubs with bird-dispersed fruits dominated, with more shade-tolerant species in the oldest site (67 years old).

In the eastern Hutt Valley, pine trees suppressed surrounding mānuka, but were predicted to be replaced by fivefinger (*Pseudopanax arboreus*) and kāmahi (*Weinmannia racemosa*) (Wardle 1991). Although native vegetation is generally predicted to replace *P. radiata* if left unharvested, pine seedlings might outcompete native species in drier habitats (Brockerhoff et al. 2003).

Dehlin et al. (2008) studied tree seedling performance under monospecific stands of native mountain beech (*Nothofagus solandri* var. *cliffortioides*), and exotic lodgepole pine (*Pinus contorta*) and Douglas fir (*Pseudotsuga menziesii*). Seedlings of all three species were grown in a glasshouse and then transplanted to the field. Both exotic species appear to inhibit tree seedling establishment compared with the native mountain beech. Mountain beech provided the most favourable conditions for seedling performance, which was attributed to reduced light availability beneath Douglas fir and altered soil conditions beneath both exotic tree species. Seedling survival was significantly greater under beech and pine (which both had higher light levels) than under Douglas fir stands (which had the lowest light intensity). Although light levels were greatest under pine, seedling growth was three times greater in mountain beech stands, which had the highest levels of soil organic matter, microbial biomass, and abundance and diversity of nematodes. Seedlings beneath Douglas fir decreased in biomass during the experiment.

Scion is currently conducting research on the establishment of natives under a range of conifer species (Ledgard 2007). It has been found that poisoning of *P. radiata* in the Marlborough Sounds hastened the process of native succession. Researchers are also testing the effects of thinning the pine canopy and spreading native seeds (to date, the latter approach has been reported as 'promising'). Natives struggled to establish under living conifers in drier regions around Lake Tekapo, but felling of conifers had a significant benefit for native grasses and woody species. In high-country grasslands, fertiliser addition doubled resident vegetation cover compared with unfertilised plots and suppressed the emergence of nine conifer species. However, dominant resident species included hawkweeds (*Hieracium* spp.) and browntop (*Agrostis capillaris*), along with hard tussock (*Festuca novaezelandiae*). Researchers have also investigated vegetation successions where wilding lodgepole pines were left unmanaged. Wildings spread steadily after their introduction in 1975, suppressing all existing vegetation after 10 years. By 2007, canopy openings enabled limited ground cover establishment (<5% cover and only exotic species). Light levels may be suitable for the establishment of shade-tolerant natives if a seed source is available.

At DOC, Clayson Howell and Kate McAlpine are researching native plant succession in high-altitude stands of wilding *P. contorta*. They are also testing the effects of different methods of *P. contorta* control (felling v. poisoning) on subsequent native regeneration to see if native succession can be facilitated.

7. DOC weed staff observations

The authors contacted DOC weed staff and asked where, when and why they made decisions to not control weeds with the intention that natives would eventually take over. The results of this survey are shown in Table 3.

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Table 3.   Situations where weed managers currently base weed control decisions (in part) on the probability of natives replacing weeds naturally.

WEEDS	HABITAT WHERE NATIVE SUCCESSION OCCURS	HABITAT WHERE NATIVE SUCCESSION DOES NOT OCCUR	NATIVE COLONISERS	PREDICTED VEGETATION	LOCATION	NOTES	SOURCE
Acacia mearnsii (black wattle) and *A. dealbata* (silver wattle)	Regenerating bush				Hauraki Gulf (Motuora Island)	Several mature acacia plants among mature native bush. No sign of acacia seedling spread, presumably too shady.	Helen Lindsay
Buddleja davidii (buddleia)	Riverbank, possibly burnt— native regeneration			Predominantly podocarp-broadleaf forest	Te Maire Scientific Reserve (Whanganui River below Taumarunui)	Use of herbicide would create bare areas and more of a problem. Native regeneration interspersed within weed area making it difficult to target single species. This is an erosion-prone site.	Jim Campbell
Calluna vulgaris (heather)	Previously forested				Tongariro-Taupo		Nick Singers
Chrysanthemoides monilifera ssp. *monilifera* (bone-seed)	Coastal forest at top of steep cliffs	Where a bone-seed seed source is nearby	*Coprosma macrocarpa* and *C. robusta* (karamu)		Hauraki Gulf (Motuora Island)	Pine shelterbelt cleared. Natives out-competed bone-seed where there were enough natives in soil seed bank.	Helen Lindsay
Cytisus scoparius (broom)	Previously forested		*Leptospermum scoparium* (mānuka), *Pseudopanax arboreus* (fivefinger), *Phormium* spp. (flax)		Tongariro-Taupo	NH says: 'Nick Singers believes the mānuka and other natives will overtop the broom. I have not seen this happen yet and I'm not convinced it will.'	Nick Singers; Nicki Hughes
	Montane rocky river bed		*Olearia* sp., *Coriaria arborea* (tutu)	Broadleaf forest (plus podocarps sometimes)	West Coast		Dave Eastwood
	Regenerating shrublands, peatlands, coastal sites		*Kunzea ericoides*, *Leptospermum scoparium*		Northland (Te Paki, Kaimaumau, Waipoua)	Broom has short-lived seed viability and only germinates in well-lit open areas.	Tony McCluggage

Table 3 continued

WEEDS	HABITAT WHERE NATIVE SUCCESSION OCCURS	HABITAT WHERE NATIVE SUCCESSION DOES NOT OCCUR	NATIVE COLONISERS	PREDICTED VEGETATION	LOCATION	NOTES	SOURCE
Hakea sericea (needle bush)	Regenerating farmland (c. 1920s–30s) and mānuka (*Leptospermum scoparium*), kānuka (*Kunzea ericoides*)			Uncertain, best guess is mānuka then podocarp forest	Mangapurua Valley, tributary of Whanganui River	Use of herbicide would create bare areas and more of a problem. Native regeneration is interspersed within weed area making it difficult to target single species.	Jim Campbell
Leycesteria formosa (Himalayan honeysuckle)	Fertile and damp soil		*Melicytus ramiflorus* (māhoe), karamū, *Macropiper excelsum* (kawakawa)		Wellington, West Coast, Banks Peninsula	Especially historically disturbed sites and where grazing has ceased.	Peter Russell
Rubus fruticosus (blackberry)	Hill slopes		*Pittosporum tenuifolium* (tarata)	Beech (*Nothofagus* spp.)-broadleaf forest	Marlborough (Clarence and Molesworth)	Other native species present in the area are not regenerating, e.g. lacebark (*Hoheria* spp.), Hall's tōtara (*Podocarpus hallii*).	Simon Moore; Cathy Jones; Claire Wooldridge-Way
Rosa rubiginosa (sweet briar)	Wide unstable riverbeds in lower catchments, previously forested disturbed land, forest edges	Alpine areas above natural bushline, coastal dunes, wide semi-stable riverbeds in upper catchments where natural cover is native herbs and grasses, wetlands, ultramafic scrub	*Coriaria arborea*, *Melicytus ramiflorus*, *Aristotelia serrata* (wineberry), *Weinmannia racemosa* (kāmahi), *Schefflera digitata* (patē)	Podocarp-broadleaf and/or beech (*Nothofagus* spp.) forest	West Coast		Tom Belton
Ulex europaeus (gorse)	Previously forested				Tongariro–Taupo		Nick Singers
		Ultramafic scrub			Marlborough		Simon Moore
	Forest edges		*Aristotelia serrata*, *Coprosma* spp., *Coriaria arborea*	Could include rimu (*Dacrydium cupressinum*) and kahikatea (*Dacrycarpus dacrydioides*) (close seed source)	West Coast (Hokitika)	Ex-opencast gold mining sites close to native forest edge.	Dave Eastwood
	Rocky river floodplain			Beech or beech-podocarp forest	West Coast	Good seed source and good growing climate for natives.	Dave Eastwood

Table 3 continued on next page.

Table 3 continued

WEED	HABITAT WHERE NATIVE SUCCESSION OCCURS	HABITAT WHERE NATIVE SUCCESSION DOES NOT OCCUR	NATIVE COLONISERS	PREDICTED VEGETATION	LOCATION	NOTES	SOURCE
Ulex europaeus (gorse) continued	Forest and regenerating bush	Coastal dunes	*Leptospermum scoparium*		Warkworth	In coastal dunes pampas (*Cortaderia* spp.) is establishing instead of natives, e.g. *muehlenbeckia* spp.; area must be fenced from stock otherwise no regeneration.	Thelma Wilson
		Steep coastal cliffs			Hauraki Gulf (Tiritiri Matangi and Motuora Island)		Helen Lindsay
	Wetland areas where woody vegetation establishes	Dry tussock sites	*Leptospermum scoparium* and other natives		Southland (Awarua wetland)	Gorse controlled 15 years prior to November 2006 fire; now it is not controlled when natives are predicted to outcompete the gorse.	Graeme Miller

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8. Research

8.1 Knowledge gaps

There are many aspects of native succession through weeds where our understanding is far from complete. For example, canopy tree influences on belowground processes can have important, and perhaps unexpected, effects on seedling recruitment (Dehlin et al. 2008). In a study by Dehlin et al. (2008), root competition and mycorrhizal connections with canopy trees (mountain beech, lodgepole pine, and Douglas fir) somewhat surprisingly had no effect on seedling performance (of all three species) under native or exotic species. Instead, seedling performance was influenced by reduced light intensity and altered soil conditions beneath woody weeds (reduced soil organic matter, microbial biomass, and microbe-consuming nematode diversity and abundance). Nematodes are important in regulating plant-available nutrients; nematode feeding on microbial tissue releases previously immobilised nutrients from the microbes, thus enhancing nutrient availability and plant growth (Dehlin et al. 2008). However, most international studies have found that weeds promote decomposer organisms and processes relative to native plants. Our knowledge of complex ecosystem-level processes such as this appears to be too rudimentary to enable generalisations to be made at this stage.

Most research on native succession through weeds has been conducted on a small number of weed species (e.g. gorse, broom and *Pinus radiata*), mostly in areas suitable for forest. Little research has been conducted in non-forested ecosystems, although some studies have been undertaken in streambeds on weed species such as buddleia (Smale 1990; Bellingham et al. 2005).

Much of the existing research is descriptive, with very few quantitative studies testing the actual mechanisms limiting or facilitating succession. Comparative studies that test for correlations are unable to rule out alternative explanations for the patterns they describe. None of the studies to date have tested the effects (across multiple weed species) of weed or site attributes on the likelihood of replacement by natives (but see Dehlin et al. 2008 for a comparison of seedling performance under two exotic tree species).

8.2 Future research

One of the difficulties in investigating the potential for replacement of weeds by natives is the long timeframe over which successional processes can occur. Studies that compare sites that differ in time since weed invasion can be useful for determining successional outcomes (e.g. Brockerhoff et al. 2003; Sullivan et al. 2007). Such studies need to be carefully designed, with particular attention to site selection to avoid confounding effects (Ogden et al. 1997) and ensure adequate site replication. However, as discussed earlier, this type of study is unable to rule out alternative explanations for the succession patterns observed.

Experimental research to understand the mechanisms by which weeds facilitate or inhibit succession by natives may be the most useful approach for developing generalisations (see Dehlin et al. 2008 for an interesting example). Experiments could be conducted with a few weed species of particular interest; for example, widespread species that are problematic or expensive to control that managers feel are likely to be replaced by native succession. Such a study could include variation between weed species in attributes such as life form, seed size, nitrogen-fixing ability, and light intensity beneath the weed canopy, with replication of traits across weed species. Using this approach would probably enable an assessment of seedling performance only. However, the seedling stage is key in the plant recruitment cycle.

9. Decision-making tools

Several approaches could be used to predict whether natives will replace a given weed species at a particular site and to aid decision-making on whether to undertake weed control.

9.1 Mathematical models

Mathematical models can be used to predict successional outcomes and these models are well developed for forest ecosystems outside New Zealand (Luken 1990). One advantage of models is that they help ecologists to understand what they do or do not yet know (Luken 1990). However, mathematical models tend to be complex and require large amounts of quantitative data. Because current knowledge is limited, any mathematical model would be based on many assumptions and may be be of limited utility (i.e. a model is only as good as the data it is based on).

9.2 Expert systems

An alternative approach is to use an expert system. Expert systems are usually more practical than mathematical models because they are based on a wide variety of information, not just quantitative data and mathematically derived functions (Prach et al. 1999). Expert systems consist of a series of rules, and for each management problem or biotic system, a different set of rules must be developed (Luken 1990). Luken (1990) stated that 'the rules are an expression of the knowledge that experts have about a particular type of problem. Because the rules are not mathematically derived functions, a large variety of observations can go into the rules. However, in the best expert systems an attempt is made to distil the experts' knowledge so that only important rules emerge. Ideally, the user of an expert system is not involved in any aspect of rule development'. The user applies the expert system by answering a series of multi-choice questions (Luken 1990). Once the entire series of questions has been answered, the rules system is activated and a decision is made.

Expert systems are usually constructed by system planners in the form of 'if-then' statements (Luken 1990). Expert systems should be designed so that the rules can be modified as more data become available (Luken 1990).

9.3 Example expert system

A simplified example of an expert system for predicting the probability of a particular weed being replaced by natives and for deciding whether weed control is needed is shown below:

- Possible management decisions:
    1. No control needed
    2. Control needed
- Example series of questions asked by such a system:
    1. Can disturbance be excluded?
    2. Is there a native seed source?
    3. Can the site support woody native vegetation?
    4. Is the weed shade tolerant at the seedling stage?

Only if the user answers yes to questions 1, 2, and 3 and no to question 4 would the system decide that there is a high likelihood of the weed being replaced by natives and that no control is necessary. The system could be refined with the inclusion of other weed and site attributes (e.g. is the annual water deficit greater than 100 mm?) from Tables 1 and 2 to give a probability of replacement (e.g. high, medium, low, zero). This could also identify other management actions that could be taken to increase the likelihood of natural succession (e.g. fencing, seed addition), or predict the timeframe over which succession will occur. For example, succession can take longer, or be less likely to occur, in cold or dry areas where native vegetation growth is slower (Lee et al. 1986; Brockerhoff et al. 2003). For this type of expert system to work, research may be required to determine weed seedling shade tolerances.

McAlpine (2010) proposed a similar expert system for predicting the replacement of woody weeds by native plant succession in New Zealand (Fig. 1). The assumptions behind this system are that a) disturbance is absent or minimal, b) there is a native seed source available and c) managers are willing to take the risk that some native species may be lost if the weed is allowed to persist.

In both expert systems mentioned above, it is also assumed that there is not some additional reason that managers might decide to control the weed, for example to prevent spread to adjacent areas.

9.4 Decision-making tables

Another approach is to use decision tables, whereby the user gives each attribute of a particular weed and site a score (Table 4) and a second table is then used to determine the probability of natives replacing the weed (Table 5).

Decision-making matrices could also be used, but are constrained by the fact that only two attributes can be included (Figs 2 and 3).
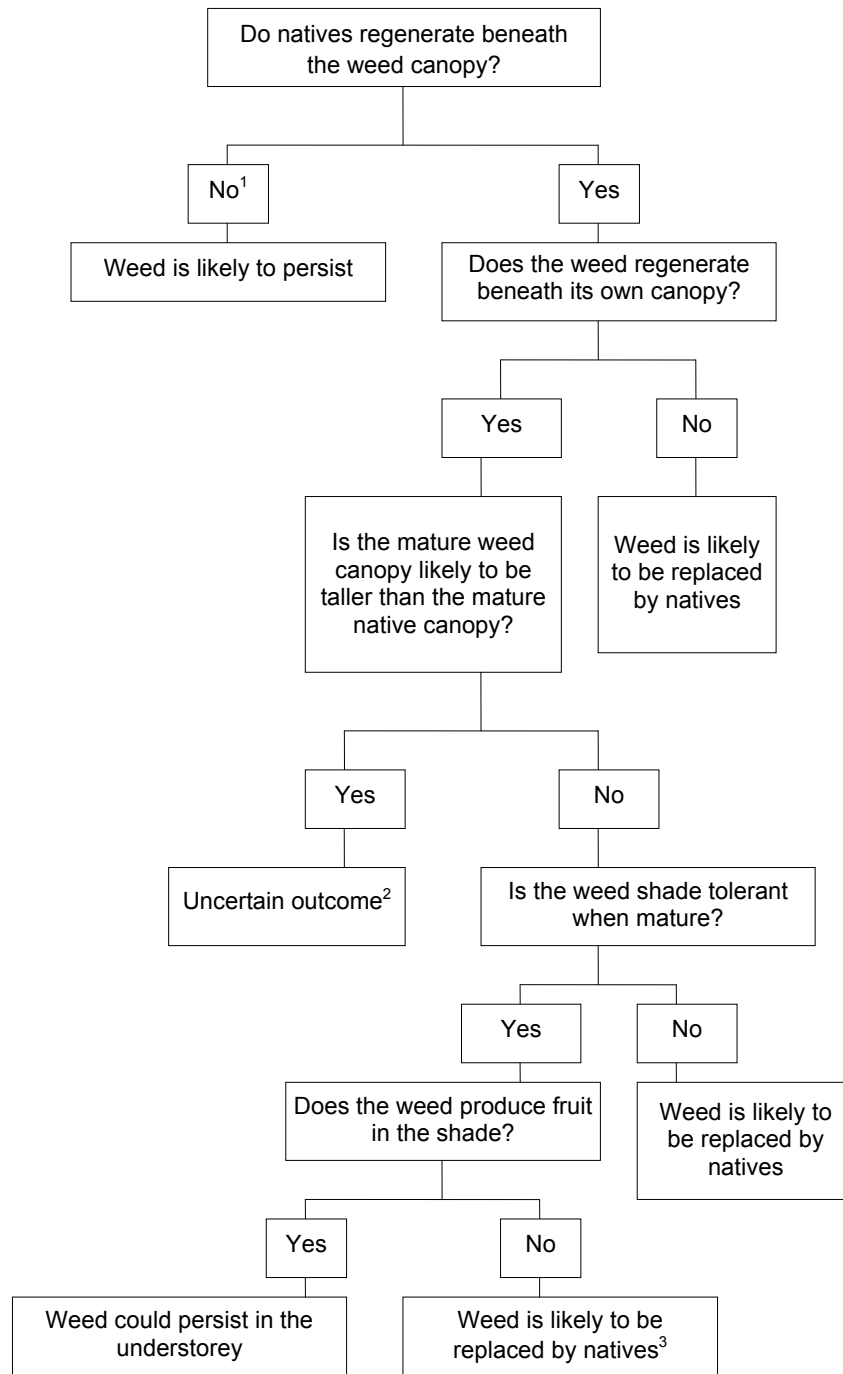
Figure 1.   Example of an expert system for predicting the replacement of woody weeds by native plant succession in New Zealand (reproduced from McAlpine 2010).

[1] It is important to determine why native seedlings are not establishing beneath the weed canopy, because this may change over time. If, for example, the lack of seedling regeneration is due to the fact that the weed stand is extremely dense and thus dark, this may change as the population ages and naturally thins out. If, however, seedling regeneration is being suppressed by some innate mechanism such as allelopathic interference, this is less likely to change over time.

[2] This is largely dependent upon whether weed or native seedlings 'win' when the adult weed population dies. This could be tested experimentally by controlling the weed in a way that imitates natural senescence, then monitoring subsequent seedling regeneration.

[3] Although weed seedlings may continue to establish in the understorey if weed seeds are being dispersed into the site.

Table 4. Scoring system for weed and site attributes.

ATTRIBUTES	DESCRIPTION	RANKING					SCORE
		1	2	3	4	5	(1–5)
Weed attributes							
Life-form	Pre-empts space	Grass	Liane	Tree	Shrub	Herb	
	Provides shelter	Herb	Grass	Liane	Shrub	Tree	
Shade tolerance	Determines regeneration requirements	Tolerant		Partially tolerant		Intolerant	
Site attributes							
Native seed source	Distance (km)	>40	20–40	5–20	1–5	<1	
Native frugivorous birds	Movement of birds between site and native remnant(s)	Never	Rarely	Sometimes	Often	Daily	
Climate (LENZ Level 1)	Annual water deficit (mm)	>100 (B,I,J,N)	51–100 (C,G)	31–50 (A,E,K,L)	11–30 (D,F,Q)	0–10 (H,M,O,P, R,S)	
Mammal	Browsing intensity	Extreme	High	Moderate	Low	Absent	
						TOTAL SCORE	

Table 5. Relationship between total score (Table 4) and the probability of native succession occurring.

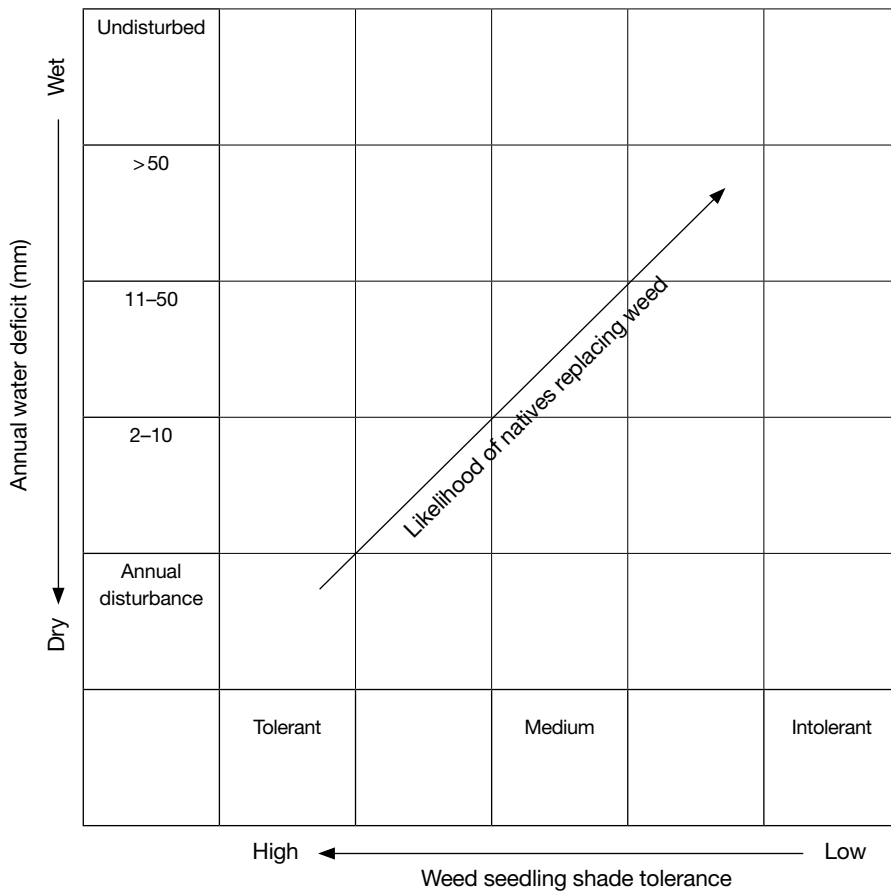| TOTAL SCORE	PROBABILITY OF REPLACEMENT BY NATIVES
31–35	Very good
25–30	Good
19–24	Moderate
13–18	Poor
7–12	Very poor

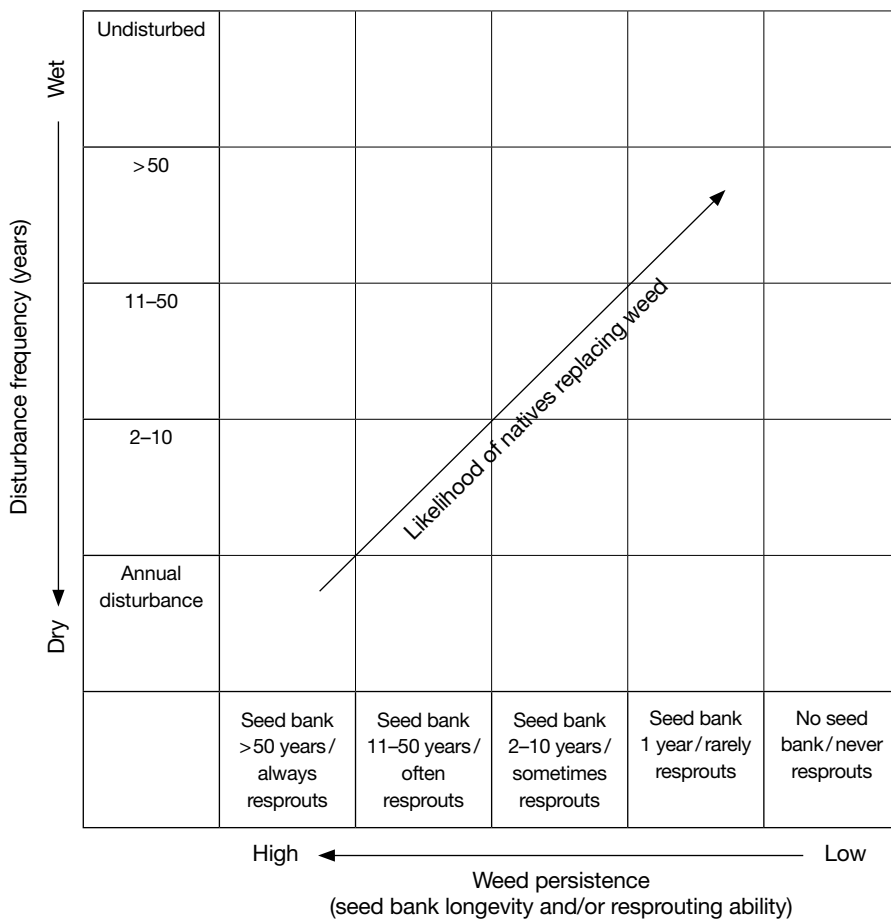Figure 2. Example decision-making matrix for areas suitable for the establishment of native forest.

Figure 3. Example decision-making matrix for non-forest ecosystems prone to disturbance (e.g. riverbeds, dunes).

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10. Discussion

Although there are many factors that could influence the succession of weeds by native plants, some of these will be more important than others. In New Zealand, key weed attributes are likely to be seed bank persistence, seedling shade tolerance (in woody ecosystems) and life form relative to native successional species. Critical site attributes are likely to be native seed source availability, disturbance regime, climate, and the presence of herbivorous mammals. However, it remains largely unknown which factors are the most important drivers of succession, and how or if they vary according to environmental conditions and the plant species (both weed and native) involved. Additionally, attributes such as seed bank persistence and weed seedling shade tolerance are often unknown, which makes it difficult to make predictions. Seed size could possibly be used as a proxy for seedling shade tolerance, however, as there is often a close positive correlation between the two variables (Fenner & Thompson 2005).

It may not always be feasible to leave a weed population uncontrolled in order for native succession to replace it. For example, this may not be the best option at sites where the presence of the weed is compromising biodiversity values, or where further spread of the weed needs to be contained. Additionally, this may not be a feasible option if the ecosystem has been irreversibly damaged, if succession through the weed will result in the loss of desirable native species (see Sullivan et al. 2007) or if environmental conditions do not promote sufficient native regeneration. Sullivan et al. (2007) demonstrated that native species richness was lower where succession had proceeded through gorse rather than the native kānuka, and that there were fewer small-leaved shrubs and orchids in gorse. Other studies have also shown that the presence of early-successional invasive species can result in the loss of native species (Yoshida & Oka 2000; Gorchov & Trisel 2003; Fagan & Peart 2004). If woody weeds are at an early stage of invasion, it may be worth managers considering the potential loss of important native species before deciding to allowing the weed to dominate the next stage of succession. Unfortunately, however, in most situations we do not have sufficient information to predict whether native species will be lost if woody weeds are allowed to dominate successional processes. It may also be difficult to predict successional outcomes in some situations; for example, where the weed is ecologically similar to the dominant native species, or where a suite of co-dominant weeds is present. The best strategy in the face of uncertainty may be to ensure heterogeneity during early succession; for example, by clearing weeds from some parts of a site but leaving them in others.

In considering whether a particular weed can be left uncontrolled at a particular site, a few site conditions must be met. A native seed source must be available, either at the site (seed bank or remnant native vegetation) or through dispersal from nearby native vegetation remnants—otherwise, native seed will need to be sown or native seedlings planted. The site must be kept free from disturbance (including fire, stock and mechanical clearing), or weeds will dominate in most systems. If a site remains undisturbed, weed persistence in the soil seed bank will be less important. However, disturbance is a major natural factor in some ecosystems, including streambeds and coastal dunes. Controlling introduced mammalian herbivores may also be necessary at some sites to allow natives to regenerate.

Despite these uncertainties, DOC weed managers can and do base weed control decisions—at least in part—on their particular understanding of the likelihood of native succession replacing the weed. Our survey indicated that there are at least ten weed species that are not actively controlled because managers believe that they will be replaced by native plant succession. In some cases, these approaches are supported by published studies (e.g. for gorse and broom). However, for the majority of species (e.g. Himalayan honeysuckle, sweet briar) there are no data, and managers are basing their decisions on experience and what they observe in the field.

11. Summary

There are likely to be critical weed-species-specific and site-specific variables that determine successional outcomes where weeds and native plants co-occur in New Zealand, but it is uncertain which are most critical, and how they might vary in different habitats and under different environmental conditions. For most woody weed species in New Zealand, the likelihood of weed replacement by native succession has not been quantified. There are a range of options for making 'best guess' predictions about which weeds are likely to persist and which are likely to be replaced by native succession, but much uncertainty remains. Ongoing research and observations by weed managers in the field should reduce this uncertainty, and allow better decision making around which weed species do and do not require active control.

12. Acknowledgements

13. References

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