SHORT COMMUNICATION

Composition of the understory in 132 woody weed populations and implications for succession

Kate G. McAlpine[1]*, Susan M. Timmins[1], Sarah D. Jackman[2] and Shona L. Lamoureaux[2]

[1]Department of Conservation, PO Box 10420, Wellington 6143, New Zealand
[2]AgResearch Ltd, Private Bag 4749, Lincoln 8140, New Zealand
*Author for correspondence (Email: kmcalpine@doc.govt.nz)

Published online: 22 June 2018

Abstract: The species composition of the understory can be a key indicator of successional trajectories in the absence of disturbance at forested sites. We surveyed species composition and percent cover in the understory of 132 closed-canopy stands of 41 woody weed species throughout New Zealand as a first step in understanding potential successional trajectories in these weed populations. Twenty-seven weed species had zero, or very few, conspecific seedlings or saplings present beneath their own canopy. Fourteen weed species had medium to high numbers of conspecific seedlings and/or saplings present. Some weed species had variable understory regeneration, with high numbers of conspecific seedlings and saplings present at some sites, but none at others. Twenty-eight weed species had native understory cover of ≥ 50% at one or more sites. Native understory cover was higher at sites close to remnants of native vegetation compared to sites distant from native vegetation. Overall, many more native than non-native species were present in woody weed understories. *Melicytus ramiflorus* (māhoe) was the most common native species, present at 67% of sites. At least 76 other native species were recorded at five or more sites. Our results demonstrate that (1) woody weed species vary in the extent to which they regenerate under their own canopy, and (2) closed canopy woody weed stands frequently have a predominantly native understory. Further research to determine whether the composition of the understory can be used to predict successional trajectories in woody weed populations would be valuable.

Keywords: facilitation; nurse plants; invasive species; shade tolerance; weed impacts; weed persistence

Introduction

A central tenet of forest successional theory states that, in the absence of disturbance, light demanding pioneer species are gradually replaced by shade tolerant, secondary successional species that establish in the understory (Connell & Slatyer 1977; Bazzaz 1979). This means that the species present in a forest understory can be a key indicator of the species likely to be present in later successional stages at that site under stable conditions (Pacala 1997; Kimmins 2004). Individuals already present in the understory can respond quickly to canopy gaps created when adult plants die, and therefore have a competitive advantage over light-demanding species that can only germinate and establish after adult plants die (Swaine & Whitmore 1988). Conversely, species absent from the understory are unlikely to be present in later successional stages unless further disturbance occurs.

Although succession theory is usually considered with regard to native forest dynamics, it should be equally applicable to non-native forests (Young et al. 2001). In fact, succession theory has profound implications for the management of invasive non-native trees or shrubs ('woody weeds'): weed species that do not regenerate under their own canopy are likely to die out naturally as succession proceeds (providing further disturbance does not occur). If the later successional species regenerating in the understory are predominantly native, then the site could be on a natural trajectory to native dominance, without active management (Lugo 2004). Conversely, woody weed species that do regenerate under their own canopy are more likely to be self-replacing and thus persistent in the long term (Wyckoff & Webb 1996; Vanhellemont et al. 2009). Sites dominated by these invasive species are unlikely to return to native dominance without active management of the weed.

A native understory is most likely to develop in woody weed stands where there is a native seed source within dispersal distance, and environmental conditions (e.g. rainfall, temperature, altitude, aspect, soil fertility) are amenable to native seedling establishment (Wilson 1994; Carswell et al. 2013). Woody weeds may even facilitate native plant establishment if they ameliorate harsh conditions (Ewel & Putz 2004; Svriz et al. 2013; Burrows et al. 2015), although the composition of vegetation that has regenerated under a woody weed canopy may differ from vegetation that has regenerated under native canopy species (Sullivan et al. 2007; Lorenzo et al. 2012). Conversely, native plant establishment in the understory could be impeded if the canopy weed is allelopathic, or if dense populations of herbivorous mammals, exotic grasses, or other shade-tolerant weed species are present (Wilson 1994; Wardle et al. 2001; Smale et al. 2005; McAlpine et al. 2015).

Woody weeds are among the most widespread and damaging of invasive organisms worldwide (Richardson & Rejmánek 2011). In New Zealand, almost half of the 328 environmental weeds present are trees or shrubs (Howell 2008), and many of these establish dense, closed-canopy patches over large areas. Some of these woody weed species are known to be replaced by native plant succession in some circumstances (Williams 2011; Wotton & McAlpine 2013), but in general, the potential successional role of these species is unclear. As a first stage in addressing this knowledge gap, the understory vegetation was surveyed in mature, closed-canopy woody weed stands to document which species regenerate under their own canopies, and the extent to which native and other non-native species colonise the understory.

Methods

Species and sites

The aim was to include all woody weed species that occur in patches of greater than 80% cover and that exceed 0.25 ha in area (sensu Williams 2011) in lowland areas of New Zealand. Weed experts (including the authors) determined that 56 of the 328 species on the Department of Conservation (DOC) environmental weeds list (Howell 2008) met these criteria.

To locate study sites, weed managers and experts at DOC, regional councils, universities and crown research institutes throughout New Zealand were asked about lowland areas where mature, closed-canopy populations of any of the 56 woody weed species were known to be present. Additional sites were found fortuitously from the road. Sites were accepted into the survey if a minimum of 10 mature individuals of the target weed species comprised ≥ 80% of the canopy over an area ≥ 25 m × 25 m, and there was no active management of the vegetation underway. Fortuitously found sites were only included if the site appeared to be unmanaged, i.e. no sign of planting or weeding or any other human activity. Sites for the same species had to be a minimum of 500 m apart. Sites were rejected if seedling recruitment appeared likely to be severely restricted by herbivorous livestock (e.g. sheep, cows), dense populations of pest animals (e.g. rabbits, goats), dense cover of exotic grasses or ground cover weeds, or frequent disturbance (e.g. riverbanks). Some weed populations were obviously old plantation sites, but these were included in the study if they were unmanaged and met all the other criteria, because the same successional processes were assumed to be underway.

Ideally, a minimum of three sites per species was sought. However, sites were included even if they were the sole site surveyed for a species. The rationale for this approach was that even a single site could indicate the potential successional trajectory for that weed species, particularly if understory regeneration was at one of the extreme ends of the spectrum (i.e. dense native cover and no canopy weed regeneration, or no native cover and dense canopy weed regeneration).

Site assessments

All assessments were made by one person (KGM) to maximise consistency. At each site, vegetation assessments were made over an area of approximately 20 × 20 m (400 m^2) nested within the weed population and at least 5 m from any patch edge.

To broadly classify woody weed species by the extent to which they regenerate under their own canopy, the number of conspecific understory plants was estimated for each of two height classes: beyond cotyledon stage but < 1 m (seedlings), and ≥ 1 m but below adult canopy (saplings). Seedlings were considered established, and thus were counted, only if they were beyond the cotyledon stage. Weed regeneration in both height classes was allocated to one of six categories, based on the nearest number of plants estimated to be present: 0 = 0 plants, 1 = 10 plants, 2 = 100 plants, 3 = 500 plants, 4 = 5000 plants, 5 = 10 000 plants. Percent cover in the understory of the canopy weed species, native species, and other non-native species was assessed visually. In many sites, the understory was growing in two distinct layers, one relatively close to the ground, and one in between the ground layer and the canopy. This separation made it difficult to estimate the extent to which layers overlapped, and thus determine overall understory cover. In order to be conservative, only the maximum value of the two layers is reported. This likely resulted in an underestimate of understory cover at some sites. Other understory species were recorded to species level where possible. Priority was given to the identification of woody species, because they were considered most important for the formation of forest through successional processes. Small herbs, grasses, rushes and sedges were classified by lifeform, and by provenance (native or non-native) if known.

Proximity to the nearest native seed source was estimated on the ground at each site: adjacent (native canopy adjoins weed canopy), near (not immediately adjacent, but within ~300 m), or distant (≥ 300 m) to a patch of native vegetation ≥ 0.25 ha in size. A one-way ANOVA was conducted to test for an effect of proximity to remnant native vegetation (adjacent, nearby, or distant) on native understory cover at sites, followed by Bonferroni-corrected multiple pairwise comparisons. Results in which $P < 0.05$ were reported as significant. Statistical analyses were conducted in R v. 3.2.1 (R Core Team 2016).

Results

In total, 132 populations of 41 woody weed species were surveyed (Figs. 1 and 2). The number of sites surveyed for each species ranged from one to eleven (Fig. 2). Three or more

Figure 1. Distribution of the 132 woody weed sites surveyed around New Zealand.

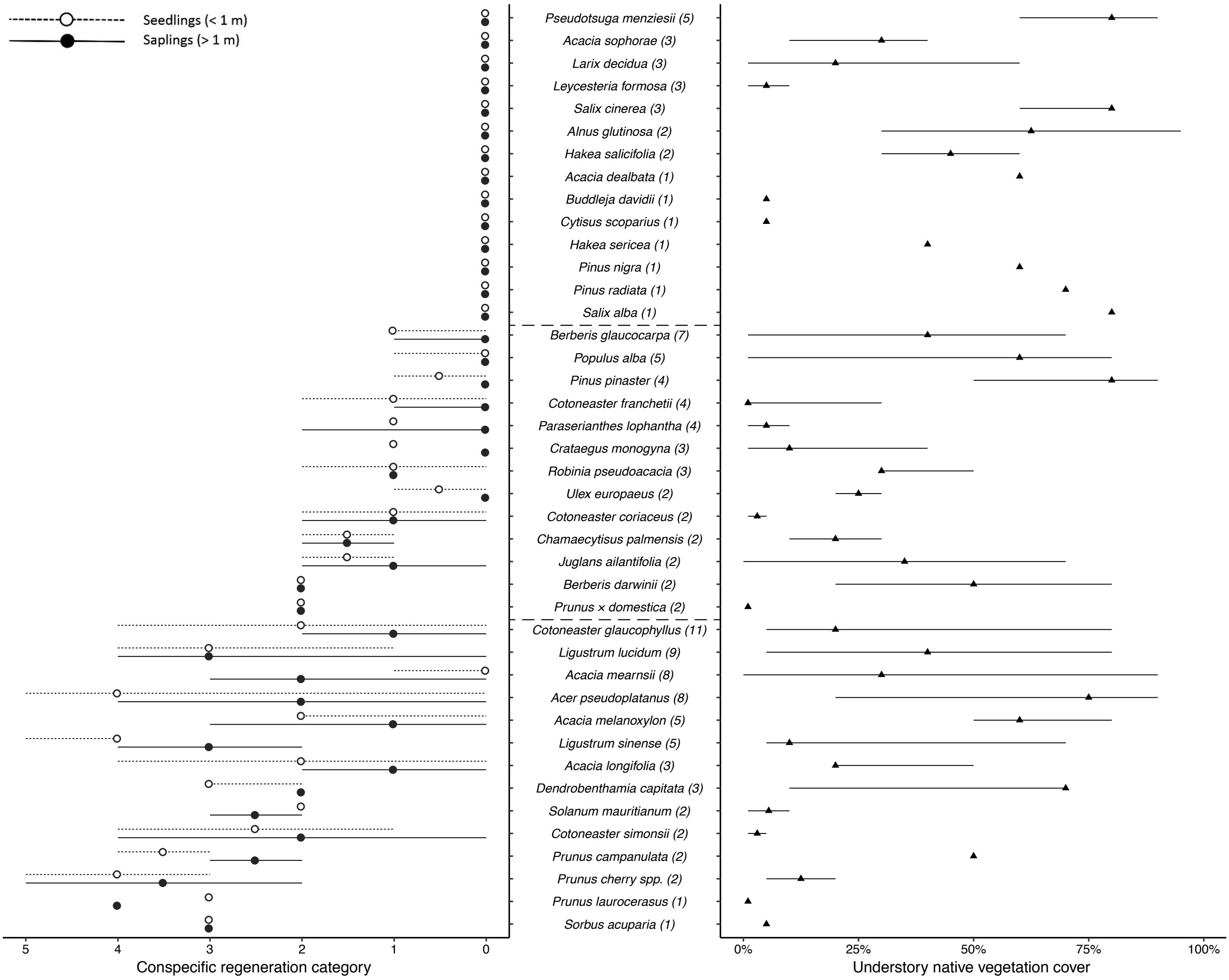

Figure 2. Conspecific regeneration of the canopy weed species and native understory cover at woody weed sites. Numbers in brackets indicate the number of sites surveyed per species (where it was the canopy species). Regeneration of the canopy weed species in the understory at each site (~400 m^2) was allocated to the category that was closest to the observed number of plants: 0 = 0 plants, 1 = 10 plants, 2 = 100 plants, 3 = 500 plants, 4 = 5000 plants, 5 = 10 000 plants. The dashed lines divide the species into three groups based on the extent to which they regenerate under their own canopy (left panel): zero regeneration, low regeneration (categories ≤ 2), and medium to high regeneration (categories ≥ 3). Within each group, species are ordered by number of sites surveyed. Central markers indicate the median, and the bars indicate the range of values across sites.

sites were surveyed for 20 species, but only one or two sites were surveyed for the other 21 species (Fig. 2). Although many more sites could probably have been located for all species, time constraints meant an exhaustive search was not possible.

The 41 woody weed species fell into three broad groups according to the extent to which they regenerate under their own canopy. Fourteen species had no conspecific seedlings or saplings under their own canopies at any site (*Pseudotsuga menziesii* to *Salix alba* in Fig. 2). An additional 13 woody weed species had low numbers of conspecific seedlings and/or saplings (regeneration categories 0–2) under their own canopies (*Berberis glaucocarpa* to *Prunus* × *domestica* in Fig. 2).

Fourteen woody weed species had medium to high numbers of conspecific seedlings and/or saplings (regeneration categories 3–5) under their own canopies (*Cotoneaster glaucophyllus* to *Sorbus acuparia* in Fig. 2). *Ligustrum sinense* had the most consistently high numbers of conspecific seedlings and saplings under its own canopy across multiple sites (Fig. 2). Six of the woody weed species with multiple (≥ 3) sites had high numbers of conspecific seedlings or saplings under their own canopies at some sites, but none, or very few, at others: *Acacia longifolia*, *Acacia mearnsii*, *Acacia melanoxylon*, *Acer pseudoplatanus*, *Cotoneaster glaucophyllus*, and *Ligustrum lucidum* (Fig. 2).

The effect of proximity to remnant native vegetation on native understory cover was significant (ANOVA, $F_{2,129}$ = 16.17, P = < 0.001). Average (± 1 SD) percent cover in the understory was 48.0 ± 30.6% at sites adjacent (n = 63) to remnant native vegetation, 37.0 ± 31.6% at sites nearby (n = 44) remnant native vegetation, and 11.1 ± 16.4% at sites distant (n = 25) from remnant native vegetation. Native understory cover was significantly lower at sites distant from native vegetation compared to sites nearby ($P < 0.001$) or adjacent ($P < 0.001$) to native vegetation. There was no significant difference in native understory cover at sites adjacent to native vegetation compared to sites nearby native vegetation ($P = 0.131$).

Percent cover of native species in the understory across all sites ranged from 0% to 90%, and averaged 37.4 ± 30.5%. All but 13 of the 41 weed species had native understory cover of ≥ 50% at one or more sites (Fig. 2). Percent cover of the canopy weed species in the understory across all sites ranged from 0% to 40%, and averaged 4.3 ± 7.1%. Percent cover of other non-native species in the understory across all sites ranged from 0% to 90%, and averaged 12.9 ± 22.3%.

There were far more native than non-native tree and shrub species recorded at sites (Table 1). Seventy-six native species were present at five or more sites (Table 1). *Melicytus ramiflorus* (māhoe) was by far the most commonly recorded species, present at 88 of the 132 sites (67%) (Table 1). Overall, the number of native species (not including sedges and rushes) present per site ranged from zero to 24, and averaged 8.9 ± 5.2. The number of non-native species (not including sedges and rushes) present per site ranged from zero to nine, and averaged 2.3 ± 1.6. *Rubus fruticosus* agg. (blackberry) was the most commonly recorded non-native species, present at 40 sites (Table 1).

Discussion

The suggestion that some woody weed species may be replaced by native plant succession in the absence of disturbance in New Zealand is not new (McQueen 1993; Williams 2011). However, this is the first study to systematically survey woody weed populations throughout New Zealand to determine which species regenerate under their own canopy, and which have predominantly native understories. Twenty-seven woody weed species had zero, or very few, conspecific seedlings or saplings beneath the parent canopy, and most had ≥ 50% cover of native species in the understory at one or more sites. Accordingly, these 27 species appear to have the most potential to be replaced by native succession in the absence of disturbance. Most of these 27 species are widely established throughout New Zealand (Howell & Terry 2016), so the management implications are significant. It should be noted, however, that the current study excluded sites where domestic livestock or dense populations of pest animals, exotic grasses or ground cover weeds were present; successional trajectories under these scenarios are uncertain. Additionally, data from a single site should be interpreted with caution; there may be considerable variation at different types of sites and/or under different conditions. For example, no *Pseudotsuga menziesii* seedlings were recorded at any of the five sites surveyed in the current study, but other authors have suggested that *P. menziesii* can invade New Zealand beech forest, particularly where the canopy and/or understory is relatively open (Ledgard 2002; Burmeister et al. 2016). Given increasing concerns over the invasive potential of *P. menziesii* in New Zealand (Froude 2011), further research into the shade tolerance of this species would be valuable.

Canopy species with high numbers of conspecific seedlings and saplings in the understory are most likely to be self-replacing and thus persistent, because this indicates that both recruitment *and* survival of seedlings is occurring (Grime 2001; Vanhellemont et al. 2009). Accordingly, fourteen species or species groups in the current study appear most likely to be self-replacing and thus persistent – particularly where the understory is otherwise sparse. The worst of these may be *Ligustrum sinense* (Chinese privet), which had consistently high numbers of conspecific seedlings and saplings across multiple sites, and generally low understory cover of native species, despite all five sites being either ‘adjacent’ or ‘near’ to native vegetation (data not shown). Another New Zealand study also documented the high regeneration of *L. sinense* under its own canopy and apparent exclusion of native species, and concluded that *L. sinense* is capable of continually occupying a site (Grove & Clarkson 2005). Many studies from the USA have also demonstrated a reduction in native plant colonisation under a *L. sinense* canopy compared to uninvaded sites (Morris et al. 2002; Merriam & Feil 2003; Wilcox & Beck 2007; Greene & Blossey 2012; Hart & Holmes 2013), but causal mechanisms appear to be unknown.

Some species were highly variable in the extent to which they were regenerating beneath their own canopies. For example, *Ligustrum lucidum* (tree privet) and *Acer pseudoplatanus* (sycamore) had very high numbers of conspecific seedlings and saplings in the understory at some sites, but none at others. There was no obvious reason for this variability between sites, but it might be due to site-specific differences that could affect understory weed regeneration, such as drought, flooding, nutrient availability, or herbivory (Metz et al. 2008; Valladares & Niinemets 2008). Additionally, the age of the weed population can influence native regeneration in the understory (Wilson 1994; Carswell et al. 2013). Studies from several countries, including New Zealand (Brockerhoff et al. 2003), South Africa (Geldenhuys 2013) and Puerto Rico (Lugo 2004), have demonstrated that abundance and diversity of native species in the understory of non-native tree stands tend to increase as the stand matures and thins out. It would be useful to know what restricts regeneration of these weed species at some sites, and whether management actions could be applied to elicit the same result.

The current study demonstrates that many native species can establish beneath woody weed canopies in New Zealand, including canopy-forming species such as *Beilschmiedia tawa* (tawa), *Alectryon excelsus* (tītoki) and *Dacrycarpus dacrydioides* (kahikatea). Closed-canopy stands of shade-intolerant woody weeds may even offer ideal conditions for native vegetation to re-establish, and could represent considerable opportunity for large-scale native forest regeneration (Brockerhoff et al. 2003; Chazdon & Guariguata 2016). The closed canopy reduces competition from non-native grass swards and enables colonisation by the many shade-tolerant native species present in the New Zealand flora. However, close proximity to native seed source is important – natural understory development may not occur otherwise.

Non-native species other than the canopy weed species were present at most sites, but they were generally a minor component of the understory. However, some of the ground-covering species recorded are capable of persisting in the understory and inhibiting native seedling establishment, for example, *Tradescantia fluminensis, Asparagus scandens* and *Hedychium* spp. (Williams et al. 2003; McAlpine et al. 2015). Non-native tree and shrub species were also present at some sites, and species such as *Ligustrum sinense* that can reach maturity in the shade could increase in abundance over time and dominate the canopy under some circumstances.

This study has added to knowledge about the regeneration ecology of 41 woody weed species in New Zealand. It has demonstrated that (1) woody weed species vary in the extent to which they regenerate under their own canopy, and (2) closed

Table 1. Species recorded in the understory at five or more of the 132 woody weed sites. The 41 study weed species were not included in species counts except when present beneath the canopy of a different species. Where identification to species level was not possible, taxa were grouped by genus or structural class. *Non-native species. **Provenance uncertain.

Trees	**No. sites**	**Shrubs**	**No. sites**
Melicytus ramiflorus	88	*Coprosma robusta*	52
Myrsine australis	51	*Piper excelsum*	45
Pseudopanax arboreus	41	*Geniostoma ligustrifolium*	44
Cyathea dealbata	39	*Rubus fruticosus**	40
Hedycarya arborea	36	*Coprosma grandiflora*	27
Carpodetus serratus	29	*Brachyglottis repanda*	23
Leucopogon fasciculatus	23	*Ulex europaeus**	18
Pittosporum eugenioides	18	*Coprosma lucida*	16
Podocarpus totara	18	*Coprosma dumosa*	11
Pittosporum tenuifolium	18	*Coprosma rhamnoides*	11
Beilschmiedia tawa	17	*Pseudowintera colorata*	11
Cyathea medullaris	16	*Leycesteria formosa**	9
*Ligustrum sinense**	16	*Coprosma rotundifolia*	8
Dacrycarpus dacrydioides	15	*Coprosma propinqua*	7
Rhopalostylis sapida	15	*Cytisus scoparius**	7
Alectryon excelsus	14	*Rosa rubiginosa**	6
Aristotelia serrata	13	*Solanum mauritianum**	6
*Berberis glaucocarpa**	13	*Coprosma colensoi*	5
Dysoxylum spectabile	13	*Cordyline banksii*	5
Schefflera digitata	13	*Hebe stricta*	5
*Acer pseudoplatanus**	12		
*Crataegus monogyna**	12	**Ferns**	
Griselinia littoralis	12	*Microsorum pustulatum*	38
Pennantia corymbosa	12	*Blechnum novae-zelandiae*	28
Pseudopanax crassifolius	12	*Asplenium flaccidum*	27
Prunus cherry spp.*	11	*Asplenium oblongifolium*	20
Cordyline australis	10	*Pteridium esculentum*	19
Pittosporum crassifolium	10	*Pyrrosia eleagnifolia*	18
Knightia excelsa	9	*Adiantum* spp.	17
Kunzea spp.	9	*Asplenium bulbiferum*	17
Dicksonia squarrosa	9	*Blechnum parrisiae*	17
Fuchsia excorticata	7	*Polystichum neozelandicum*	17
Litsea calicaris	7	*Pneumatopteris pennigera*	14
Sophora spp.	7	*Polystichum vestitum*	13
Corynocarpus laevigatus	6	*Hypolepis ambigua*	11
Prumnopitys taxifolia	6	*Pteris macilenta*	9
Weinmannia racemosa	6	*Blechnum chambersii*	7
Leptospermum scoparium	6	*Blechnum filiforme*	7
*Paraserianthes lophantha**	6	*Blechnum fluvatile*	7
Olearia rani	5	*Pellaea rotundifolia*	6
*Sambucus nigra**	5	*Asplenium polyodon*	5
Vines		**Other**	
Muehlenbeckia australis	32	Small dicot herb spp.*	62
Parsonsia spp.	18	Sedge spp.**	52
*Lonicera japonica**	15	Grass spp.*	36
*Hedera helix**	14	*Oplismenus hirtellus*	17
Ripogonum scandens	9	*Microlaena stipoides*	12
*Asparagus scandens**	8	*Cortaderia selloana**	11
*Clematis vitalba**	7	Rush spp.**	7
Metrosideros diffusa	5		

canopy woody weed stands frequently have a predominantly native understory. Further research to determine how understory composition can be used to predict successional trajectories in weed populations would have considerable management utility.

Acknowledgements

This project was funded by the Ministry of Business, Innovation and Employment through Landcare Research's Core Funded programme Beating Weeds II, and the New Zealand Department of Conservation. Clayson Howell and Ian Popay provided expert comment on which woody weed species met the criteria for inclusion in the study. Many thanks to the 100+ people who assisted with site location. Comments from James Griffiths, Clayson Howell, Colin Miskelly, Olivia Burge, Clare Veltman, Rod Hitchmough and anonymous reviewers improved the manuscript. James Griffiths and Clayson Howell also assisted with figure production.

References

Bazzaz FA 1979. The physiological ecology of plant succession. Annual Review of Ecology and Systematics 10: 351–371.

Brockerhoff EG, Ecroyd CE, Leckie AC, Kimberley MO 2003. Diversity and succession of adventive and indigenous vascular understorey plants in *Pinus radiata* plantation forests in New Zealand. Forest Ecology and Management 185: 307–326.

Burmeister EL, Kelly D, Ledgard N 2016. Environmental factors influencing the Douglas fir invasion of *Nothofagus* forest. Paper presented at the joint conference of the Society for Ecological Restoration Australasia & the New Zealand Ecological Society. 19–23 November 2016, Hamilton, New Zealand.

Burrows L, Cieraad E, Head N 2015. Scotch broom facilitates indigenous tree and shrub germination and establishment in dryland New Zealand. New Zealand Journal of Ecology 39: 61–70.

Carswell F, Mason N, Holdaway R, Burrows L, Payton I, Sutherland A, Price R, Pearce G, Corich-Hermans O, Williams PA 2013. Indirect estimation of gorse and broom 'non-forest land' to 'forest land' transition. MPI Technical Paper No. 2013. Wellington, Ministry for Primary Industries. 61 p.

Chazdon RL, Guariguata MR 2016. Natural regeneration as a tool for large-scale forest restoration in the tropics: prospects and challenges. Biotropica 48: 716–730.

Connell JH, Slatyer RO 1977. Mechanisms of succession in natural communities and their role in community stability and organization. The American Naturalist 111: 1119–1144.

Ewel JJ, Putz FE 2004. A place for alien species in ecosystem restoration. Frontiers in Ecology and the Environment 2: 354–360.

Froude VA 2011. Wilding conifers in New Zealand: Status report. Report prepared for the Ministry of Agriculture and Forestry. Bay of Islands, New Zealand Pacific Eco-logic. 206 p.

Geldenhuys CJ 2013. Converting invasive alien plant stands to natural forest nature's way. In: Jose S, Harminder P, Batish DR, Kohli RK eds. Invasive plant ecology. Boca Raton, CRC Press. Pp. 217–237.

Greene BT, Blossey B 2012. Lost in the weeds: *Ligustrum sinense* reduces native plant growth and survival. Biological Invasions 14: 139–150.

Grime JP 2001. Plant strategies, vegetation processes, and ecosystem properties. 2nd edn. Chichester, John Wiley & Sons. 456 p.

Grove E, Clarkson B 2005. An ecological study of Chinese privet (*Ligustrum sinense* Lour.) in the Waikato Region. Prepared for Environment Waikato Regional Council. Hamilton, CBER. 17 p.

Hart JL, Holmes BN 2013. Relationships between *Ligustrum sinense* invasion, biodiversity, and development in a mixed bottomland forest. Invasive Plant Science and Management 6: 175–186.

Howell CJ 2008. Consolidated list of environmental weeds in New Zealand. DOC Research & Development Series 292. Wellington, Department of Conservation. 42 p.

Howell CJ, Terry JA 2016. The creation of a New Zealand weed atlas. New ZealandScience for Conservation Series 328. Wellington, Department of Conservation. 21 p.

Kimmins JP 2004. Forest ecology: a foundation for sustainable forest management and environmental ethics in forestry. Upper Saddle River, Prentice Hall. 611 p.

Ledgard N 2002. The spread of Douglas-fir into native forests. New Zealand Journal of Forestry 47: 36–38.

Lorenzo P, Pazos-Malvido E, Rubido-Bará M, Reigosa MJ, González L 2012. Invasion by the leguminous tree *Acacia dealbata* (Mimosaceae) reduces the native understorey plant species in different communities. Australian Journal of Botany 60: 669–675.

Lugo AE 2004. The outcome of alien tree invasions in Puerto Rico. Frontiers in Ecology and the Environment 2: 265–273.

McAlpine KG, Lamoureaux SL, Westbrooke I 2015. Ecological impacts of ground cover weeds in New Zealand lowland forests. New Zealand Journal of Ecology 39: 50–60.

McQueen DR 1993. A review of interaction between naturalised woody plants and indigenous vegetation in New Zealand. Tuatara 32: 32–56.

Merriam RW, Feil E 2003. The potential impact of an introduced shrub on native plant diversity and forest regeneration. Biological Invasions 4: 369–373.

Metz MR, Comita LS, Chen Y, Norden N, Condit R, Hubbell SP, Sun I, Noor NS, Wright SJ 2008. Temporal and spatial variability in seedling dynamics: a cross-site comparison in four lowland tropical forests. Journal of Tropical Ecology 24: 9–18.

Morris LL, Walck JL, Hidayati SN 2002. Growth and reproduction of the invasive *Ligustrum sinense* and native *Forestiera ligustrina* (Oleaceae): implications for the invasion and persistence of a nonnative shrub. International Journal of Plant Sciences 163: 1001–1010.

Pacala SW 1997. Dynamics of plant communities. In: Crawley M ed. Plant Ecology. Oxford, Blackwell Scientific. Pp. 532–555.

R Core Team 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Richardson DM, Rejmánek M 2011. Trees and shrubs as invasive alien species—a global review. Diversity and Distributions 17: 788–809.

Smale MC, Ross CW, Arnold GC 2005. Vegetation recovery in rural kahikatea (*Dacrycarpus dacrydioides*) forest fragments in the Waikato region, New Zealand, following retirement from grazing. New Zealand Journal of Ecology 29: 261–269.

Sullivan JJ, Williams PA, Timmins SM 2007. Secondary forest succession differs through naturalised gorse and native kānuka near Wellington and Nelson. New Zealand Journal of Ecology 31: 22–38.

Svriz M, Damascos M, Zimmermann H, Hensen I 2013. The exotic shrub *Rosa rubiginosa* as a nurse plant. Implications for the restoration of disturbed temperate forests in Patagonia, Argentina. Forest Ecology and Management 289: 234–242.

Swaine M, Whitmore T 1988. On the definition of ecological species groups in tropical rain forests. Plant Ecology 75: 81–86.

Valladares F, Niinemets U 2008. Shade tolerance, a key plant feature of complex nature and consequences. Annual Review of Ecology, Evolution, and Systematics 39: 237–257.

Vanhellemont M, Baeten L, Hermy M, Verheyen K 2009. The seedling bank stabilizes the erratic early regeneration stages of the invasive *Prunus serotina*. Ecoscience 16: 452–460.

Wardle DA, Barker GM, Yeates GW, Bonner KI, Ghani A 2001.

Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. Ecological Monographs 71: 587–614.
Wilcox J, Beck CW 2007. Effects of *Ligustrum sinense* Lour. (Chinese privet) on abundance and diversity of songbirds and native plants in a southeastern nature preserve. Southeastern Naturalist 6: 535–550.
Williams PA 2011. Secondary succession through non-native dicotyledonous woody plants in New Zealand. New Zealand Natural Sciences 36: 73–91.
Williams PA, Winks C, Rijkse W 2003. Forest processes in the presence of wild ginger (*Hedychium gardnerianum*). New Zealand Journal of Ecology 27: 45–54.

Received 17 February 2017; accepted 28 May 2018
Editorial board member: Tom Etherington

Wilson HD 1994. Regeneration of native forest in Hinewai Reserve, Banks Peninsula. New Zealand Journal of Botany 32: 373–383.
Wotton DM, McAlpine KG 2013. Predicting native plant succession through woody weeds in New Zealand. DOC Research and Development Series 336. Wellington, Department of Conservation. 28 p.
Wyckoff PH, Webb SL 1996. Understory influence of the invasive Norway maple (*Acer platanoides*). Bulletin of the Torrey Botanical Club 123: 197–205.
Young TP, Chase JM, Huddleston RT 2001. Community succession and assembly: comparing, contrasting and combining paradigms in the context of ecological restoration. Ecological Restoration 19: 5–18.