Post-fire recovery of a dryland forest remnant in the Wither Hills, Marlborough

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Abstract: Fire is a major threat to remnant native woody vegetation in dry, lowland New Zealand. This is because the woody flora lacks specific adaptations to survive fire, and seedling regeneration is constrained by summer drought, limited native seed rain and intense competition from non-native grasses that are often favoured by fire. In December 2000, a fire burnt a 41 ha remnant of mature *Kunzea robusta* (Myrtaceae) forest in the Wither Hills, Marlborough, a dry region with little remaining native woody vegetation. Shortly after the fire the area was fenced to exclude grazing animals and oversown with pasture species to stabilise the soil. A study was then initiated in June 2001 to determine the rate and direction of native forest recovery using 15 randomly located monitoring plots. Plots were re-measured in summer 2001, 2002, 2003 and 2015. Additional strategically located plots monitored the survival and re-growth of burnt individuals of *Kunzea robusta*, *Sophora prostrata* (Fabaceae) and *Clematis quadribracteolata* (Ranunculaceae). In spite of the dry climate, limited seed rain, oversowing and absence of grazing, woody biomass has started to recover after fire in the Wither Hills – but slowly as non-native grasses are overwhelmingly dominant. After 15 years, woody biomass and cover are less than 5% of the original estimate for the area. However, while fire-damaged *Kunzea* mostly died, *Sophora* and *Clematis* individuals have recovered through resprouting. Our study site is typical of many dryland areas in New Zealand in which native biodiversity is part of a productive landscape and is under threat from fire, weeds and grazing. It is inevitable that a proportion of dryland reserves will be burnt each decade and our results underscore the need for conservation planning to incorporate fire and for experimental investigations to assist with accelerating native vegetation recovery.

Keywords: *Clematis quadribracteolata*; conservation planning; *Dactylis glomerata*; fire ecology; *Kunzea robusta*; resprouting; seed limitation; *Sophora prostrata*; state and transition models

Introduction

Before human settlement, natural fires were relatively uncommon in New Zealand and were only a significant evolutionary driver in a few, low-statured vegetation types such as wetlands and heathlands (Perry et al. 2014). Consequently, most of the tall forest trees lack specific fire adaptations such as thick bark, serotiny, fire-resistant seed banks, deep roots and lignotubers, and the ability to resprout following fire (Wardle 1991; Ogden et al. 1998; Perry et al. 2014; Richardson et al. 2015). The high frequency and intense fires that followed human settlement burnt all woody vegetation throughout the drier parts of New Zealand resulting in shrub- or grass-dominated communities (McGlone 1983). Surviving areas of native secondary and remnant woody vegetation contend with grazing, non-native pastoral and weed species, and are vulnerable to ongoing and repeated fire (Ecroyd et al. 2005; Perry et al. 2010).

Conservation managers need to understand post-fire successions in dryland forests to determine whether interventions are necessary to restore or reinvigorate successional processes (Standish et al. 2008). Quantification of the rate and trajectory of recovery following fire in modified landscapes is essential to this task. Post-fire forest successions in dryland production landscapes in New Zealand tend to stall because of two factors: (1) competition from non-native sward-forming grasses prevents seedling establishment (Ledgard & Davis 2004); and (2) limited seed sources, which include both low survival of seeds on burned adults or in soil seed banks

(Rowarth et al. 2007; Perry et al. 2014) and low seed input when remnant populations of native woody species are small and distant. These stall the establishment of woody seedlings, slow biomass accumulation and limit the recovery of pre-fire biomass. In turn, this increases the recovery period to tall forest during which vegetation is more flammable, hence increasing fire frequency and reducing further the chances for forest recovery (Perry et al. 2010, 2015; Tepley et al. 2016).

There are surprisingly few longitudinal studies quantifying post-fire recovery of woody biomass in New Zealand dryland ecosystems and production landscapes. The duration of the lag period between the fire and initial woody establishment, the rate of biomass recovery and the form of that recovery rate curve (Mack et al. 2008), and the amount of pre-fire biomass that recovers are all poorly quantified, particularly in relation to post-fire management of remnants. Globally, fire-adapted ecosystems can have rapid rates of biomass recovery through vigorous resprouting and establishment from fire-resistant seed banks (Whelan 1995). Given the scarcity of such traits in the New Zealand tall forest tree flora (Perry et al. 2014), post-fire biomass recovery rates are likely to be slow. We report on post-fire recovery of a secondary *Kunzea robusta* forest (a type typical of many dryland conservation covenants) over a 15-year period. Our goals were to determine whether, when and how much woody regeneration had occurred, and quantify resilience of three species (*K. robusta*, *Sophora prostrata* and *Clematis quadribracteolata*) to fire.

Methods and materials

Study site

Sutherland Stream (41.56°S, 173.97°E) is near Blenheim in the northern Wither Hills, eastern Marlborough, New Zealand. The Wither Hills are formed of weakly indurated conglomerate and claybound gravels overlain by loess (Begg et al. 2000). Elevations range from c. 60–422 m. The topography is steeply-incised and the loess-rich soils subject to tunnel gully erosion and slips (Begg et al. 2000). Mean annual temperature in Blenheim (1981–2010) is 12.6°C, with a summer (December to February) mean of 17.4°C and a winter (June to August) mean of 7.7°C. Mean annual rainfall in Blenheim (1981–2010) is 711 mm with a summer mean of 156 mm and a winter mean of 207 mm (The National Climate Database, www.cliflo.niwa. co.nz, accessed August 2016).

Fire and management history

Before humans settled New Zealand, the Wither Hills were likely covered by a forest of drought-tolerant tree species such as *Podocarpus totara*, *Prumnopitys taxifolia*, *Kunzea robusta* and *Sophora microphylla*. Site-specific charcoal or macrofossil data are lacking but regional charcoal records indicate that Polynesian fires removed these forests and by the time of early European surveys (1840–1860 AD) the vegetation was dominated by grasses and shrubs with scattered areas of remnant and secondary forest (McGlone 1983).

In 1994, a 41 ha area was covenanted by the Queen Elizabeth II National Trust and Marlborough District Council to safeguard mature *Kunzea robusta* (Myrtaceae) forest with subordinate tree species including *Coprosma robusta* (Rubiaceae), *Coriaria arborea* (Coriariaceae), *Discaria toumatou* (Rhamnaceae), *Melicytus ramiflorus* (Violaceae), *Olearia paniculata* (Asteraceae) and *Pseudopanax arboreus* (Araliaceae) (Queen Elizabeth II National Trust 1997). With the exceptions of *O. paniculata* and *D. toumatou*, these subordinate trees were largely confined to gullies and toe slopes, with *K. robusta* dominating the open slopes and ridgelines. A wider matrix of open grassland protected native species such as *Sophora prostrata* (Fabaceae – a shrub), *Clematis quadribracteolata* (Ranunculaceae – a liane), *Cheilanthes sieberi*, *C. distans* and *Pellaea calidirupium* (all Pteridaceae) and herbs such as *Convolvulus waitaha* (Convolvulaceae) and *Carex inopinata* (Cyperaceae). Pre-fire photographs indicate that the forest understorey was often sparse and non-native pasture grasses common. Pastoral grazing is not practised in the covenant but rabbits, hares and possums are present. The covenant is managed using practices that balance biodiversity conservation, recreation and soil stabilisation and is embedded in a productive landscape, typical of many lowland reserves in New Zealand. Like many such areas it has a long history of weed infestation and species such as *Cytisus scoparius* (Fabaceae), *Berberis glaucocarpa* (Berberidiaceae), *Euonymus europaeus* (Celastraceae), *Ulex europeaus* (Fabaceae), *Salix cinerea* (Salicaceae) and *Nassella trichotoma* (Poaceae) are manually controlled in the reserve.

On 26 December 2000, an accidental fire across the Wither Hills region burnt most of the forest. The fire was more intense in the mature *K. robusta* stands where the fuel loadings were high and few trees survived. In some places the surface litter and soil organic horizon were also incinerated (Fig. 1b). There are no vegetation data to define pre-fire composition and structure, and insufficient unburnt forest to

act as a control site. Live tree aboveground biomass in tall *K. robusta* forest from nearby Peggioh Station (41.9° S, 174.0° E, c. 35 km to the south) ranges from c. 30 Mg ha^{-1} in 40-year old stands, to c. 130 Mg ha^{-1} in mature 100-year old stands (RJH unpubl. data). As prior to the fire the covenant forest was at least 4 m tall with a continuous canopy in many areas (Fig. 1a), we conservatively estimate that stands were at least 40 years old and therefore the pre-fire biomass at least 30 Mg ha^{-1}. National biomass estimates for a similar forest and tall shrubland association dominated by *Kunzea* sp. (*Kunzea*
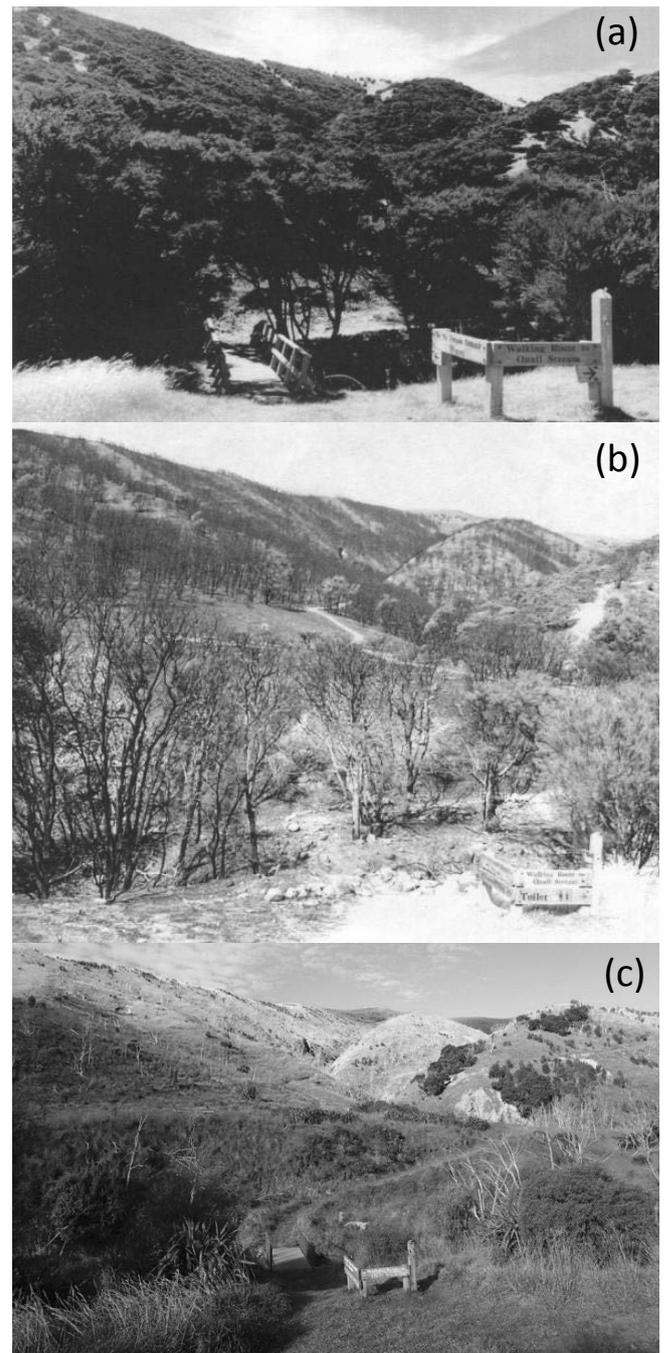

Figure 1. (a) Photo of mature *Kunzea robusta* forest in the Wither Hills in 1999 before the fire. (b) Photo from January 2001, 11 months after fire showing extensive ash beds beneath dead standing trees. (c) Photo from September 2014 showing limited recovery of woody cover and dominance by non-native grass species. Photographs: Queen Elizabeth II National Trust (Robyn Smith).

ericoides – *Cyathea dealbata* – (*Leptospermum scoparium*)/*Leucopogon fasciculatus*– (*Coprosma rhamnoides*); Wiser et al. 2011) has a mean live tree aboveground biomass of 48 Mg ha^{-1} (6 ± 1 SE, n = 32 plots) (Holdaway et al. 2017).

Immediately after the fire, the Wither Hills area (including the covenant) was oversown with a mixture of non-native pasture grasses and forbs (*Dactylis glomerata* (Poaceae), *Phalaris aquatica* (Poaceae), *Lotus corniculatus* (Fabaceae), *Lotus pedunculatus* (Fabaceae), and *Cichorium intybus* (Asteraceae)) to mitigate the risk of post-fire erosion.

Measuring vegetation recovery

In June 2001, 6 months after the fire, we established fifteen 10 m × 10 m (100 m^2) plots along three transects to sample the full range of topographic positions (spur crests, faces and gullies) and elevations (175–350 m) in the covenant. The three transects were selected on a restricted random basis. Transects were evenly-spaced to achieve full elevational coverage of the covenant. Transects were pre-determined on an aerial photograph, and ran north across the topography from origins on the southern boundary of the covenant. The first plot location in each transect was determined by a random number and then plots were located every 100 m along each transect. We measured the landform index as the arithmetic mean of eight angles to the horizon on the cardinal and intercardinal bearings (McNab 1993). We measured vascular plant composition in June 2001 (6 months after the fire), December 2001 (12 months), December 2002 (24 months), December 2003 (36 months) and December 2015 (180 months) using a modified Braun-Blanquet method (Hurst & Allen 2007). We visually assessed cover of each species overhanging each plot in classes (1 = < 1%, 2 = 1–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 => 76%) and height tiers (< 0.3 m; ≥ 0.3–2.0 m; > 2.0–5.0 m). We measured the heights of all woody plants ≥ 135 cm tall on each plot and if they had a diameter of ≥ 2.5 cm at 135 cm, we tagged them and measured their stem diameter at that height.

In addition to the 15 randomly located plots, we also established three strategically-located plots in June 2001 to follow recovery of burned individuals of three species.

(1) We followed the fate of an isolated stand of *Kunzea robusta* where foliage was burned but stems survived (plot size of 35 m × 10 m; 350 m^2). At each measurement we recorded the heights of all stems with live foliage taller than 135 cm and where stems had a diameter of ≥ 2.5 cm at 135 cm, we tagged them and measured their stem diameter.

(2) We tagged 40 *Sophora prostrata* (Fabaceae) which before the fire had been growing in grassland and had all burned to the base. Plot size was 15 m × 50 m (750 m^2). At each measurement we recorded survival and measured the widest orthogonal dimension of living tissue. In 2015, we also measured the perpendicular orthogonal width and height.

(3) We tagged 10 multi-stemmed individuals of *Clematis quadribracteolata* (Ranunculaceae) in December 2001 that had burned to the base. Plot size was 10 m × 10 m (100 m^2). In December 2002 and 2003 we relocated these individuals and measured the length of the longest shoot and the number of shoots from each cluster. In 2015, we revisited the plot and visually determined whether the species was still present within the plot as individuals could no longer be practicably separated and measured.

Data analyses

All statistical analyses were completed in R v.3.4.1. (R Core Development Team 2017). We analysed vegetation composition data by taking the percentage midpoint for each cover class and summing these across height tiers to estimate percentage cover. We categorised species as native woody, non-native woody, native herbaceous or non-native herbaceous following Ngā Tipu Aotearoa (accessed June 2016) and summed cover in each plot in these four groups. We used a linear mixed effects (LME) model to test whether summed cover (transformed as $\log_{10}$(cover + 0.5), to homogenise variance) and the rate of change in cover was similar across these four groups across our five measurements. We tested five models predicting $\log_{10}$ cover from log-transformed time since fire (in months) and group (one allowing each group to have a different slope and intercept, one allowing each group to have a different slope but a shared intercept, an additive model between the two terms, a model fitting a different intercept to each group without a slope term for change through time, and a model with a slope for change through time and a single intercept fitted to all groups). We used small sample Akaike's Information Criteria (AICc) to select the most parsimonious model (Anderson 2008). We included plot as a random effect as repeated measures within permanent plots are non-independent. We visually inspected the relationship between fitted values and residuals in the final model to check that residuals were randomly distributed with respect to fitted values. Post-hoc tests for differences in mean cover for each group at each measurement were made using the glht function in the multcomp v.1.4-0 package (Hothorn et al. 2008). Tree dimensions were converted to aboveground biomass following standard allometric methods for the species sampled (Coomes et al. 2002; Holdaway et al. 2014, 2017). We determined the relationships between aboveground biomass and landform index using a general linear model (GLM) with Gaussian error model.

Results

Vegetation composition

Vegetation cover increased over the 15-year post-fire period in three of the groups (native woody, native herbaceous and non-native herbaceous), but not in the non-native woody group (Fig. 2). The most parsimonious LME model included a different intercept and slope for each group, reflecting the substantial difference in mean cover between non-native herbaceous species and all other groups and the difference in trend through time across the four groups (interaction term between time and group $F_{3,278}$ = 13.1, P < 0.001, coefficient of determination = 0.78, slope between observed and predicted values = 1.01; Fig. 2). Non-native grasses dominated post-fire vegetation cover (Fig. 2) and non-native taxa accounted for 58% of taxa recorded across all measurements, and at least 85% of total cover in all measurements (Fig. 2). Five non-native grass taxa were found on ≥ 65% of plots in 2015 (*Anthoxanthum odoratum*, *Dactylis glomerata*, *Rytidosperma* spp., *Anthosachne scabra*, *Phalaris aquatica*) of which *D. glomerata* was the most abundant in terms of cover (97% where present ± 12% 1 SE). The only native grass species found on ≥ 50% of plots in 2015 was *Microlaena stipoides* (2% ± 0.5% 1 SE, where present). Woody cover has recovered slowly and was < 15% in 2015 (Fig. 2). The most frequent native woody species in 2015 were *Kunzea robusta* and *Muehlenbeckia complexa* (both on 27% of plots). Two non-native woody species (*Berberis glaucocarpa* and *Cytisus scoparius*) were found on ≥ 40% of plots in 2015.
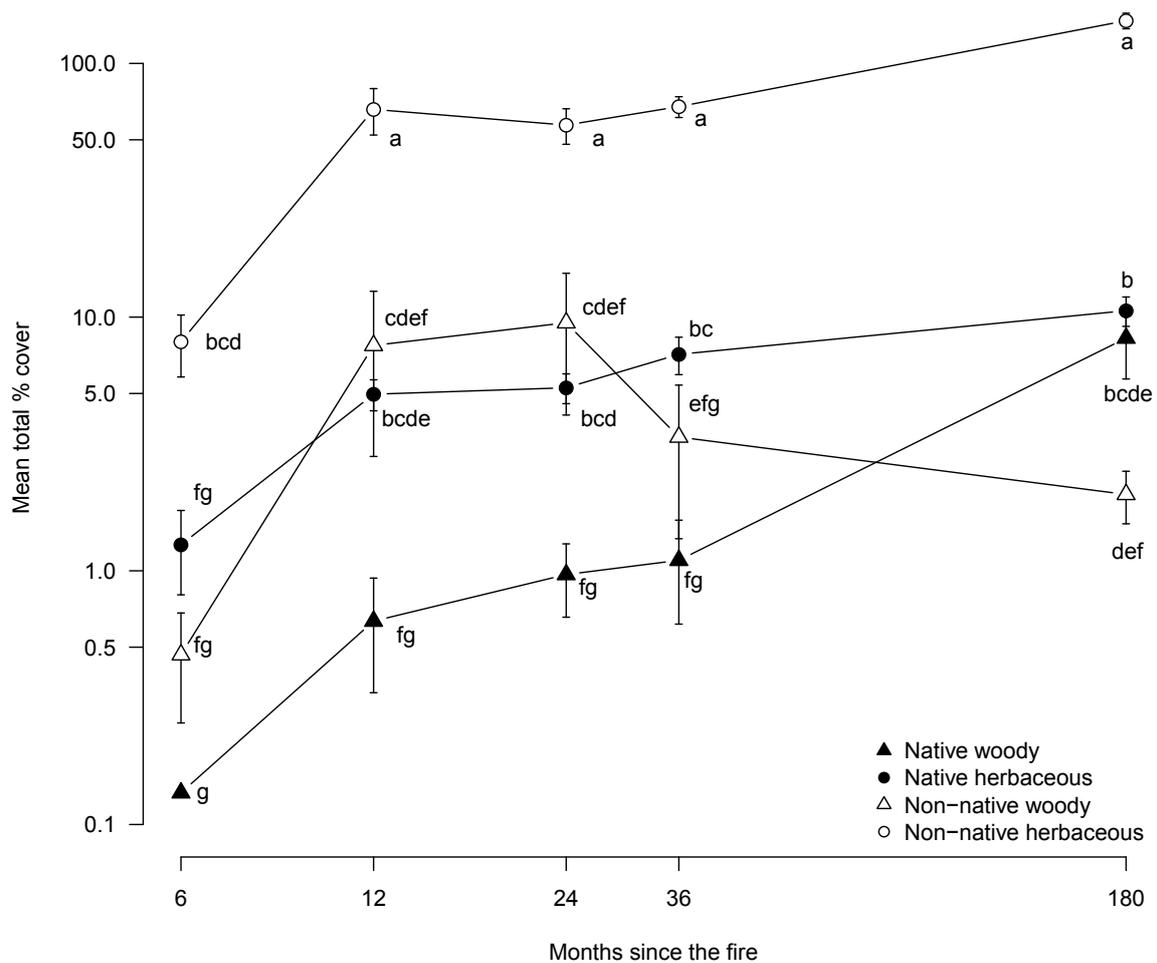
Figure 2. Post-fire vegetation recovery over 15 years in the Wither Hills, Marlborough. Changes in mean foliar cover in four groups (native woody, native herbaceous, non-native woody, non-native herbaceous). Note that cover sums to > 100% across tiers and both axes use a log-scale. Error bars are ± 1 SE. Means that share a letter are not significantly different at P < 0.05.

Tree regeneration

No *Kunzea robusta* or other trees survived the fire in the 15 randomly-located plots. In 2002 and 2003, *K. robusta* was present as seedlings on six and seven plots, respectively, but no stems were ≥ 1.35 m tall. In 2015, *K. robusta* was present on eight plots (53% of plots) but there were only 25 individuals ≥ 1.35 m tall (46 ha^{-1} ± 24 1 SE), which were confined to just six plots and their mean height was 2.4 m (± 0.1 m SE). The only other tree species recorded was a single 1.5 m tall individual of *Coprosma robusta*, which we assume to have come from seed. These live individuals equate to a stem density of 167 ha^{-1} (±85 1 SE), a basal area of 0.03 m^2 ha^{-1} (± 0.03 1SE) and aboveground biomass of 0.59 Mg ha^{-1} (± 0.33 1 SE) (Fig. 3a). Using standing dead tree diameters 6 months after the fire (i.e. not including fallen or incinerated trees), pre-fire basal area was at least 13 m^2 ha^{-1} (range 0.3–24.4 m^2 ha^{-1}). Recovery of aboveground live tree biomass was not linearly related to landform index (GLM χ^2_1 = 0.12, P = 0.73; Fig. 3b) although plots with aboveground live tree biomass were all on upper slopes (intermediate values of landform index; non-linear model not fitted because of low sample size).

In the stand of surviving *K. robusta*, 20 stems recovered from burned foliage in the period 0–36 months after the fire, but only three of these stems survived until December 2015.

Regeneration of *K. robusta* has been much greater in this stand than in the randomly-located plots where all adult trees died. In 2015 there were 36 new stems ≥ 1.35 m tall (34 *K. robusta*, one *Coprosma robusta* and one *Leptospermum scoparium*). Including the three stems that survived the fire, these live stems equate to a stem density of 1114 ha^{-1}, a basal area of 0.39 m^2 ha^{-1} and aboveground biomass of 1.83 Mg ha^{-1}.

Sophora and *Clematis*

Thirty of the 40 *S. prostrata* tagged in June 2001 survived until December 2015, equivalent to an annual mortality rate of 2.9% yr^{-1}. Mean width of surviving individuals was 1.2 m (± 0.09 1 SE) with a width growth rate of 8.6 cm yr^{-1} (± 0.69 1SE) (Fig. 3c). Mean height of surviving individuals was 1.2 m (± 0.08 1 SE) with a height growth rate of 8 cm yr^{-1} (± 0.5 1 SE). Maximum width and height of surviving individuals in December 2015 were strongly positively related (GLM, log(height) = 0.04 + 0.61 × width, r^2 = 0.62, P < 0.001). In December 2015, at least one individual bore mature seed pods.

Ten clusters of *Clematis quadribracteolata* resprouts had appeared 1 year after the fire with a mean shoot length of 71 cm (± 6.9 1 SE). Eight of these clusters survived until 3 years after the fire by which time mean shoot length was 76 cm (± 14 1 SE). Mean shoot extension rates in the 3-year
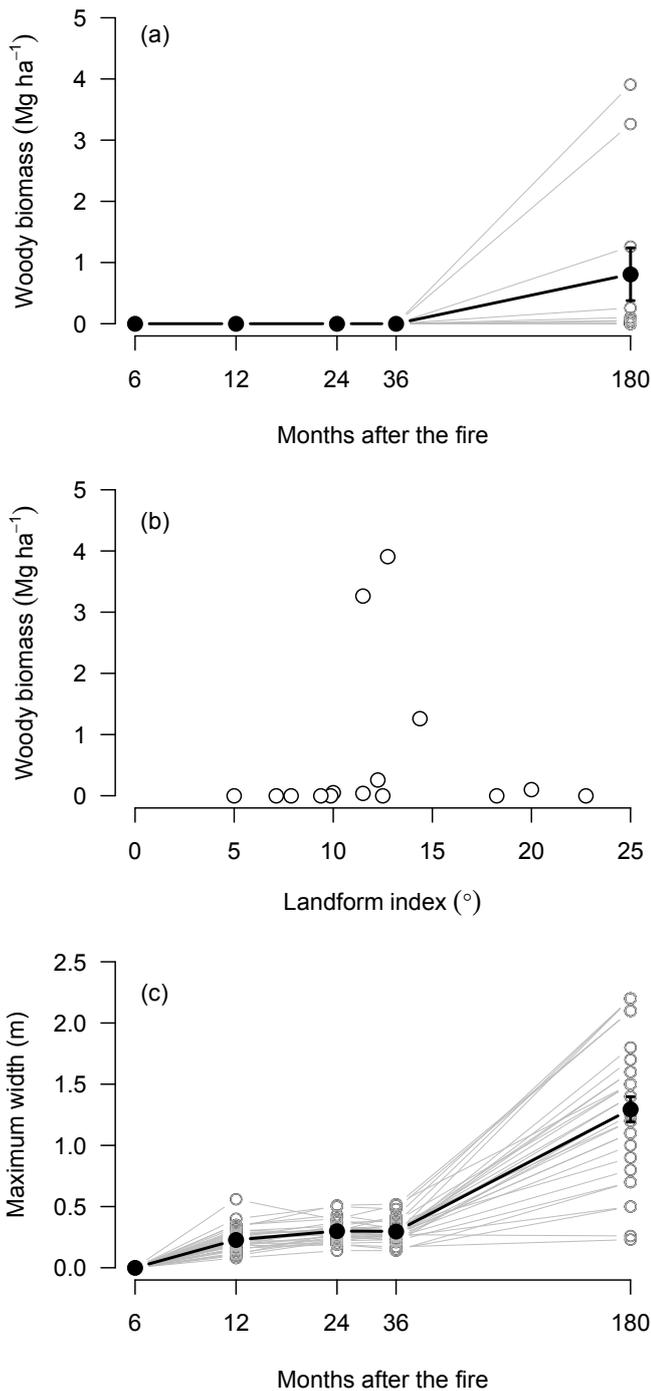
Figure 3. Post-fire vegetation recovery over 15 years in the Wither Hills, Marlborough. (a) Woody biomass. Grey lines are individual plots. Black line is the mean across all plots. Error bars are 1 SE. (b) Woody biomass in 2015 (180 months after the fire) relative to landform index. Each data point is a plot. Low values of landform index are raised topographic positions (e.g. ridges) and high values are depressed positions (e.g. gullies). (c) Recovery of burned *Sophora prostrata* plants (n = 40, 35, 32, 32, 30, at each measurement). Grey lines are individual shrubs and the black line shows the mean across all shrubs. Error bars are 1 SE.

period following the fire was 25 cm yr^{-1} (± 5 1 SE). Flowering and seeding was observed on one individual in 2002 and by 2015, the area was densely covered in a tangle of this species and plants were flowering and fruiting prolifically. Individual marked clusters and shoots could no longer be distinguished.

Discussion

Fire is a significant threat to remnant woody vegetation in dryland production landscapes where competition from non-native grass species and depauperate seed rain constrain opportunities for tree regeneration. In this study, it was at least 3 years before woody biomass began to accumulate and recovery has been slow and spatially restricted. However, this recovery is important because it suggests that oversowing did not stall native woody regeneration entirely. A liane and a small shrub recovered well by resprouting, while regeneration of dominant tree species from seed and tree seedling regeneration was localised around surviving trees and in a few midslope topographic positions. We anticipate that future recovery will be from lateral spread around these foci.

Forest recovery

The post-fire succession is dominated by non-native grasses, particularly *Dactylis glomerata*. Sward-forming non-native grasses prevent native species establishment by blocking light (Sessions & Kelly 2000), smothering seedlings and accumulating a deep litter layer and fibrous root mat that limit seedling root access to the soil (Miller & Wells 2003). The importance of each factor varies with grass species (e.g. short-statured, root mat-forming *Agrostis capillaris* vs tall, litter-accumulating *Dactylis glomerata*), and according to the regeneration niche of the native species (Sessions & Kelly 2000). In our study, forest was lost from the gullies and *D. glomerata* accumulated litter depths in excess of 50 cm in them, sufficient to prevent seedlings accessing the mineral soil, and cast significant shade. Gullies elsewhere often support source populations for reinvasion (Perry et al. 2010) but not in this area. Recovery of the bird-dispersed species recorded in gullies prior to fire (e.g. *Coprosma robusta*, *Pseudopanax arboreus*) is likely to be further impeded by the paucity of surviving individuals to act as perching sites (Albornoz et al. 2013). Restoration plantings in gullies are likely to be necessary to restore these species. Litter depths were less on ridges than in gullies but ridge crests are often more drought-prone than other topographic positions, and this might constrain woody seedling establishment (Ashton & Larson 1996). These limitations may explain why woody biomass only developed on intermediate topographic positions (Fig. 2c).

Dominance by pasture grasses is likely to have occurred in the Wither Hills covenant, regardless of oversowing, but oversowing may have amplified suppression of woody regeneration early in succession. Ledgard and Davis (2004) tested whether the addition of pasture grasses suppressed woody regeneration after fire in native mountain beech (*Fuscospora cliffortioides*, Nothofagaceae) forest, in the eastern South Island (elevation c. 840 m). They found that pasture grasses diminished woody cover (35% in control plots; 15% in oversown plots), suggesting grass oversowing delayed, but did not preclude, woody regeneration. Furthermore, seedling densities of trees and shrubs were equivalent after 18 years (5.6 plants m^{-2} in controls vs 5.9 plants m^{-2} in plots seeded with pasture grasses) so in numerical terms of woody seedlings, the outcomes of

sowing pasture grasses were indistinguishable from not sowing pasture grasses.

At our study site, regeneration of *Kunzea* was limited where no trees survived the fire but abundant around individuals that survived. We suggest that this reflects one or more of three factors. First, the fire was less intense where trees survived and this reduced fire damage to the soil and seed reserves. Second, surviving trees were a source of new seed as many flowered heavily in the summers following the fire (RJH pers. obs.). Lastly, surviving trees provided summer shade and winter shelter to emerging seedlings, and may have depressed grass sward development. We cannot disentangle these factors in our observational study, and experimental studies are needed to understand the relative importance of fire intensity, seed limitation, microhabitat (shade) and competition from sward-forming grasses in determining successional outcomes. Wilson (1994) reported on post-agricultural succession at Hinewai Reserve in Canterbury and noted that while *Kunzea* was unable to establish into ungrazed non-native grass swards, consistent with our observations, other species such as *Muehlenbeckia complexa* (a liane) and *Pteridium esculentum* (a fern) were more competitive in the regeneration phase, and were able to establish into ungrazed pastures of non-native grasses. Based on these observations, we suggest that small-scale adaptive management of grazing or selective herbicides could be a promising tool for expediting *Kunzea* reestablishment, particularly around regeneration foci such as surviving seed trees.

Fire resilience traits in *Sophora* and *Clematis*

Godley (1979) reported that *Sophora prostrata* could sucker and we demonstrate that this suckering habit provides fire resilience. *Sophora prostrata* favours dry open hillsides, terraces and plains (Godley 1979) and while these habitats experienced infrequent fires in the period 7000 BP to 750 BP (Perry et al. 2014), resprouting is unlikely to be a fire-adapted trait in this species because infrequent fire over a period of less than 7000 years would have been insufficient for a fire-specific trait to have evolved. We suggest instead that resprouting is exaptive (i.e. it increases fitness in response to fire, but did not evolve in response to fire; Gould & Lewontin 1979) and part of the divaricating habit that was advantageous during the lengthy and repeated glacials, because it facilitated persistence on periodically-disturbed alluvial river terraces, and recovery from snow damage and herbivory (Bellingham & Sparrow 2000; Bond & Midgley 2001, 2003). We also demonstrate vigorous resprouting in *Clematis quadribracteolata*. This species is widespread throughout central New Zealand, favouring shrublands and forest margins in which fire-specific adaptations would not be expected. Many lianes are deep-rooting to access deep water resources (Wyka et al. 2013) and this extensive belowground investment enables them to survive fire and resprout (Janzen 1975). However, as with *S. prostrata*, we argue that fire is unlikely to be the primary driver of this resprouting trait in *C. quadribracteolata* because of insufficient time for a specific adaptation to have evolved. Nonetheless, both species showed resilience to fire through resprouting and recovery of individuals and populations within 15 years.

Recovery of a native dryland forest understorey

Many short-statured herbaceous forest and shrubland species favour open microsites either beneath a woody canopy or in clearings in woody vegetation and these are particularly vulnerable to extirpation through competition from non-native grasses (Ecroyd & Brockerhoff 2005). Nevertheless, some short-statured herbaceous species have persisted in microrefugia. Three 'hot rock' fern species were recorded (*Cheilanthes sieberi*, *C. distans*, *Pellaea calidirupium*, all Pteridaceae) and *Cheilanthes* spp. were always recorded on 25–50% of plots from 2002 to 2015. These ferns do not compete directly with non-native grasses but persist on small rocky outcrops and dry ridge crests where grass cover is thinner and shorter. Similarly, the ground-creeping vine *Convolvulus waitaha* (Convolvulaceae) and small herb *Drosera auriculata* (Droseraceae) persisted at low abundance.

Conclusion

Longitudinal studies of succession provide valuable case studies for understanding the rate and direction of vegetation change in relation to disturbance types and specific management actions (Bakker et al. 1996). Woody regeneration in the Wither Hills has been spatially restricted and after 15 years, vegetation is still dominated by non-native grasses that were sown to mitigate erosion risk. Given the management imperative to stabilise hill slopes through oversowing and the potential of non-native grasses to slow successional processes of native species, we suggest that experimental manipulations of low intensity grazing and selective herbicides would be informative to test whether modulating competition from grasses can accelerate woody biomass accumulation.

Acknowledgements

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