

Native plant species richness in non-native *Pinus contorta* forest

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Abstract: *Pinus contorta* (lodgepole pine) is invasive in many southern hemisphere countries, having spread extensively from original plantings. It is widely controlled to limit its spread and negative impacts, and is generally assumed to have little value for native plant biodiversity. We surveyed vegetation in two stands of montane wilding *P. contorta* forest, and recorded a subcanopy of more than 50 native plant species from 35 genera, including trees, shrubs, ferns, and orchids. Canopy openness ranged between 5 and 20% and was positively related to native plant species richness at both sites. Native plant species richness was negatively related to *P. contorta* stem density at one site but not the other, where richness was positively related to soil available phosphorus concentrations. A diverse native subcanopy in wilding *P. contorta* forest may represent an important seed source for further native regeneration in invaded areas. *Pinus contorta* control methods that minimise disturbance to the native subcanopy may be prudent if a return to native vegetation is a long-term management goal.

Keywords: canopy openness; *Fuscospora*; wilding pines

Introduction

Invasive trees are recognised as a major problem worldwide (Richardson et al. 2014). In New Zealand, freely regenerating non-native conifers are referred to as wildings (Ledgard 2003), and collectively it is estimated that they have encroached upon 1.3 million ha (Clifford et al. 2013). Of the ten species that currently cause almost all wilding conifer problems in New Zealand (Froude 2011), *P. contorta* is the most widespread and has been estimated to comprise as much as two-thirds of the total wilding area (Ledgard 2001). *Pinus contorta* predominantly invades human-induced, seral grasslands and shrublands (Ledgard 2003; Dehlin et al. 2008). It is considered an environmental weed (sensu Falk-Petersen et al. 2006) because as stands of *P. contorta* coalesce, native grass, herb and shrub species present at establishment are displaced (Ledgard & Paul 2008).

In New Zealand, it is widely assumed that dense *P. contorta* stands have little or no value for native plant biodiversity, but, to our knowledge, this has not been investigated. Studies from North America demonstrate that shade-tolerant species can establish in (native) *P. contorta* forest in the absence of disturbance (Sullivan et al. 2000), with canopy-forming species eventually replacing much of the *P. contorta* if conditions remain suitable (Habeck 1968; Kobe & Coates 1997). Additionally, *P. contorta* establishment within closed canopy *P. contorta* is rare (Johnson et al. 1994), as seedlings require at least 40% full sunlight to grow (Lotan & Perry 1983), and saplings do not persist below 25% full sunlight (Claveau et al. 2002). This suggests that in New Zealand, where native seed sources are available, there is potential for native plant species to persist in or colonise the understorey of *P. contorta* forests, thus representing native biodiversity values. In this study, we set out to describe vegetation beneath *P. contorta* prior to a manipulative experiment investigating native plant responses to *P. contorta* control.

Methods

This study was established in April 2011, in two large stands ('Black Birch' and 'Don Juan') of wilding *P. contorta* in the Kaweka Forest Park, North Island, New Zealand. The Black Birch site (39.30° S, 176.44° E) was located between 1040 and 1080 m a.s.l. on the Black Birch ridge, to the north of Trig A8A8. The Don Juan site (39.34° S, 176.47° E) was located between 880 and 940 m a.s.l., to the north of Trig A3R0. *Pinus contorta* began to spread at these sites in the 1960s following establishment trials designed to reduce soil erosion (Cunningham & Roberts 1970). Remaining native montane (sensu Wardle 1991) forests in this area are dominated by mountain beech (*Fuscospora cliffortioides*) and red beech (*F. fusca*) with occasional podocarp species, including mountain tōtara (*Podocarpus cunninghamii*), and mountain toatoa (*Phyllocladus alpinus*). Extensive tracts (>5 ha) of native forest occur within 400 m of both sites, and smaller patches (<1 ha) of native trees and shrubs are scattered throughout. The pattern of distribution of these species reflects the highly modified nature of the area after several hundred years of sporadic burning (Rogers 1994) and attempted conversion to grazing (Elder 1941).

Twelve locations were established in 7–14 m-high *P. contorta* forest at both sites. At each location, a patch of trees 30 m in diameter was marked out, giving a total of 24 patches. Each patch was a minimum of 20 m from any forest edge or tree fall gap, and a minimum of 20 m from any other patch. Four 2 × 2 m plots were established in each patch, 2 m from the patch centre on north, east, south and west bearings, giving a total of 96 plots. In the 2 × 2 m plots, vegetation was assessed according to the Recce method (Hurst & Allen 2007). Species were assessed individually, and each plot was also scored for overall native vegetation cover. Seedlings were generally only included if they were beyond the cotyledon stage. However, *P. contorta* seedlings at the cotyledon stage were included, because they were easily identifiable and their

presence, even if ephemeral, was germane to our study. For each plot the number of native species (native richness) was calculated.

Canopy openness was used as an index of light availability. To measure this we took photographs of the forest canopy from approximately 1 m above the middle of each plot using a digital SLR camera (Canon EOS 50D, Canon Inc.) and 4.5 mm hemispherical (fisheye) lens (Sigma EX DC, Sigma Corporation of America, New York, USA). Photographs were then digitally analysed using the HemiView image processing software (HemiView Forest Canopy Analysis System v8, Delta-T Devices, Cambridge, UK).

All *P. contorta* stems within a 5-m radius of the patch centre were counted (stem density) and their dbh (diameter at breast height of 1.3 m) was measured. Within the 5-m radius, 10 soil samples were taken in a 'Z' pattern. Surface litter was excluded and samples were taken from the top 10 cm of soil using a 2.5 cm diameter soil corer. Patch samples were pooled and analysed by R.J. Hill Laboratories Limited for the organic carbon, total nitrogen, carbon to nitrogen ratio (C:N) and available phosphorus (Olsen P) concentrations using standard tests. We compared soil characteristics of the two sites using Welch two sample t-tests in statistical software package 'R' (version 2.15.3) (R Core Team 2013).

We used the package 'lme4' (Bates et al. 2012) in 'R' for analyses. We used mixed effects models with Poisson error structures to model the response of native species richness to factors we considered most likely to be important. Plot and patch were included as nested random effects to account for spatial clustering. Other covariates assessed for inclusion in the model were dbh, canopy openness, stems per ha, C:N ratio and Olsen P. Akaike's Information Criterion (AICc) was used to rank models (package 'AICmodavg') (Mazerolle 2013) within each site, with the lowest AICc ranked first. We calculated the evidence ratio between first and second ranked models, the marginal and conditional R^2 (Nakagawa & Schielzeth 2013) and weight of the highest ranked model, and the ranking of the null model including only the random effects.

Results

A total of 49 species, from 35 native plant genera, was recorded (Table 1). More than half (55%) of the native species were woody trees or shrubs, 20% were ground ferns, and the remaining 25% were herbs, orchids, grasses, and vines. Native plants were predominantly found in lower tiers, but 12 plots contained some native cover greater than 2 m tall (Table 1). *Griselinia littoralis* and *Gaultheria antipoda* were common at both sites but some species common at Black Birch were rare or absent at Don Juan (e.g. *Coprosma dumosa*, *Phyllocladus alpinus*) and vice versa (e.g. *C. grandifolia*). Beech species were found in six plots, but all were less than 1 m tall.

Pinus contorta was the dominant component of the vegetation, but saplings and seedlings of *P. contorta* were scarce, with only four seedlings recorded, all of which were at the cotyledon stage (Fig. 1). *Pinus contorta* stem density ranged from 2299 to 15 915 live stems per ha and average dbh ranged from 11.5 to 32.9 cm per patch. Counting annual rings on a subset of these trees that were later felled suggested typical ages of between 30 and 40 years. Canopy openness was variable, and ranged from 5.0 to 20% (Fig. 2). The most open sites were those with small mean diameter *P. contorta* (Fig. 2). The soils beneath the two sites varied significantly: soils from Don Juan had much greater available phosphorus, but contained less organic carbon and total nitrogen than those at Black Birch (Table 2).

The density of *P. contorta* stems, extent of canopy openness, and their interaction were important predictors of native species richness at Black Birch, with the greatest richness found under relatively widely-spaced trees with open canopies (Table 3). The best model (stems per ha, canopy openness and their interaction) had a marginal R^2 of 0.52, conditional R^2 of 0.54 and was 96 times more likely than the second-ranked model to be the best model in the candidate set (Table 2). At Don Juan, the greatest native species richness was associated with high levels of Olsen P under open canopies. The best model (canopy openness and Olsen P) had a marginal R^2 of

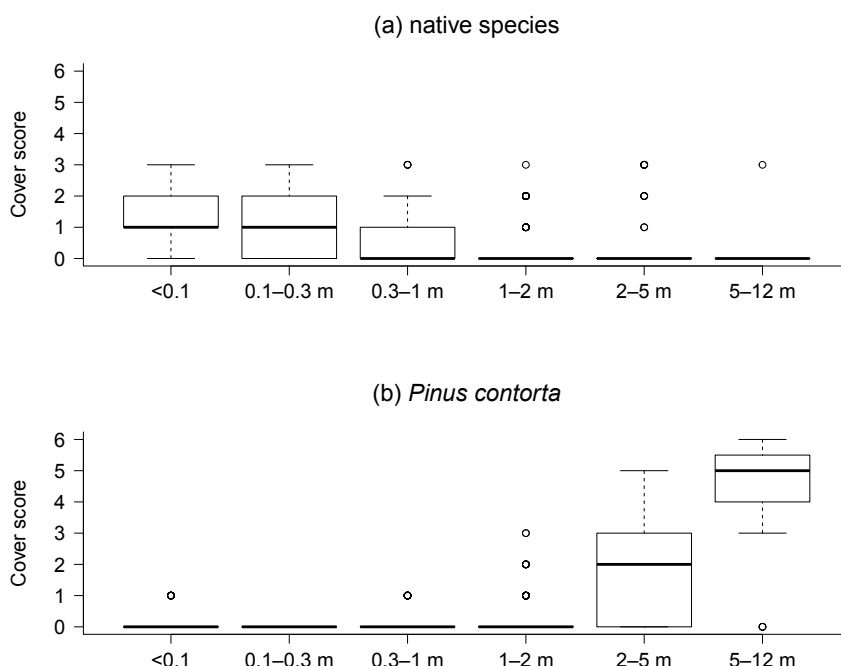


Figure 1. Cover of (a) native species combined and (b) *Pinus contorta*. Each box plot represents the average cover score by height tier across all plots. Cover scores represent % cover of live foliage in each height tier: 1 = <1%, 2 = 1–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–100%.

Table 1. Plant species recorded in *Pinus contorta* forest. Values indicate the number of plots (out of a potential 96) in which each species was recorded, both overall (Total plots) and for each site (Black Birch and Don Juan) separately. Bracketed values are number of plots where plants were recorded in tiers above 2 m.

| Growth form | Species | Total plots | Number of plots per site | |
|---------------|---|-------------|--------------------------|----------|
| | | | Black Birch | Don Juan |
| trees | | | | |
| | <i>Carpodetus serratus</i> | 2 | 0 | 2 |
| | <i>Coprosma grandifolia</i> | 31 | 6 | 25 (1) |
| | <i>Coprosma robusta</i> | 11 | 1 | 10 (1) |
| | <i>Fuscospora cliffortioides</i> | 1 | 1 | 0 |
| | <i>Fuscospora fusca</i> | 5 | 2 | 3 |
| | <i>Griselinia littoralis</i> | 27 | 15 | 12 |
| | <i>Leptospermum scoparium</i> | 10 | 6 (4) | 4 (2) |
| | <i>Phyllocladus alpinus</i> | 20 | 20 (2) | 0 |
| | <i>Pinus contorta</i> * | 96 | 48 (48) | 48 (48) |
| | <i>Podocarpus cunninghamii</i> | 4 | 4 | 0 |
| | <i>Pseudopanax colensoi</i> | 13 | 13 | 0 |
| shrubs | | | | |
| | <i>Coprosma colensoi</i> | 1 | 1 | 0 |
| | <i>Coprosma dumosa</i> | 42 | 40 | 2 |
| | <i>Coprosma foetidissima</i> | 3 | 3 | 0 |
| | <i>Coprosma linariifolia</i> | 8 | 8 | 0 |
| | <i>Coprosma microcarpa</i> | 1 | 1 | 0 |
| | <i>Coprosma propinqua</i> | 6 | 6 | 0 |
| | <i>Coriaria arborea</i> | 2 | 0 | 2 (2) |
| | <i>Gaultheria antipoda</i> | 23 | 10 | 13 |
| | <i>Gaultheria depressa</i> | 1 | 1 | 0 |
| | <i>Helichrysum lanceolatum</i> | 2 | 1 | 1 |
| | <i>Leptecophylla juniperina</i> | 12 | 6 | 6 |
| | <i>Leucopogon fasciculatus</i> | 6 | 6 | 0 |
| | <i>Leucopogon fraseri</i> | 1 | 1 | 0 |
| | <i>Lupinus arboreus</i> * | 4 | 0 | 4 |
| | <i>Myrsine divaricata</i> | 11 | 11 | 0 |
| | <i>Olearia arborescens</i> | 15 | 2 | 13 |
| | <i>Olearia nummulariifolia</i> | 2 | 2 | 0 |
| | <i>Pseudowintera colorata</i> | 5 | 5 | 0 |
| lianas | | | | |
| | <i>Clematis</i> sp. | 4 | 1 | 3 |
| dicot herbs | | | | |
| | <i>Celmisia spectabilis</i> × <i>gracilentata</i> | 2 | 2 | 0 |
| | <i>Lagenophora strangulata</i> | 10 | 9 | 1 |
| | <i>Nertera ciliata</i> | 3 | 3 | 0 |
| | <i>Nertera villosa</i> | 9 | 9 | 0 |
| | <i>Ranunculus reflexus</i> | 2 | 0 | 2 |
| monocot herbs | | | | |
| | <i>Astelia fragrans</i> | 6 | 6 | 0 |
| | <i>Chiloglottis cornuta</i> | 10 | 10 | 0 |
| | <i>Phormium cookianum</i> | 5 | 5 | 0 |
| | <i>Pterostylis</i> sp. | 1 | 1 | 0 |
| | <i>Uncinia</i> sp. | 1 | 1 | 0 |
| grasses | | | | |
| | <i>Microlaena stipoides</i> | 11 | 9 | 2 |
| ferns | | | | |
| | <i>Asplenium flaccidum</i> | 5 | 0 | 5 |
| | <i>Blechnum discolor</i> | 1 | 0 | 1 |
| | <i>Blechnum fluviatile</i> | 1 | 1 | 0 |
| | <i>Blechnum penna-marina</i> | 5 | 1 | 4 |
| | <i>Blechnum procerum</i> | 5 | 1 | 4 |
| | <i>Hymenophyllum flabellatum</i> | 8 | 5 | 3 |
| | <i>Microsorium pustulatum</i> | 7 | 0 | 7 |
| | <i>Notogrammitis billardierei</i> | 5 | 0 | 5 |
| | <i>Polystichum vestitum</i> | 1 | 0 | 1 |
| | <i>Pyrrosia eleagnifolia</i> | 1 | 0 | 1 |

*non-native species

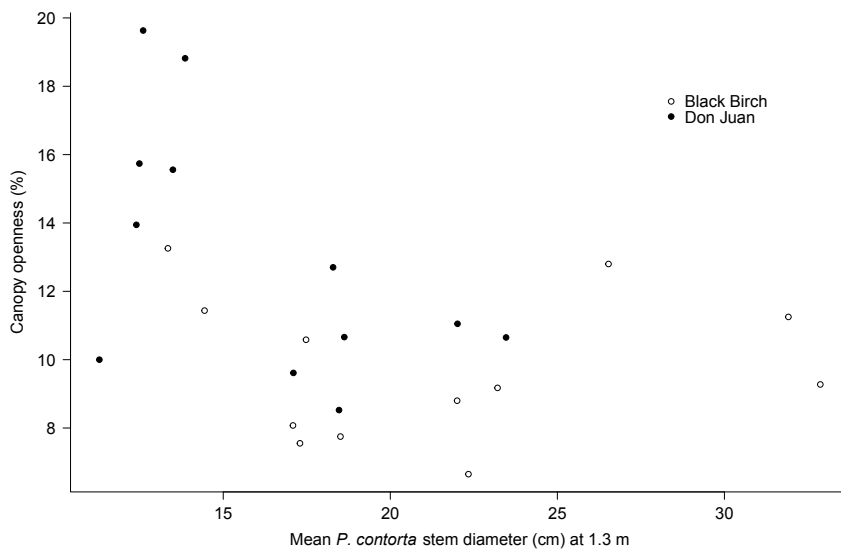


Figure 2. Canopy openness (%) and mean *P. contorta* stem diameter at 24 patches in the Kaweka Forest Park.

Table 2. Estimates of mean (and standard error) of soil parameters and significance resulting from Welch two-sample *t* test to investigate differences between sites.

| | Black Birch | Don Juan | <i>t</i> | df | <i>P</i> |
|--------------------------------|---------------|---------------|----------|-------|----------|
| Olsen P (mg kg ⁻¹) | 0.85 (0.046) | 3.36 (0.267) | -4.47 | 11.64 | 0.0008 |
| Organic C (%) | 4.09 (0.215) | 2.31 (0.088) | 3.68 | 14.59 | 0.0023 |
| Total N (%) | 0.16 (0.007) | 0.08 (0.002) | 5.09 | 13.14 | 0.0002 |
| C:N ratio | 25.17 (0.397) | 28.97 (0.764) | -2.14 | 16.53 | 0.0480 |

Table 3. Candidate models for predictors of native species richness under *Pinus contorta* canopy at Black Birch and Don Juan sites. Openness = canopy openness, Stems = stems ha⁻¹. Models are ranked on AIC_c (Akaike Information Criterion adjusted for small sample size). *k* = number of parameters, ΔAIC_c shows AIC_c relative to the best model, AIC_c *w_i* shows the weight (relative strength) of support for each model, Cum. *w* indicates cumulative weight of models in the candidate set, LL = log likelihood.

Black Birch

| Models of native species richness | <i>k</i> | AIC _c | ΔAIC _c | <i>w_i</i> | Cum. <i>w</i> | LL |
|-------------------------------------|----------|------------------|-------------------|----------------------|---------------|---------|
| Stems + Openness + Stems × Openness | 7 | 76.798 | 0.000 | 0.966 | 0.966 | -29.999 |
| dbh + Openness | 6 | 85.925 | 9.128 | 0.010 | 0.976 | -35.938 |
| Openness | 5 | 86.471 | 9.673 | 0.008 | 0.984 | -37.521 |
| dbh + Openness + dbh × Openness | 7 | 87.086 | 10.288 | 0.006 | 0.989 | -35.143 |
| Stems + Openness | 6 | 87.639 | 10.841 | 0.004 | 0.993 | -36.795 |
| Openness + C:N | 6 | 88.233 | 11.435 | 0.003 | 0.997 | -37.092 |
| Openness + Olsen P | 6 | 88.589 | 11.791 | 0.003 | 0.999 | -37.270 |
| dbh | 5 | 93.480 | 16.682 | 0.000 | 0.999 | -41.026 |
| Null model (random effects only) | 4 | 93.502 | 16.704 | 0.000 | 1.000 | -42.286 |
| dbh + C:N | 6 | 94.643 | 17.845 | 0.000 | 1.000 | -40.297 |
| Stems | 5 | 94.847 | 18.049 | 0.000 | 1.000 | -41.709 |
| Stems + C:N | 6 | 96.690 | 19.892 | 0.000 | 1.000 | -41.321 |

Don Juan

| Models of native species richness | <i>k</i> | AIC _c | ΔAIC _c | <i>w_i</i> | Cum. <i>w</i> | LL |
|-------------------------------------|----------|------------------|-------------------|----------------------|---------------|---------|
| Openness + Olsen P | 6 | 81.387 | 0.000 | 0.850 | 0.850 | -33.669 |
| Openness | 5 | 87.514 | 6.127 | 0.040 | 0.890 | -38.043 |
| Openness + C:N | 6 | 88.014 | 6.627 | 0.031 | 0.921 | -36.982 |
| dbh + Openness | 6 | 88.026 | 6.639 | 0.031 | 0.951 | -36.988 |
| Stems + Openness | 6 | 88.842 | 7.456 | 0.020 | 0.972 | -37.397 |
| dbh + Openness + dbh × Openness | 7 | 90.312 | 8.925 | 0.010 | 0.982 | -36.756 |
| dbh | 5 | 90.496 | 9.109 | 0.009 | 0.991 | -39.534 |
| Stems + Openness + Stems × Openness | 7 | 91.580 | 10.194 | 0.005 | 0.996 | -37.390 |
| dbh + C:N | 6 | 92.983 | 11.596 | 0.003 | 0.998 | -39.467 |
| Null model (random effects only) | 4 | 95.537 | 14.151 | 0.001 | 0.999 | -43.304 |
| Stems + C:N | 6 | 96.183 | 14.796 | 0.001 | 1.000 | -41.067 |
| Stems | 5 | 97.006 | 15.619 | 0.000 | 1.000 | -42.789 |

0.37, conditional R^2 of 0.41 and was 21.4 times more likely than the second ranked model to be the best model in the candidate set.

Discussion

We found a diverse assemblage of native species beneath the *P. contorta* canopy, including orchids, ferns, shrubs and trees. Some differences in the species present at each site could be due to differences in altitude, e.g. *Coprosma grandifolia* was detected at the lower altitude site only. Given that this is a point-in-time study, we cannot determine whether commonly occurring native plant species have persisted through or colonised during *P. contorta* establishment, but it seems likely that both scenarios have occurred. *Leptospermum scoparium* above 2 m have probably persisted since *P. contorta* establishment, numerous dead *L. scoparium* stems suggests that in some plots this species was formerly more abundant. Conversely, the presence of seedlings and small saplings (<2 m tall) of *Fuscospora fusca*, *Griselinia littoralis* and *Phyllocladus alpinus* strongly suggest that they are much younger than the *P. contorta* canopy and that there is at least some potential for native species to colonise wilding *P. contorta* forests in New Zealand.

Despite abundant seed, *P. contorta* seedlings and saplings were almost completely absent in this study. This is consistent with previous findings that *P. contorta* is unable to regenerate beneath a closed canopy (Johnson et al. 1994). As we observed several cotyledon stage seedlings, it appears that seeds can germinate under a closed canopy, but seedlings fail to establish.

Our results demonstrate a positive correlation between *P. contorta* canopy openness and native species richness at both sites. However, it is difficult to establish whether this is the result of increasing canopy openness as stands age, incomplete canopy closure, or both. Canopy closure of *P. contorta* in Wyoming, U.S.A., typically peaks at 40 to 45 years; canopies then slowly become more open over the next 80 years (Long & Smith 1992). As *P. contorta* stands age, they tend to become more structurally complex, with greater variability of canopy cover (Sampson & Smith 1993). Several studies of the understory in *P. radiata* plantation forests in New Zealand have demonstrated a positive correlation between native plant species richness and stand age (Allen et al. 1995; Ogden et al. 1997; Brockerhoff et al. 2003), and it has been suggested that this can be partly attributed to a more favourable light environment in older stands (Brockerhoff et al. 2008). In our study, native species richness was highest under widely-spaced trees with open canopies at the Black Birch site. However, at Don Juan the highest levels of canopy openness were associated with small diameter *P. contorta*, which suggests incomplete canopy closure. The trees in our study are still relatively young; *P. contorta* can live for at least 350 years (Smithwick et al. 2005). It is unclear if the canopy of wilding *P. contorta* stands in New Zealand will become more open as stands age beyond 40 years, but this seems likely.

The reasons behind the much higher available phosphorus concentrations in soils at Don Juan remain unclear, but it is an important predictor of native plant diversity at this site. High levels of available phosphorus may have resulted from physical processes or biotic processes related to the encroachment of *P. contorta* (Dickie et al. 2014) or both.

Pinus contorta is one of the most light-demanding conifers (Coates 2000). It is generally regarded as a pioneer species

(Long & Smith 1990) and can be gradually replaced by more shade tolerant forest species in its native range (Habeck 1968). Our results demonstrate that native species can survive in *P. contorta* forest in New Zealand, but it is unclear whether they could eventually replace the *P. contorta*. Beech seedlings can survive deep shading (Wardle 1970) and are certainly more shade tolerant than *P. contorta*. Planted beech seedlings can survive beneath *P. contorta* canopy (Dehlin et al. 2008) and beech saplings up to 3 m tall have been observed in 60-year-old *P. contorta* stands (Ledgard & Paul 2008). However, the presence and possibly greater shade tolerance of some native species is no guarantee that they will eventually dominate; under certain conditions, establishment of other species under *P. contorta* canopies may be insignificant until after 200 years (Johnson et al. 1994) or not occur at all (Despain 1983). It may be possible to facilitate establishment of beech and other native species in *P. contorta* stands, for example by sowing seed, or controlling *P. contorta* in a way that promotes native seedling establishment but inhibits *P. contorta* establishment. Future research will address these possibilities.

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