



FORUM

Understory vegetation provides clues to succession in woody weed stands

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Published online: 18 September 2020

Abstract: Invasive exotic tree and shrub species (woody weeds) form dense, monospecific stands in many areas of New Zealand. At some sites, the weed dies out naturally and is replaced by native species as succession proceeds, but at others the weed persists indefinitely. The ability to distinguish between these different trajectories is critical to effective weed management, but the conditions that determine successional outcomes remain poorly understood. However, clues to the successional trajectory at any given woody weed site can be found in the understory, because understory plants represent the potential future plant community (in the absence of disturbance). Of key relevance is whether the woody weed species is regenerating under its own canopy, because this enables it to replace individuals as they die, and thus persist as succession proceeds. Conversely, if the understory is comprised entirely of native species, there is potential for the natives to take over the community as the weed dies out. This process is often termed “passive restoration”, because native vegetation is restored without any active management other than (in some cases) the removal of environmental stressors or degrading processes. The likelihood of a native understory developing is affected by site-specific traits such as the natural (historical) vegetation type, proximity to native seed sources, climate, stand age and the presence of herbivores. We present a framework to help land managers use their observations of understory vegetation to assess likely successional trajectories in woody weed stands.

Keywords: facilitation, invasion, natural regeneration, passive restoration, recruitment, shade tolerance, successional trajectory

Introduction

Invasive exotic trees and shrubs (woody weeds) have established in many areas and ecosystem types throughout New Zealand and globally (Richardson & Rejmánek 2011). They often create apparent monocultures, occurring as the sole canopy species in large, relatively even-aged stands. Such stands can be highly conspicuous and persistent in the landscape, and so appear to have permanently supplanted any natural ecosystems that would be expected to occupy these sites. However, the long-term impacts of such monocultures can vary among weed species and sites (Pyšek et al. 2012; Kiswaga et al. 2020). In some cases, woody weeds have transformative, persistent effects on the natural vegetation and ecosystem processes, but in others, successional replacement by native species occurs (McQueen 1993; Richardson et al. 1994; Williams 2011). Here we examine the drivers that lead to these different outcomes and describe how the understory vegetation can provide clues to the likely successional trajectory at any given woody weed site.

In forests and shrublands, the understory can be a key driver of succession (in the absence of disturbance) because it is the main source of species and individuals that will comprise the next successional stage (Connell & Slatyer 1977; Bazzaz

1979; Pacala 1997). This general ecological theory applies regardless of the provenance (native or exotic) of the species involved (D'Antonio & Chambers 2006). In woody weed stands, this means that the composition of the understory (i.e. the identity and abundance of resident plants) can indicate whether the woody weed is likely to persist in the long-term or be replaced naturally as succession proceeds (McAlpine et al. 2018).

A key trait determining long-term persistence in the absence of disturbance is the extent to which the weed regenerates under its own canopy. This trait is largely driven by shade tolerance, although site-specific factors such as soil moisture and nutrient availability can also play a role (Valladares & Niinemets 2008). A species that can regenerate under its own canopy can replace individuals as they senesce (van der Valk 1992; Grime 2001), and thus can potentially persist indefinitely. Conversely, a species that does not regenerate under its own canopy can be replaced by other species that are regenerating in the understory. If those understory species are native, then the site may be on a trajectory to a community dominated by native species (Aide et al. 2000). This successional replacement can occur when understory plants overtop and shade-out the adult weed plants; i.e. successional replacement is ‘from above’ the weed canopy. We suggest that it can also occur

'from below' the weed canopy, if shade from the understory vegetation prevents another generation of weed seedlings from establishing when adult weed plants senesce. Presumably, this is most likely if canopy senescence is gradual and patchy and thus does not result in major damage to understory plants. Successional replacement 'from below' means that even tall woody weed species that would never be overtapped by natives could be replaced by native succession at sites where a native understory is present. However, this second mechanism is poorly understood.

Several site-specific factors influence the likelihood of woody, forest-forming natives colonising and replacing woody weed stands in New Zealand. A critical factor is whether the original (pre-human arrival) native vegetation at the invaded site was forest or non-forest. Sites that historically supported native forest readily revert back to native vegetation (forest) under suitable conditions when a native seed source is available, and disturbance is minimal (Wardle 1991). This reversion can occur even when the early colonising species is exotic (e.g. gorse (*Ulex europaeus*), Wilson 1994). Given that much of lowland New Zealand was cloaked in native forest prior to human arrival (McGlone 1989; Leathwick 2001), there is potential for many, if not most, lowland woody weed sites to be colonised by native forest species, including anthropogenically induced grasslands that were historically forested (McGlone 2001). Conversely, succession back to communities dominated by native species is unlikely where the woody weed has invaded naturally non-forested sites, such as frost flats and herbfields. The low stature plant species that comprise non-forest ecosystems typically cannot colonise, or survive under, a forest canopy.

Exotic conifer stands in New Zealand illustrate how site traits can affect the development of a native understory, and thus the likelihood of succession to natives (Brockerhoff et al. 2003; Froude 2011). Although most evidence comes from exotic plantation pine (*Pinus* species) forests, it should be applicable to wild pine populations and to other invasive conifers with similar regeneration ecology. Where exotic conifers occur in historically forested sites with adequate rainfall and a nearby

seed source of shade-tolerant native species, a dense, species-rich native understory can develop (Henry 1954; Norton 1989; McQueen 1993; Porteous 1993; Brockerhoff et al. 2008; Forbes et al. 2019). In the absence of disturbance, such sites appear to have the potential to return to native forest naturally. However, where exotic conifers invade historically non-forested sites such as herbfields and high elevation shrublands, they can suppress the native vegetation and have severe and long-lasting impacts both above and below ground (Richardson et al. 1994; Froude 2011; Dickie et al. 2014). A return to native vegetation in these non-forested ecosystems is usually only possible with active management. Accordingly, we do not consider naturally non-forested sites further here.

Stand age can also influence understory development. When a woody weed population is young and actively growing, stem density is high and light levels in the understory may be insufficient for native (or exotic) seedling establishment. However, as the stand ages and thins, light levels increase, and native seedlings may be better able to recruit (Wilson 1994; Lugo 2004; Carswell et al. 2013; Geldenhuys 2013). This process has been observed in exotic tree plantations in New Zealand (Allen et al. 1995; Ogden et al. 1997; Brockerhoff et al. 2003; Forbes et al. 2019) and South Africa (Geldenhuys 1997). High-density populations of exotic pest mammals and domestic livestock can also severely restrict native plant establishment in New Zealand (Wardle et al. 2001; Dodd et al. 2011; Perry et al. 2015).

A framework to assess succession in woody weed stands

We present a framework to help land managers assess the likelihood of any given woody weed site returning to native dominance naturally. Our framework is based on the extent to which canopy weed and/or woody (forest-forming) natives are regenerating under the weed canopy (Fig. 1). For the sake of simplicity, our starting point is a mature, seed-producing,

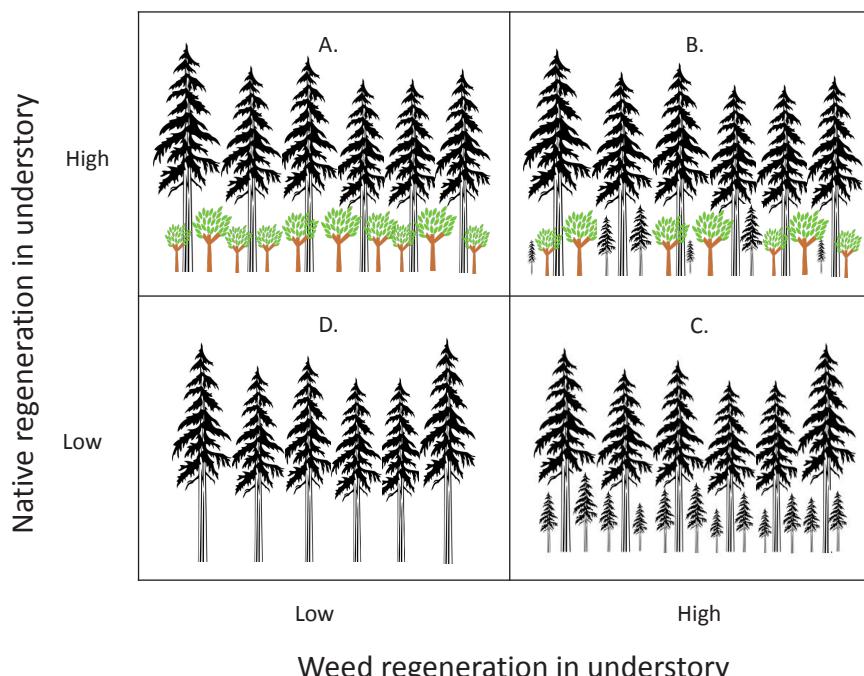


Figure 1. Framework of four potential native/weed regeneration understory composition scenarios found in woody weed stands. Black plant = woody weed (single species in canopy and understory), green and brown plant = woody native (could be multiple species).

closed canopy, largely monospecific (in the canopy) woody weed stand at a site that historically supported native forest. We do not attempt to determine how the invasion occurred or what species were present at the time; our focus is on interpreting the current vegetation to predict what is likely to happen next, under the assumption that major disturbance does not occur (because disturbance would reset succession). We consider the management implications of each scenario, but we do not address the question of whether the weed should or should not be controlled, because a myriad of factors beyond the scope of this paper affect that decision (e.g. risk of spread to sensitive areas, economic and social considerations). Our focus is on woody weed stands in New Zealand, but the principles should be largely applicable elsewhere, given that they are based on general succession theory (D'Antonio & Chambers 2006).

Scenario A. Understory is predominantly native

In this scenario, the woody weed dominates the canopy but is absent from the understory. This may be because the weed is a typical pioneer (early successional) species: highly competitive after disturbance, but shade-intolerant and therefore unable to survive when the canopy closes (Bazzaz 1979). In this sense, the canopy weed is essentially performing a similar functional role to a pioneer native species such as mānuka (*Leptospermum scoparium*) (Porteous 1993). Typically, mānuka establishes en masse after disturbance and can dominate large areas for decades (Stephens et al. 2005). However, mānuka is shade intolerant and does not regenerate under its own canopy. Instead, a diverse understory of other, more shade-tolerant, native species develops, and those species gradually take over as mature mānuka plants senesce (Esler & Astridge 1974; Wardle 1991; Bray et al. 1999). Indeed, the understory of a typical mānuka stand is exactly as Scenario A, except the canopy species is native.

Studies from other countries also suggest that superior shade-tolerance is the mechanism by which natives replace woody weeds (DeWine & Cooper 2008; Cunard & Lee 2009; Motta et al. 2009; Svirz et al. 2013). However, there may be reasons other than shade-intolerance that explain why a species does not regenerate under its own canopy. In New Zealand for example, the shade-tolerant woody weed species sycamore (*Acer pseudoplatanus*) and tree privet (*Ligustrum lucidum*)

regenerate under their own canopy at some sites, but not at others (McAlpine et al. 2018). A potential explanation for this variability in regeneration across sites is that interspecific competition varies across one or more resource gradients (D'Antonio & Chambers 2006). For example, a species' ability to tolerate shade may be affected by stress factors like drought, flooding, nutrient availability, or herbivory (Valladares & Niinemets 2008). Further research to determine what restricts regeneration of these woody weed species at some sites — and whether management actions could be applied to elicit the same result — would be informative.

Woody weed stands with a native understory (Fig. 2) appear to be relatively common in lowland areas of New Zealand. McAlpine et al. (2018) reported 14 woody weed species that had a native understory of > 50% cover and no conspecific weed regeneration at one or more sites (including unmanaged plantations): silver wattle (*Acacia dealbata*), blackwood (*Acacia melanoxylum*), sycamore, alder (*Alnus glutinosa*), common barberry (*Berberis glaucocarpa*), willow-leaved hakea (*Hakea salicifolia*), larch (*Larix decidua*), black pine (*Pinus nigra*), cluster pine (*Pinus pinaster*), radiata pine (*Pinus radiata*), white poplar (*Populus alba*), Douglas fir (*Pseudotsuga menziesii*), silver willow (*Salix alba*) and grey willow (*Salix cinerea*). Additionally, radiata pine plantations in New Zealand are commonly recorded as having a native understory (Ogden et al. 1997; Brockerhoff et al. 2003; Forbes et al. 2019).

Likely successional outcome

This is the best-case scenario from a conservation perspective. Providing disturbance does not occur, the long-term successional trajectory at these sites is likely a return to native dominance: natives will gradually take over as the adult weed plants senesce. There is much anecdotal, and some empirical, evidence that many woody weed species can be replaced by native plant succession in New Zealand, with gorse being the best-known example (Smale 1990; McCracken 1993; McQueen 1993; Wilson 1994; Williams 2011). The resulting vegetation may not be exactly the same composition as succession through natives (Sullivan et al. 2007), but any mix of natives is presumably preferable to exotic domination, particularly if it can be achieved 'for free'. Missing native species could be added later, for example by planting saplings or sowing seed (Overdyck et al. 2013; Forbes et al. 2020).

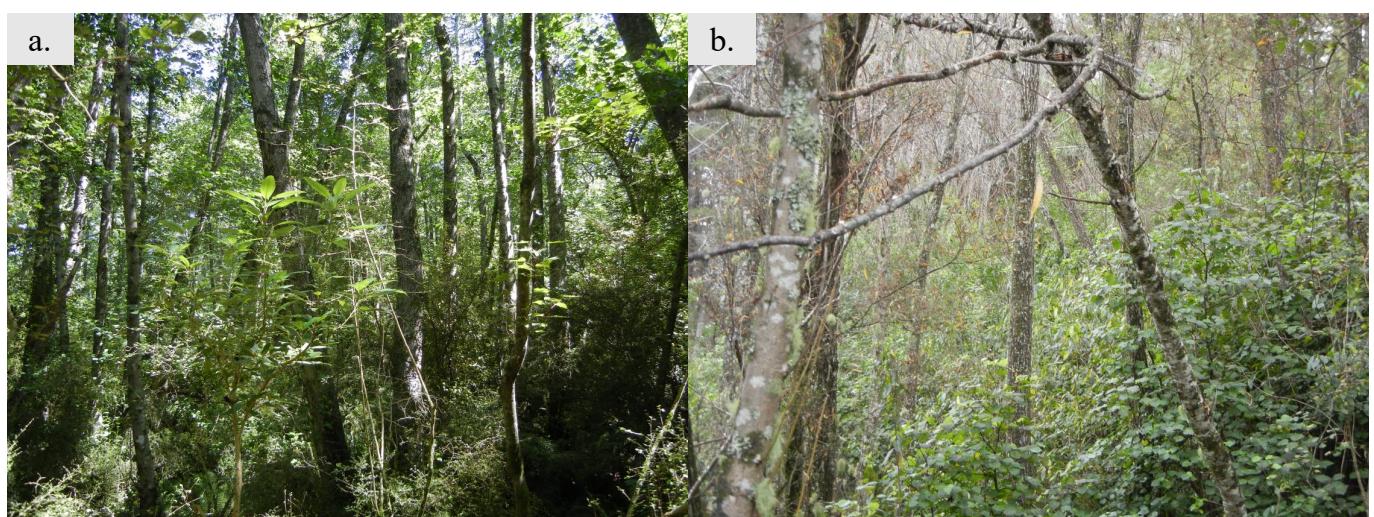


Figure 2. Examples of Scenario A, woody weed stands with a dense native understory: a) alder (*Alnus glutinosa*), b) silver willow (*Salix alba*).

Woody weeds can even facilitate native plant establishment by acting as nurse plants in modified environments (Svriz et al. 2013; Burrows et al. 2015). Nurse plants can improve survival and growth of other species by reducing excessive solar radiation, moderating temperature extremes, conserving soil moisture and reducing competition from exotic grasses (Callaway 1995). In some countries, exotic woody plant species are even deliberately planted to out-compete undesirable species and ‘trigger’ natural succession in deforested areas (Lamb et al. 2005; Douterlungne et al. 2013). This approach has been trialled on a small scale in New Zealand, largely with tree lucerne (*Chamaecytisus palmensis*), but uncertainties around successional trajectories and the risk of weed spread generally restrict the planting of exotics as a restoration tool. However, existing woody weed stands with a native understory represent a significant pool of ‘passive restoration’ sites in New Zealand and, as such, could be considered to have conservation value. Passive restoration is far easier and cheaper than active restoration and is also more likely to succeed than planting a bare site, where plants have to contend with competition from exotic grasses and other weeds, water evaporation and exposure (Chazdon 2008; Crouzeilles et al. 2017). Passive restoration may also result in a more natural forest structure and species composition than active restoration, although this is likely to depend on a range of site-specific factors, such as the severity of land degradation and the extent to which naturally occurring native species remain in the landscape (Holl & Aide 2011; Meli et al. 2017).

Management implications

To maximise the chance of native species replacing the canopy weed, protect the status quo by avoiding disturbance if possible (e.g. prevent fire), excluding domestic and wild herbivorous mammals, and monitoring for dispersal and establishment of shade-tolerant weed species into the understory. Seek expert advice on whether missing native species could be introduced to the understory, for example by planting saplings or sowing seed.

Scenario B. Canopy weed and natives are abundant in the understory

In this scenario, a critical question is whether the canopy weed is actively recruiting in the understory, because this determines whether it can maintain a presence in the understory as succession proceeds. A key indication of active recruitment of the canopy weed species is the presence of seedlings and saplings of multiple size/age classes, indicating continuous recruitment, survival and growth (Grime 2001). If the canopy weed species has only seedlings present, understory conditions are likely not suitable for survival beyond the seedling stage. If the canopy weed species has only saplings present, conditions are no longer suitable for new seedlings to establish; saplings may be survivors of the initial colonisation event, still undergoing self-thinning (Peet & Christensen 1987). Alternatively, the presence of a single size-class (only seedlings or only saplings) might be because plants of that size class are long-lived and can persist in the understory for years or decades, waiting for a canopy gap. However, it is not known whether any of the woody weed species present in New Zealand have this trait.

Native species must be actively recruiting to maintain a presence as succession proceeds. However, as we are not concerned with predicting the persistence of individual native species, there only needs to be a mix of seedlings and saplings of native species as a group (rather than seedlings and saplings

of each species). In a survey of 132 woody weed stands around New Zealand, McAlpine et al. (2018) recorded as many as 24 native species in the understory at some sites, and 55 sites had ten or more native species in the understory (KGM unpubl. data). Woody weed species recorded as having understory Scenario B (i.e. that regenerated strongly under their own canopy, but also had at least 50% cover of natives) at some sites included stands of black wattle (*Acacia mearnsii*), blackwood, Sydney golden wattle (*Acacia longifolia*), sycamore, large-leaved cotoneaster (*Cotoneaster glaucophyllus*), tree privet, Chinese privet (*Ligustrum sinense*), Taiwan cherry (*Prunus campanulata*) and strawberry dogwood (*Dendrobenthamia capitata*) (McAlpine et al. 2018).

Likely successional outcome

Successional trajectories are difficult to predict where the canopy weed and native species are both abundant in the understory, because it depends on whether natives or the weed ‘win’ over the long-term. If the canopy weed is not actively recruiting, the natives could win (i.e. same as Scenario A). If the canopy weed is actively recruiting, the successional outcome likely depends upon how competitive different species are for resources both above and below ground (light, water, nutrients), and how long plants can persist in the understory in the absence of disturbance (Sanford et al. 2003; Closset-Kopp et al. 2007; Goria & Osborne 2014). In a modelling study of succession in a pine-oak (*Pinus sylvestris-Quercus robur*) forest in the Netherlands, Vanhellemont et al. (2011) suggested that the relatively short life span of the invasive tree species black cherry (*Prunus serotina*) precluded its dominance over a long-lived native tree species (*Quercus robur*), despite both being able to regenerate in the understory.

The successional outcome of Scenario B may also depend on which species are able to respond most quickly to increasing resources when canopy plants start to die and canopy gaps open up (Riegel et al. 1995). Sycamore and black cherry (both present in New Zealand) are examples of invasive tree species that have been shown to reproduce under forest canopies in the northern hemisphere, and rapidly exploit any newly formed canopy gaps with greater efficiency than resident native species (Closset-Kopp et al. 2007; Collet et al. 2008; Hein et al. 2009). In general, however, little is known about competition between weeds and native species under closed canopies in New Zealand, and there is likely to be high variability across sites.

Management implications

If the canopy weed is not actively recruiting, management implications are similar to those for Scenario A: protect the status quo and avoid disturbance. Replacement of the weed may take longer than Scenario A, particularly if understory weed saplings survive long enough to reach the canopy. If the canopy weed is actively recruiting, local weed experts might be able to advise on the likely successional outcome based on similar sites, and/or relevant ecological studies on the canopy weed. It may also be worth investigating whether there is an effective biocontrol agent available for the weed that might reduce the biomass and/or vigour of the weed and tip the balance in favour of natives. Further research into where and when biocontrol could achieve this outcome would be informative.

Weed species that can actively recruit in the shade may be able to invade intact native vegetation, so it may be prudent to watch for spread into any sensitive or high-value natural areas within seed dispersal distance of the woody weed stand.

Scenario C. Understory is predominantly canopy weed

In this scenario, one or more factors appear to be limiting regeneration of native species, but not the canopy weed. The canopy weed is obviously shade-tolerant and can recruit and survive in the understory, so it has the potential to persist for future generations. Assuming active recruitment (as described in Scenario B), understory weed plants can replace adult weed plants as they senesce, with no competition from natives. In a study of understory regeneration of the woody weed black cherry in Belgium, Vanhellemont et al. (2009) suggested that the ‘massive’ presence of black cherry seedlings in the understory could ensure future site occupancy to the detriment of the native species present. Similar studies from North America have shown that the woody weed Norway maple (*Acer platanoides*) regenerates strongly under its own canopy, which enables the species to persist (Wyckoff & Webb 1996; Martin 1999; Reinhart et al. 2005).

The absence of native regeneration in the understory might be because there is no native seed source (remnant forest patch) within dispersal distance. Although most seeds are typically deposited within c. 100 m of the parent plant, longer dispersal distances of several kilometres are not unusual, particularly for seeds dispersed by birds (Clout & Hay 1989; Burrows 1994; Anderson et al. 2006; Wotton & McAlpine 2015). Isolated woody weed stands may attract seed-dispersing birds seeking perching sites and/or food sources (Wunderle 1997; Ferguson & Drake 1999; Corbin et al. 2016). Examples of widespread, stand-forming woody weed species in New Zealand that are attractive to frugivorous birds include Darwin’s barberry (*Berberis darwinii*), hawthorn (*Crataegus monogyna*), large-leaved cotoneaster, tree privet, Chinese privet and Taiwan cherry (Wotton & McAlpine 2015). Along with proximity to seed source, the effectiveness of seed dispersal will depend on the size and species diversity of the seed source, the availability of long-distance dispersal agents such as birds, and the attractiveness of the weed to those birds (Schupp et al. 2010). In general, however, landscape-scale seed dispersal data from New Zealand studies are scarce.

It is also possible that seeds of shade-tolerant native species are being dispersed into the woody weed stand, but for some reason native seedlings are unable to establish and survive. Allelopathy, or the ability to release phytotoxic

substances, is often invoked as a mechanism underlying the success of invasive plants. However, although allelopathy appears to offer a plausible explanation for the absence of native understory regeneration (Hierro & Callaway 2003), evidence from field studies is scarce. Woody weed species present in New Zealand that are purportedly allelopathic include Chinese privet (Merriam & Feil 2003; Foard 2014), black wattle (Tassin et al. 2009), patula pine (*Pinus patula*) (Schumann et al. 1995), silver wattle (Lorenzo et al. 2011), blackwood (Hussain et al. 2011) and woolly nightshade (*Solanum mauritianum*) (Florentine & Westbrooke 2003; Van Den Bosch et al. 2004). However, native plant species readily establish under these species in New Zealand (McAlpine et al. 2018) and/or elsewhere (Geldenhuys 2002; Lemenih et al. 2004; Elgar et al. 2014; Randriambanona et al. 2019), so it seems unlikely that allelopathy plays a major role in preventing the establishment of natives in woody weed stands in New Zealand.

Alternative explanations for the lack of native seedling establishment could include herbivory of more palatable natives (Wardle et al. 2001), or the absence of some critical mutualism, e.g. arbuscular mycorrhiza (Bever et al. 2010). Some woody weed species may suppress native vegetation by altering the quantity of light in the understory (Reinhart et al. 2005). It may also be that weed seedlings simply outcompete native seedlings, for example by growing bigger and/or faster (Van Kleunen et al. 2010). In general, however, the mechanisms that allow weed species to favour the growth and establishment of their own seedlings at the expense of natives remain poorly understood.

Likely successional outcome

This is the worst-case scenario from a conservation perspective: the canopy weed is likely to persist indefinitely under current conditions, with no chance of native succession. Examples of woody weed species in New Zealand that have been observed to have an understory resembling Scenario C (at least at some sites) include sycamore, tree privet, Chinese privet (Fig. 3a), and Taiwan cherry (Fig. 3b) (KGM pers. obs.; McAlpine et al. 2018). The same principles should apply in mixed species woody weed stands; species regenerating in the understory are most likely to persist.

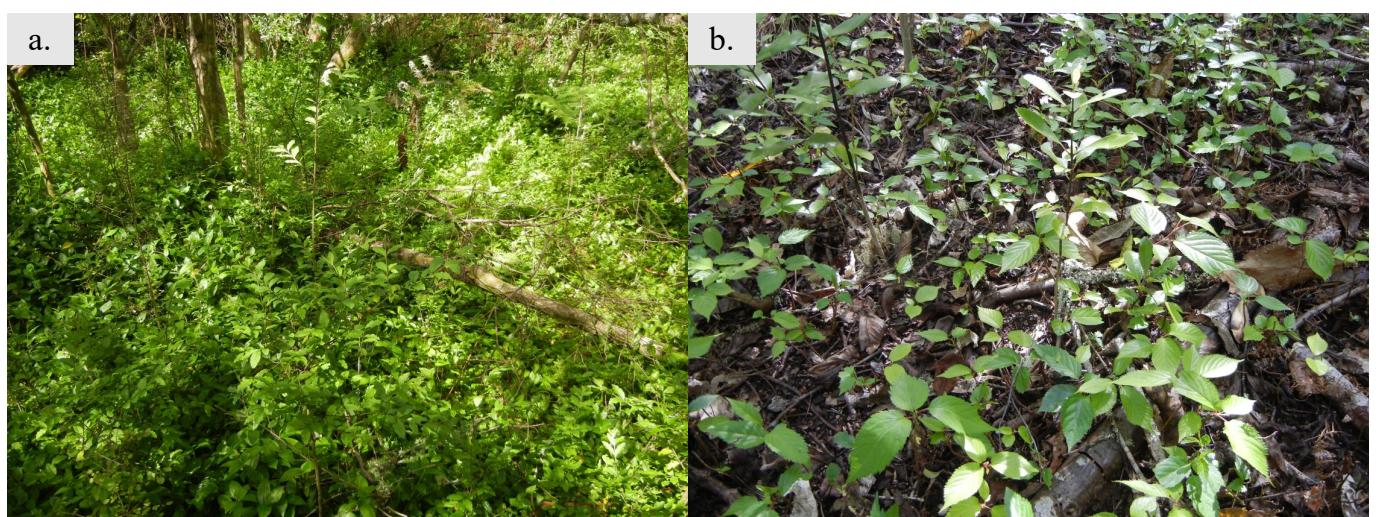


Figure 3. Examples of Scenario C, woody weed species regenerating under their own canopy: a) Chinese privet (*Ligustrum sinense*), b) Taiwan cherry (*Prunus campanulata*).

Management implications

There are no easy options for returning a site to native vegetation if the main component of the understory is active regeneration of the canopy weed. It might be possible to identify and mitigate barriers to native recruitment in the understory, but the weed species will presumably have a competitive advantage that will be difficult to overcome. Eradication of the weed is likely to be extremely difficult (Howell 2012; Panetta 2015) but might be feasible if sufficient resources and expertise were available. Biological control programmes, such as those currently being developed for Chinese privet in New Zealand (Q. Paynter, Landcare Research, pers. comm.) and the U.S.A. (Zhang et al. 2016) might offer some hope.

Scenario D. Understory is sparse or absent

In this scenario, one or more factors are limiting the regeneration of natives and the canopy weed. The absence of understory regeneration may be the result of a combination of conditions described under previous scenarios, for example the canopy weed is shade intolerant and a native seed source is lacking. Thus, potential reasons for the absence of weed regeneration could be the same as Scenario A, and the absence of natives could be the same as Scenario C. There are also alternative explanations for the complete absence of understory regeneration. For example, herbivores may be consuming understory plants (Atkinson 2001; Smale et al. 2005), or frequent disturbance of the understory (e.g. flooding) may be preventing seedling establishment. It could also be that the woody weed stand is young and dense with light levels insufficient for seedling establishment (Wilson 1994). Alternatively, it could be a combination of these factors.

Likely successional outcome

It is difficult to predict the successional trajectory at this type of site, since there is no understory to provide clues. If the status quo remains, canopy collapse would be the eventual likely outcome, with either a transition to a completely different plant community (depending on which species arrive and survive), or the establishment of a new stand of the weed (if seeds are present and the canopy collapse removes the limiting factor preventing regeneration).

Management implications

It might be possible to assist natural successional processes by identifying, and then removing or reducing barriers to natural forest regeneration. For example, if herbivorous mammals are potentially the problem, it might be possible to fence the site, and/or undertake pest control (Burns et al. 2011). If a native seed source is lacking, it might be possible to remedy this by sowing seed or planting saplings (Clarkson & Kirby 2016). If the site is dense and dark, it might be possible to speed up succession by felling or poisoning selected trees (Forbes et al. 2016). However, all these management interventions are difficult to do over large areas and require specialist advice. Additionally, and perhaps most critically, the interventions might result in regeneration of the canopy weed.

Uncertainties

This framework is intended to help managers determine likely successional outcomes in woody weed stands, based on the current understory vegetation and current conditions. If conditions change, however, the outcome may change (Seidl et al. 2011). Disturbance, in particular, can have a major

impact on succession (Allen et al. 2013; Wyse et al. 2018). It is inevitable that disturbance will occur (e.g. drought, flooding, storm damage, fire), but whether this results in a complete reset of the successional clock depends on the severity of the disturbance (Pickett et al. 1987; Hart & Chen 2006). Major (large-scale) disturbance is likely to favour re-invasion of the woody weed if seeds (including aerial and soil seed banks) and/or vegetative propagules are present. Minor (small-scale) disturbances might allow the canopy weed to re-establish in patches but may also accelerate native succession. Studies from New Zealand where exotic canopy plants were artificially controlled show that native species present in the understory respond strongly to the increase in light (Paul & Ledgard 2009; Forbes et al. 2016; McAlpine et al. 2016). Future climate change may render some sites more prone to disturbance and drought (Renwick et al. 2016), which may favour weed invasion.

Another site-specific factor that could change, and thus alter the successional trajectory is herbivore density; herbivore populations might increase or decrease, or new species may appear. Similarly, new weed species may appear (or expand) in the understory and affect the rate or trajectory of successional processes. Shade-tolerant, ground covering weeds in particular can become highly abundant under forest canopies and inhibit seedling establishment and growth (Standish et al. 2001; McAlpine et al. 2015; Wallace et al. 2017). Tree or shrub weed species that reach maturity in the shade could increase in abundance over time and even dominate the canopy under some circumstances. However, any number of exotic successional stages, including mixed native-exotic canopies, could precede native succession. For example, Williams (1983) suggested that the woody weed broom (*Cytisus scoparius*) facilitated succession to another woody weed, elder (*Sambucus nigra*), which in turn facilitated succession to native species.

Summary

Predicting successional trajectories and outcomes is not an exact science. However, critical insights can be gained from observing the understory vegetation in woody weed stands. We recommend this as a first-step when considering control measures or other management action at sites invaded by woody weeds (Fig. 4). Key drivers that influence woody weed understory composition include the shade tolerance of the canopy weed, availability of seed — and seed dispersal vectors — of forest-forming native species, and site-specific conditions such as the natural vegetation type and climate. If the understory is comprised entirely of native species, then there is a good chance that those natives will eventually replace the weed species, providing major disturbance does not occur. Such sites may even have considerable biodiversity value and passive restoration potential. If the weed is actively regenerating under its own canopy, it has the potential to persist in the long-term, particularly if native species are sparse or absent in the understory. There is more uncertainty if natives and the weed are regenerating in the understory, or if the understory is absent/sparse. Land managers can use the information they gain from observing understory composition to determine the likely successional trajectory at woody weed sites, and thus decide their course of action (or inaction). Working with, rather than against, natural successional processes will save time and money and optimise conservation outcomes.

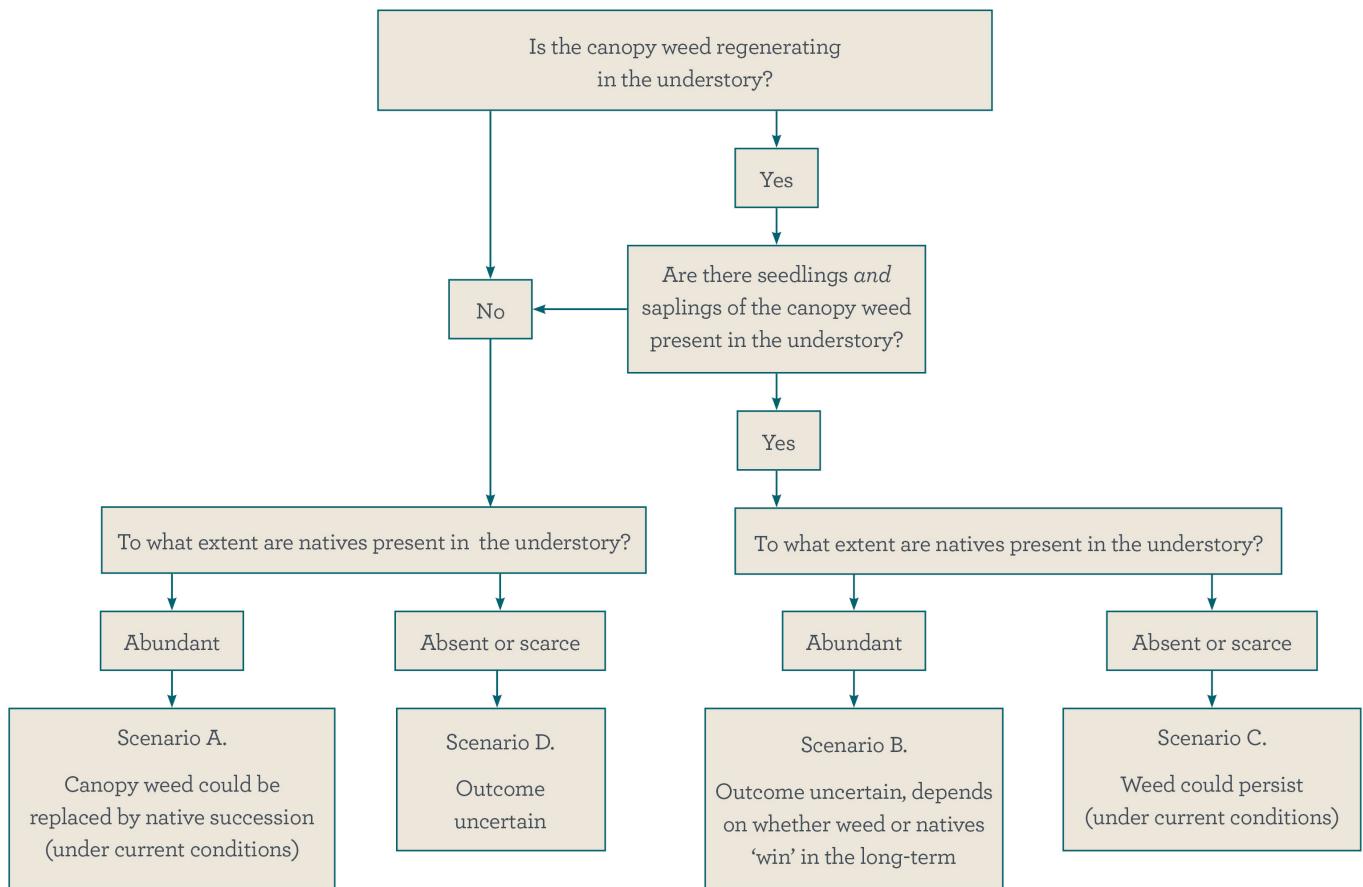


Figure 4. Decision tree to help managers determine likely successional outcomes in closed canopy woody weed stands, based on what they observe in the understory. Scenarios A, B, C, and D refer to the composition of the understory, as per Fig. 1.

Authorship statement

KGM developed the conceptual ideas and wrote the manuscript, SLL provided funding and assisted with related fieldwork, SMT contributed to the manuscript and gave intellectual guidance and support.

Acknowledgements

This project was funded by the New Zealand Department of Conservation and the Ministry of Business, Innovation and Employment through Landcare Research's Core Funded program Beating Weeds II. Comments from James Griffiths, Rachel McAlpine, Colin Miskelly, Rowan Sprague, Fiona Thompson, Debra Wotton and two anonymous reviewers improved the manuscript.

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Received 28 April 2020; accepted 17 August 2020
Editorial board member: Hannah Buckley