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Multiple competitive mechanisms underlie the effects of a strong invader on early- to late-seral tree seedlings

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Summary

1. Certain non-native invaders reduce the species diversity and alter the structure of natural communities by displacing native species with differing life histories, successional roles or resource requirements. Few studies have tested the potential for these 'strong invaders' to exert multiple mechanisms of control on natives that differ in these traits.

2. We assessed the mechanisms by which bohemian knotweed (*Polygonum* × *bohemicum*) regulates seedling growth and survival among early-, mid- and late-seral tree species in a riparian forest ecosystem in western North America. We used general linear mixed models to compare seedling performance (survival, height and diameter growth, biomass allocation and ectomycorrhizal colonization of root systems) over two growing seasons in paired experimental plots from which knotweed was either removed or retained (controls). Seedling performance was assessed relative to the effects of knotweed on light and soil resources and the traits of the native species.

3. Results from paired *t*-tests suggest that knotweed had a significant effect on light availability (> 85% reduction), but small, mostly non-significant effects on measured soil properties. Knotweed imposed strong controls on growth and survival of all three tree species. The apparent mechanisms of interaction varied in a manner consistent with species' ecophysiologies. Reduced survival of early- and mid-seral species was correlated with light limitation beneath knotweed (≤ 7% of ambient levels): light transmittance was significantly higher (79%) above surviving seedlings. Knotweed also exerted strong controls on the late-seral species, reducing survival by 24% and height and diameter growth by 91–122% and 37–55%. These effects were not correlated with reductions in light. Instead, in the presence of knotweed, ectomycorrhizal colonization was significantly reduced (64%) and root/shoot ratio was significantly increased, suggesting a disruption of soil mutualisms.

4. *Synthesis.* We demonstrate that strong invaders can displace co-occurring native species through multiple mechanisms that are consistent with the functional traits of native species. To our knowledge, this is the first study to relate community-level impacts of an invader to the combined effects of resource exploitation and interference of below-ground mutualisms. Where invaders have the ability to displace early- to late-seral dominants, the consequences for community structure and ecosystem functioning can be profound.

Key-words: competition, ectomycorrhizal fungi, interference, invasion ecology, mycorrhizae, native–alien interactions, riparian forest, species' interactions, tree seedlings

Introduction

Non-native invasive plants that develop dense monotypic stands can dramatically alter the structure and dynamics of native plant communities (Parker *et al.* 1999; Mack *et al.* 2000; Byers *et al.* 2002). The mechanisms by which invasive plants displace natives are often poorly understood (Levine *et al.* 2003). Certain 'strong' invaders (sensu Ortega & Pearson 2005) or 'transformers' (sensu Richardson *et al.* 2000; Pyšek *et al.* 2004) may reduce community diversity because they can displace native species with distinctly different life histories or resource requirements. However, little is known about the mechanisms that underlie the interactions of strong invaders (or transformers) with multiple coexisting species. The majority of studies consider interactions with individual native species or treat all native species as belonging to a common group (Parker *et al.* 1999; Ortega & Pearson 2005). In contrast, few, if any, studies have explicitly tested the potential for

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invaders to exert different mechanisms of control on species (or groups of species) with differing functional traits (Ortega & Pearson 2005). Elucidating the diversity of processes by which invasives can displace multiple native species within a community is fundamental to predicting the broader impacts of invasions and to mitigating or managing their effects (Levine *et al*. 2003; MacDougall & Turkington 2005; Reinhart *et al*. 2006; Farrer & Goldberg 2009).

Competition or interference from invasives can take multiple forms: reductions in light or soil resources (Kourtev, Ehrenfeld & Haggblom 2002; Ehrenfeld 2003; Reinhart *et al*. 2006), allelopathic interference (Bais *et al*. 2003) and disruption of mycorrhizal associations that enhance resource uptake (Marler, Zabinski & Callaway 1999; Callaway *et al*. 2008). Natives with differing life histories or resource requirements may vary in their sensitivities to the changes imposed by invading species (Chapin *et al*. 1987; Tilman 1990; Grime 2002; Ortega & Pearson 2005). For example, early- and late-successional species have inherently different resource requirements, with early-seral species characterized as sun adapted and late-seral species as shade adapted (Bazzaz 1979; Tilman 1988). Thus, whereas competition for light may be an important mechanism of interference in early successional species, late-seral species should be more sensitive to changes in below-ground resources.

When faced with competition for resources, species may adjust allocation of biomass to resource-acquiring structures depending on the nature of resource limitation or other constraints (Bloom, Chapin & Mooney 1985; Chapin *et al*. 1987; Callaway, Pennings & Richards 2003). Plants may allocate more biomass to roots and rhizomes when soil nutrients are limiting (Gedroc, McConnaughay & Coleman 1996; Hodge 2004) or to avoid allelochemical influences (Ridenour & Callaway 2001). Allocational plasticity may thus contribute to differential growth and survival in the face of invasions (D'Antonio & Mahall 1991; D'Antonio *et al*. 1998). An understanding of the interplay between invasion-induced resource changes, native plant strategies, and competitive outcomes is essential for differentiating among the mechanisms that underlie the displacement of natives by invasives.

In this study, we investigate the potential mechanisms by which a notorious strong invader – bohemian knotweed (*Polygonum* × *bohemicum*) – regulates the growth and survival of native tree seedlings in riparian forests of the Pacific Northwest, USA. Knotweed is an herbaceous perennial that invades low-elevation river corridors and tributary channels throughout North America and Europe, where it can form tall, dense stands that are difficult to eradicate (Bailey & Wisskirchen 2006; Barney 2006; Hagen & Dunwiddie 2008; Urgenson, Reichard & Halpern 2009; Holman, Carey & Dunwiddie 2010). Considered among the world's most invasive plants (Lowe, Browne & Boudjelas 2000; Bailey 2003), knotweed possesses a diversity of traits that may reduce establishment and survival of native tree species in heavily invaded sites. These include dense canopy cover (Siemens & Blossey 2007); allelopathic, antifungal, and antimicrobial chemical properties (Inoue *et al*. 1992; Beerling, Bailey & Conolly 1994; Konstantinidou-Doltsinis & Schmit 1998; Kumagai *et al*. 2005; Weston, Barney & DiTommaso 2005; Vrchotová & Šerá 2008; Murrell *et al*. 2011); an extensive rhizome system (Smith *et al*. 2007); and the ability to compete for and retain soil nutrients (Price, Gamble & Williams 2001; Urgenson, Reichard & Halpern 2009).

Knotweed exhibits wide ecological amplitude along riparian corridors in the Pacific Northwest. It commonly occurs as a pioneer on recent alluvial deposits, but also as an understory dominant in deciduous floodplain forests. In both habitats, it appears to limit recruitment of the tree species that dominate the regeneration pool (Urgenson, Reichard & Halpern 2009): early-seral, N-fixing, *Alnus rubra*, on primary successional surfaces; and mid- and late-seral conifers, *Picea sitchensis* and *Tsuga heterophylla*, under established forest canopies. The co-occurrence of species with contrasting life-history strategies and resource requirements (shade intolerant vs. tolerant; N-fixing vs. N-limited) (Fonda 1974; Minore 1979; Van Pelt *et al*. 2006) provides an ideal system for exploring the diversity of mechanisms by which a strong invader can influence the growth and survival of native species. In addition, as the primary structural elements of these forests, *Alnus*, *Picea* and *Tsuga* play critical functional roles in both terrestrial and adjacent aquatic habitats – regulating microclimate, stabilizing stream banks and water flow, and providing energy and nutrients to soil and aquatic food webs (Fetherston, Naiman & Bilby 1995; Naiman, Bilby & Bisson 2000). The nature of interaction with knotweed – particularly during the establishment phase – has important implications for the conservation and restoration of these riparian systems.

Planting of seedlings is a common method of reintroducing trees to riparian forest ecosystems during restoration (Sweeney, Czapka & Yerkes 2002; Pollock *et al*. 2005; Keeton 2007). To explore the potential mechanisms of interaction with knotweed, we transplanted seedlings of each species into replicate paired plots from which knotweed was experimentally removed or retained along a highly invaded riparian corridor on the western Olympic Peninsula (Washington). To quantify the effects of knotweed on the physical/resource environment, we measured understory light transmittance and soil physical and chemical properties. We assessed the effects of knotweed on seedling survival, diameter and height growth, biomass allocation to shoots and root systems, and ectomycorrhizal colonization of root tips after two growing seasons. We inferred the mechanisms of interaction from effects on performance and how these related to light and soil resources in the presence or absence of knotweed.

We addressed the following questions: (i) What are the effects of knotweed on light transmittance and soil physical and chemical properties? (ii) Does knotweed invasion alter native tree seedling growth, survival, biomass allocation or mycorrhizal colonization? (iii) Do tree species differ in these measures of performance in the presence of knotweed? (iv) Are patterns of performance consistent with the effects of knotweed on light and soil resources and the life histories and resource requirements of early- to late-seral tree species? We hypothesized that knotweed would differentially affect native species in a manner consistent with species' functional traits. Specifically, we expected early-seral species to be more sensitive to changes in light associated with the presence of knotweed and late-seral species to be more sensitive to changes in below-ground resources.

Materials and methods

JAPANESE KNOTWEEDS S.L.

Japanese knotweeds *s.l.* are rhizomatous perennials that were introduced to Europe and North America from Southeast Asia as horticultural species in the late 19th century. They have since become persistent invaders of riparian areas, roadsides and other disturbed habitats throughout their adventive range (Beerling, Bailey & Conolly 1994; Barney 2006; Bailey, Bímová & Mandák 2007). The primary invasive taxa include giant knotweed (*Polygonum sachalinense* F. Schmidt ex Maxim), Japanese knotweed (*Polygonum cuspidatum* Sieb. & Zucc.) and their hybrid, bohemian knotweed (*P.* × *bohemicum* J. Chrtek & Chrtková). The taxonomy is subject to debate, and some authors place these species in the genera *Fallopia* or *Reynoutria*. *Polygonum* is the most common usage in western North America. Morphologically, the plants in our study area resemble *P.* × *bohemicum,* the most abundant taxon in the Pacific Northwest (Zika & Jacobson 2003). It results exclusively from the hybridization of *P. cuspidatum* and *P. sachalinense* in their sympatric introduced ranges. Plants from Europe exhibit advanced generative capacity, higher levels of genetic variation, greater resistance to herbicide control (Bímová, Mandák & Pyšek 2001) and stronger competitive ability in *P.* × *bohemicum* compared with its progenitors, suggestive of hybrid vigour.

The phenological, morphological and chemical properties of knotweed appear to play a role in its successful invasions. It is a large herb often reaching 3 m in height, with hollow ligneous stems and broad heart-shaped leaves that can create a dense and continuous canopy. Japanese knotweeds are early-seral species in their native habitats and are well suited to the colonization of disturbed sites (Seiger 1984). The species emerges early in the growing season and growth increments can reach 8 cm day^{-1} in full sunlight (Siemens & Blossey 2007). Knotweeds can produce dense and spreading rhizome systems that extend 7 m from a source plant (Child & Wade 2000), potentially monopolizing soil water and mineral nutrients. Their bamboo-like ligneous stems are slow to decompose and can form a thick litter layer that may affect the performance of others species (Beerling, Bailey & Conolly 1994). Knotweeds also produce potent secondary compounds that may contribute to allelopathic or antifungal effects (Inoue *et al.* 1992; Beerling, Bailey & Conolly 1994; Weston, Barney & DiTommaso 2005; Vrchotová & Šerá 2008; Murrell *et al.* 2011).

Knotweed reproduces primarily through vegetative means (rhizome or stem fragments) in its introduced range (Pyšek *et al.* 2003). However, generative reproduction may play a larger role in dispersal than previously assumed (Bailey, Bímová & Mandák 2007; Gammon *et al.* 2007; Tiebre *et al.* 2007; Grimsby & Kesseli 2010). Once introduced, knotweed can spread rapidly through the riparian zone as flood waters transport rhizome fragments and redistribute them downstream (Bímová, Mandák & Pyšek 2001).

NATIVE TREE SEEDLINGS

Three native tree species were tested: *Alnus rubra* (red alder), *Picea sitchensis* (Sitka spruce) and *Tsuga heterophylla* (western hemlock). All are common in the study area, but play different successional roles and have differing resources requirements (Fonda 1974; Minore 1979; Van Pelt *et al.* 2006; Naiman *et al.* 2010). *Alnus* is an early-seral, shade-intolerant deciduous species that preferentially establishes on mineral substrates. It fixes atmospheric N through a symbiosis with the bacterium, *Frankia*; thus, it is relatively insensitive to variation in soil nitrogen (Hibbs, DeBell & Tarrant 1994). *Picea* is a mid-seral conifer that is moderately tolerant of shade and soil nutrient limitations. *Tsuga* is a late-seral conifer that is highly tolerant of shade, but more sensitive to below-ground competition (Christy 1986).

STUDY SITE

The experiment was conducted along the Dickey River (47°57′ N, 124°33′ W), a tributary of the lower Quillayute River on the west coast of the Olympic Peninsula (Washington, USA). The Dickey enters the Quillayute River *c.* 1.6 km from its estuary at the Pacific Ocean. Climate is characterized by warm summers and mild winters with consistently high relative humidity and rainfall. Annual precipitation averages 260 cm, with *c.* 25% falling between April and September; annual snowfall averages 38 cm. Average monthly maximum and minimum temperatures are 20.5 °C in August and 1.5 °C in December–January (climate-station data from nearby Quillayute Airport; 5.5 m elevation; 1996–2007, Western Regional Climate Center).

The Dickey River is a low gradient channel with riparian soils that are very deep, well drained, silt loams (Halloin 1987). The surrounding vegetation lies within the *Picea-Tsuga* forest zone (Franklin & Dyrness 1988). Flooding disturbance is a key determinant of community structure in these riparian forests. Fresh alluvial substrates are initially colonized by fast-growing deciduous trees, primarily *Alnus* (Fonda 1974; Van Pelt *et al.* 2006). *Picea* establishes subsequently and, barring repeated disturbance, *Tsuga* is able to colonize slowly. Common shrub species include *Acer circinatum*, *Rubus spectabilis* and *Sambucus racemosa,* and common understory herbs include *Polystichum munitum*, *Oxalis oregana* and *Athyrium filix-femina*. Knotweed was the dominant invasive species at the time of this study. Nomenclature follows Hitchcock & Cronquist (1973).

The study area begins *c.* 6 river km above the Dickey's confluence and extends for *c.* 5 river km. Knotweed was introduced to the Dickey from a homestead where it was planted as an ornamental. The Quileute tribe initiated the Dickey River knotweed removal programme in 2003 to enhance tree regeneration and improve in-stream fish habitat (Geyer 2004).

EXPERIMENTAL DESIGN

We used a paired removal/non-removal experiment to assess the influences of knotweed. An alternative design, pairing sites with and without knotweed, was not feasible because there were no areas lacking knotweed with comparable habitat characteristics (flood disturbance, soils, and overstorey vegetation) to those with knotweed. Nine experimental blocks were established between June and September 2006 in areas of dense knotweed invasion adjacent to the river channel (0–10 m from the ordinary high-water mark). Each block was 21 × 10 m (with the long axis parallel to the stream channel), placed in a forest patch with visually homogenous overstorey (canopy cover and composition) and geomorphology (slope and height above channel). Within each block, a knotweed removal treatment, knotweed (−), was randomly assigned to one half of each block and knotweed was left intact in the other half, knotweed (+). A 1-m buffer (in which knotweed was removed) was maintained between experimental units (plots). Knotweed was removed by a Quileute Natural Resources crew using standard methods: foliage was sprayed with a glyphosate-based herbicide two to three times between June and September 2006. Although rhizome systems were not removed (to minimize soil disturbance), they were largely killed by the application of glyphosate, as evident by limited resprouting the following growing season. Glyphosate has a soil half-life of 24 days in sandy forest soils (Roy *et al.* 1989) and thus would have minimal effect on seedlings transplanted the following growing season. During the second growing season, herbicide was painted directly onto the leaves of any re-emerging stems to avoid non-target effects.

In April 2007, we transplanted 10 seedlings of each tree species into each plot (10 seedlings × 3 species × 2 plots/blocks × 9 blocks; 540 seedlings in total). Seedlings were spaced 0.5 m apart, ≥1.5 m from the back edge of each plot. Seedlings were obtained from a local nursery (Silvaseed Co., Roy, WA, USA) and transplanted either as P + 0 plugs (1-year- old *Alnus* and *Tsuga*) or as plug + 1s (2-year-old *Picea*), the stock types most often used in restoration and other planting operations in the region.

EFFECTS OF KNOTWEED ON LIGHT AVAILABILITY AND SOILS

Stem density and modal height of knotweed were measured in a 0.25 m^2 quadrat centred on each tree seedling. If knotweed was absent, height was assigned a value of zero. Light availability and soil physical and chemical properties were also quantified. Light availability was measured as photosynthetically active radiation (PAR; $\mu mol\ m^{-2}\ s^{-1}$) in August 2007 and 2008 on clear days between 10:00 and 15:00 h. We averaged the values of three successive measurements made 0.5 m above each transplanted seedling using a sunfleck ceptometer (Decagon, Inc., Pullman, WA, USA). Light availability is expressed as the proportion of ambient PAR, with ambient PAR sampled in an adjacent opening with unobstructed sky before and after measurements in each plot.

Mineral soil samples were collected between August and October 2008. Within each plot, three soil cores were extracted from the root zones of transplanted seedlings using a bulb planter (6 cm depth, 350 cm^3). Bulk density (dry $g\ cm^{-3}$) was determined, and a sample from each core was air-dried, sieved to 2 mm and then composited for chemical analyses. The latter were conducted as a comprehensive assessment of knotweed's effects on soils, including pH, organic matter content (%), cation concentrations (phosphorus, potassium, magnesium, calcium, sodium; p.p.m.), cation exchange capacity (meq 100 g^{-1}), sulphate (p.p.m.), total carbon and nitrogen (%), and available nitrate (NO_3-N, p.p.m.) and ammonium (NH_4-N, p.p.m.). All analyses, except total C and N, were conducted at A & L Western Agricultural Laboratories (Modesto, CA, USA). Total C and N were determined by dry combustion using a CHN analyzer (Perkin Elmer model 2400; Waltham, MA, USA) at the University of Washington Analytical Services Center (Seattle, WA, USA).

TREE SEEDLING PERFORMANCE

Survival and growth

Survival was censused annually (August 2007 and July 2008). Initial height (cm) and basal diameter (mm) of each seedling were measured within 2 weeks of transplanting. Height was measured as stem length (root collar to leader tip). Basal diameter was measured with a calliper immediately above the root collar; for stems with elliptical cross-sections, diameter was calculated as the mean of two perpendicular measurements. Annual growth was expressed as $\ln(y_1 - y_0)$ or $\ln(y_2 - y_1)$, where y_0, y_1 and y_2 are initial, first-year and second-year heights or diameters, respectively. At each measurement, any herbivory from Roosevelt elk, beaver or insects was noted; however, there were no consistent patterns, thus herbivory was not explicitly addressed in analyses.

Ectomycorrhizal colonization and biomass allocation

A subset of surviving seedlings (n = 2–34, average of 12 per plot) was harvested in September 2008 to assess ectomycorrhizal colonization (ECM) of root tips (*Tsuga and Picea*) and biomass allocation to shoot and root systems (all species). To quantify ECM, we refrigerated seedlings for < 2 weeks, maintaining root moisture during storage. We selected two to four *Picea* and *Tsuga* seedlings from each plot and gently rinsed the roots to remove soil. The entire root system was placed on a sampling grid, and three random (0.10–0.12 g) sections of fine roots were selected for analysis. We restricted sampling to roots that had grown into field soil. Sections were placed in 9-cm Petri dishes with a sampling grid and examined under a dissecting microscope (10–40× magnification). Root tips were classified as ectomycorrhizal, non-mycorrhizal, broken or dead. Tips were considered to be mycorrhizal unless they exhibited several to many root hairs, sloughing epidermal cells, lack of a fungal mantle, a non-swollen appearance, a clearly visible root stele and lack of a hartig net (Brundrett *et al.* 1996; Walker *et al.* 1999). For the latter, we examined longitudinal sections of root tips mounted on slides in a lacto-glycerol solution (100 mL lactic acid, 100 mL distilled water and 100 mL glycerol). Dead root tips were blackened, wrinkled, cracked and easily fragmented. ECM colonization was expressed as a proportion of the total number of non-broken root tips.

To quantify biomass allocation, harvested seedlings (33 *Alnus*, 86 *Tsuga* and 103 *Picea*) were oven-dried at 50 °C for 5–7 days, separated into roots vs. stems and leaves (shoots) and weighed to the nearest 0.001 g.

ANALYSES

Differences in knotweed density and height, light availability (proportion of ambient PAR), and soil characteristics were compared between knotweed (+) and (–) treatments using paired t-tests (n = 9). Analyses were conducted in R ver. 2.12.1 (R Development Core Team 2010).

We evaluated eight measures of tree seedling performance: survival; height and diameter growth; total, shoot and root biomass; root/shoot ratio; and ECM colonization of root tips (conifers only). General linear mixed models (GLMM; McCulloch, Searle & Neuhaus 2008) were used to test the effects of knotweed treatment, tree species and their interaction on each measure of performance (means for each plot). Block was treated as a random factor. Separate models were run for first- (2007) and second-year (2008) responses. Seedling survival was analysed with a binary regression and logit link (McCulloch & Nedler 1989). Other measures of performance were analysed using a normal distribution and either an identity (height and diameter growth) or log-link (biomass, ECM colonization) error structure. For each response variable, we plotted the observed vs. expected values and applied the log-link error structure as needed to stabilize the error variance (McCulloch & Nedler 1989).

Due to complete *Tsuga* mortality in some knotweed (+) plots and root damage during storage, sample sizes were reduced for the analysis of ECM colonization ($n = 6$ for *Tsuga* and 8 for *Picea*). For models in which there was a significant species or species × treatment interaction, we conducted a series of post hoc comparisons. To simplify the number of comparisons, pairwise comparison among species were made using GLMMs on relative performance, that is, difference in performance between treatments. Comparisons for root/shoot ratio could not be made in this way and were conducted separately within each treatment.

Preliminary analyses revealed significant variation in light availability and tree seedling survival within knotweed (+) plots. To determine whether species responded to this variation (reflecting differing light requirements), we conducted GLMMs for each species (binary regression with logit link). Individual survival in the second growing season (2008) was used as the response variable, and light (proportion of ambient PAR) and plot were included as fixed and random factors, respectively. GLMMs were conducted in SPSS ver. 19.0 (SPSS Inc. 2011).

Results

EFFECTS OF KNOTWEED ON LIGHT AVAILABILITY AND SOILS

As expected, the removal treatment resulted in significant (>90%) reductions in the density and height of knotweed (Table 1). Light availability (proportion of ambient PAR) was significantly lower (>85%) in knotweed (+) plots. Soil pH was significantly lower and total C and N significantly greater in knotweed (+) plots, although the differences in means were very small (Table 2). Soil bulk density was significantly (24%) lower in knotweed (+) plots. No other measure of soil fertility differed between treatments (Table 2).

EFFECTS OF KNOTWEED ON TREE SEEDLING PERFORMANCE

Tree seedling survival was markedly reduced in the presence of knotweed; however, the strength of this effect varied among species (significant treatment × species interaction; Fig. 1a,b; Table 3). *Alnus* experienced significantly greater mortality than *Picea* and *Tsuga*. By the end of the second growing season, *Alnus* suffered complete mortality in six of nine knotweed (+) plots (vs. zero of nine knotweed (−) plots). As with survival, seedling height growth was greatly reduced in the presence of knotweed. Effects were similar among species in 2007 but differed in 2008 (significant treatment × species interaction) (Fig. 1c,d; Table 3). Among seedlings that survived to 2008, reductions in height growth were significantly greater in *Tsuga* (122%) and *Picea* (75%) than in *Alnus* (which increased by 60%) (Fig. 1d). Seedling diameter growth was also reduced significantly in the presence of knotweed (Fig. 1e,f; Table 3). Reductions were greater in *Alnus* (78%) than in *Picea* (64%) or *Tsuga* (55%) in the first growing season (significant treatment × species interaction; Fig. 1e), but were comparable in the second (Fig. 1f).

Measures of seedling biomass (total, root, and shoot) were greatly reduced in the presence of knotweed, but the effect did not differ among species (Fig. 2a–c; Table 3). However, patterns of biomass allocation (root/shoot ratio) differed among species in the presence of knotweed (significant treatment × species interaction; Fig. 2d; Table 3). Knotweed had no effect on allocation in *Alnus* and *Picea*, but caused significantly greater allocation to roots in *Tsuga*.

Knotweed had a strong effect on ECM colonization of *Tsuga* (64% reduction), but not of *Picea* (significant treatment × species interaction; Fig. 3; Table 3).

TREE SEEDLING SURVIVAL VS. LIGHT AVAILABILITY

Within knotweed (+) plots, seedling survival varied with light availability for *Alnus* (significance of PAR, $P < 0.025$) and *Picea* ($P < 0.01$), but not for *Tsuga* ($P < 0.90$). Light levels above surviving *Alnus* averaged 19%, but only 7–8% above surviving *Picea* and *Tsuga* (Fig. 4; Table 3). Mean PAR was significantly greater for live than for dead *Picea*, but no different for live and dead *Tsuga*.

Discussion

The results of our experiment suggest that displacement of native species by strong invaders can occur through multiple mechanisms depending on the functional traits of the resident species. Knotweed invasion of Pacific Northwestern riparian forests alters light availability and below-ground environments, differentially affecting the performance of early- to late-seral tree species in ways that are consistent with their ecophysiologies. The less shade-tolerant early- and mid-seral species were sensitive to reductions in light. However, the shade-tolerant late-seral species was not. Instead, it exhibited

Table 1. Density and height of knotweed and light transmittance in knotweed (+) and knotweed (−) plots in the first (2007) and second (2008) growing seasons after treatment. *T*-statistics and *P* values are from paired *t*-tests ($n = 9$)

		Knotweed (+)			Knotweed (−)				
Variable	Year	Mean	SE	Min.–Max.	Mean	SE	Min.–Max.	*t*	*P*
Knotweed density (stems m^{-2})	2007	18.3	1.5	11.6–26.1	1.8	0.5	0.1–4.3	11.7	<0.001
	2008	20.7	1.3	14.7–26.1	1.9	0.5	0.0–4.7	14.3	<0.001
Knotweed modal height (cm)	2007	123.3	22.3	68.6–241.1	8.5	2.0	0.5–15.3	5.3	<0.001
	2008	160.8	22.2	73.7–290.1	13.4	2.4	0.0–24.5	6.9	<0.001
Proportion of ambient photosynthetically active radiation	2007	0.1	0.04	<0.1–0.4	0.5	0.1	<0.1–0.9	3.4	0.009
	2008	0.1	0.02	<0.1–0.2	0.4	0.1	<0.1–0.9	4.1	0.003

Table 2. Soil properties in knotweed (+) and knotweed (–) plots two growing seasons after treatment (2008). *T*-statistics and *P* values are from paired *t*-tests ($n = 9$)

	Knotweed (+)			Knotweed (–)				
Soil parameter	Mean	SE	Min–Max.	Mean	SE	Min–Max.	*t*	*P*
Bulk density (g cm^{-3})	0.68	0.04	0.5–0.8	0.9	0.03	0.8–1.0	−3.4	< 0.001
pH	5.12	0.05	4.9–5.3	5.21	0.05	5.0–5.5	−2.9	0.02
Total carbon (%)	2.08	0.1	1.6–2.5	1.67	0.2	1.0–2.7	2.4	0.04
Total nitrogen (%)	0.12	0.01	0.09–0.2	0.10	0.01	< 0.1–0.2	2.6	0.03
Organic matter (%)	3.02	0.2	2.2–3.9	3.03	0.4	1.8–5.3	−0.03	0.98
P (p.p.m.)	8.67	1.1	4–14	8.56	1.2	4–14	0.1	0.90
P (NaHCO$_3$-P; p.p.m.)	36.56	3.1	20–52	30.89	2.9	18–46	2.05	0.08
K (p.p.m.)	82.11	5.9	61–109	67.11	3.5	47–79	2.11	0.07
Mg (p.p.m.)	185.89	13.8	120–241	192.67	12.3	143–236	−0.8	0.44
Ca (p.p.m.)	936.0	59.0	697–1196	1018.11	69.7	757–1322	−1.6	0.14
Na (p.p.m.)	21.78	1.5	16–29	23.33	2.0	18–37	−1.1	0.30
CEC (meq 100 g^{-1})	10.33	0.6	7.7–12.7	10.56	0.7	8.3–14.3	−0.5	0.62
NO$_3$-N (p.p.m.)	11.6	1.4	8–20	9.0	1.0	6–15	1.4	0.19
NH$_4$-N (p.p.m.)	2.4	0.2	2–3	2.56	0.2	2–4	−0.4	0.73
SO$_4$-S (p.p.m.)	7.9	0.9	5–13	9.67	2.0	4–24	−1.3	0.23

reduced ectomycorrhizal colonization and increased root/shoot ratio, suggesting a disruption of soil mutualisms by knotweed.

The breadth of knotweed effects – spanning early- to late-seral dominants – has profound implications for the structural development of riparian forests. In the presence of knotweed, rates of tree establishment and growth are greatly reduced, with the potential to alter the ecological functioning of terrestrial and aquatic habitats.

EFFECTS OF KNOTWEED ON LIGHT AVAILABILITY AND SOILS

Light is a key determinant of riparian forest composition and structure. PAR was reduced to 6–7% of ambient levels beneath knotweed. Data on light transmittance from comparable, non-invaded riparian communities in the Pacific Northwest are limited. However, estimates from the understoreys of coastal hardwood forests in British Columbia are considerably higher – 10.8 ± 10% (Drever 2005) and 16 ± 2% (Roburn 2003) – suggesting that knotweed has a negative effect on understorey light relative to uninvaded habitats (Siemens & Blossey 2007).

We detected significant, but small differences between treatments in a number of soil properties. Soil bulk density showed the largest change, increasing 24% after knotweed removal. It is likely that decay of the dense and extensive systems of rhizomes (Child & Wade 2000) resulted in loss of macropore space. Nevertheless, bulk density values in the presence or absence of knotweed (both < 1.0) were well below levels detrimental to root growth (Minore, Smith & Woolard 1969; Kozlowski 1999) and were within the range of values documented for riparian soils in the western United States (Wheeler *et al.* 2002; Latterell *et al.* 2006) and New Zealand (Cooper, Smith & Smith 1995). Thus, it is unlikely that effects of knotweed on soil physical structure are important in shaping tree seedling responses. Although the effects on soil pH, total C and total N were statistically significant, they were small and are unlikely to be ecologically meaningful. Small differences in total N are consistent with observations in knotweed's adventive range in Europe and eastern North America. Across a wide range of European sites (including some similar to ours), Dassonville *et al.* (2011) found slightly lower soil pH, but no difference in total C or total N in plots with and without knotweed. However, they did find a difference in denitrification enzyme activity and a significant site × treatment interaction in ammonia (AOEA) and nitrite oxidizing enzyme activity (NOEA), suggesting spatial variation in the effects of knotweed on soils. Knotweed has also been associated with increases in soil cation and P concentrations in other systems (Vanderhoeven, Dassonville & Meerts 2005; Dassonville *et al.* 2007).

Although removal of knotweed had minimal effect on measures of soil chemistry in this system, our understanding of the dynamics of soil resource availability was constrained by the static nature of our measurements. It is possible that in-situ measurements of N cycling could have yielded stronger differences. It is also possible that major floods during the course of the study redistributed soils throughout the riparian corridor, masking the effects of knotweed. Finally, we did not measure differences in soil moisture availability and cannot eliminate its potential influence on seedling survival or growth. However, the study system is characterized by high relative humidity and abundant (including summer) rainfall (260 cm year^{-1}) owing to its proximity (< 2 km) to the Pacific Ocean. Moisture limitation in the presence of knotweed appears to be a much less plausible explanation for any treatment effects.

KNOTWEED–TREE SEEDLING INTERACTIONS

Alnus rubra is an archetypal early-seral species, adapted to disturbed environments, intolerant of shade and capable of rapid

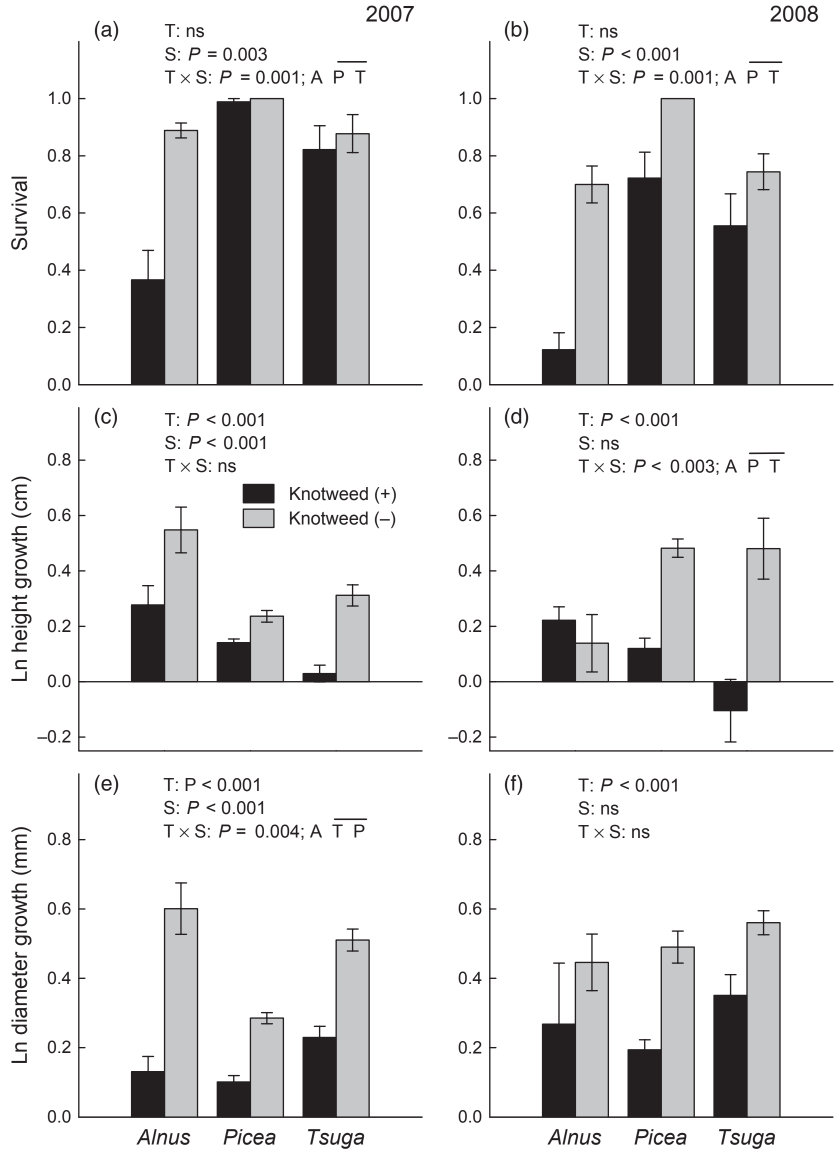

Fig. 1. Survival (a, b), ln height growth (c, d) and ln diameter growth (e, f) for *Alnus rubra, Picea sitchensis and Tsuga heterophylla* seedlings in the first (2007) and second (2008) growing seasons in the presence and absence of knotweed. Values are means (±1 SE). P values are from general linear mixed models (GLMM) with treatment (T), species (S) and treatment × species interaction (T × S) as fixed factors, and block as a random factor (see Table 3 for d.f. and F statistics). ns indicates a non-significant ($P > 0.05$) main effect or interaction. For significant treatment × species interactions, letter codes for species (A, P, T) indicate results of post hoc comparisons of relative performance

juvenile growth. Moreover, its ability to fix atmospheric N makes it less sensitive to variation in soil resources than other riparian species (Hibbs, DeBell & Tarrant 1994). Among the tree species in this study, *Alnus* was most similar to knotweed in its functional traits (seral status, shade tolerance and leaf longevity). Consistent with trait-based theories of plant competition (Tilman 1988; Bengtsson, Fagerström & Rydin 1994), *Alnus* exhibited the strongest response to the presence of knotweed, with survivorship reduced by 83% (vs. 24–28% in *Tsuga* and *Picea*).

Several lines of evidence suggest that light limitation beneath knotweed explains the greater mortality of *Alnus*. Pezeshki & Hinckley (1982) note that *Alnus* requires levels of PAR >80 μmol m^{-2} s^{-1} to survive; mean PAR beneath knotweed was only 14 μmol m^2 s^{-1} in the second growing season, far below this threshold. Second, in the presence of knotweed, light transmittance was significantly (79%) higher above live than dead *Alnus* seedlings, suggesting that survivors were growing in gaps in the knotweed canopy. Finally, height and diameter growth of surviving *Alnus* were similar between treatments suggesting an ability to maintain growth in patches of higher light, even in the presence of knotweed.

Picea sitchensis is a moderately shade-tolerant, mid-seral dominant in these riparian forests (Fonda 1974; Minore 1979; Van Pelt *et al.* 2006). Although it showed the highest survival, it was not immune to the influence of knotweed. Survival declined significantly in the second growing season, and height and diameter growth were greatly reduced in the presence of knotweed. Light appeared to play a primary role in these

Table 3. Degrees of freedom (d.f.) and *F* statistics for models of plant performance. Values are from general linear mixed models (GLMM) with treatment, species and treatment × species interaction as fixed factors, and block as a random factor; or single species models for the knotweed (+) treatments with proportion photosynthetically active radiation (PAR) as a fixed factor and block as a random factor. See Figs 1–3 for *P* values.

	Total Model		Treatment		Species		Treatment × Species		Proportion PAR	
Response variable	d.f.	*F*	d.f.	*F*	d.f.	*F*	d.f.	*F*	d.f.	*F*
Multiple species models										
2007 survival	5,48	17.3	1,48	0.01	2,48	6.7	2,48	8.1		
2008 survival	5,48	15.7	1,48	0.06	2,48	12.3	2,48	8.2		
2007 ln height growth (cm)	5,46	15.0	1,46	32.7	2,46	16.1	2,46	2.7		
2008 ln height growth (cm)	5,40	15.0	1,40	22.1	2,40	2.2	2,40	6.6		
2007 ln diameter growth (cm)	5,46	25.7	1,46	82.2	2,46	12.9	2,46	6.2		
2008 ln diameter growth (cm)	5,40	7.4	1,40	24.7	2,40	2.7	2,40	0.4		
Total biomass (g)	5,36	66.2	1,36	24.2	2,36	13.4	2,36	0.8		
Shoot biomass (g)	5,36	31.5	1,36	11.0	2,36	10.4	2,36	0.5		
Root biomass (g)	5,36	37.5	1,36	12.4	2,36	11.7	2,36	0.6		
Root/shoot biomass	5,36	5.8	1,36	1.0	2,36	3.1	2,36	5.9		
Ectomycorrhizal % colonization	3,20	4.7	1,20	5.3	2,20	14.0	1,20	6.4		
Single species models										
Alnus survival									1,88	10.0
Picea survival									1,88	6.9
Tsuga survival									1,88	0.9

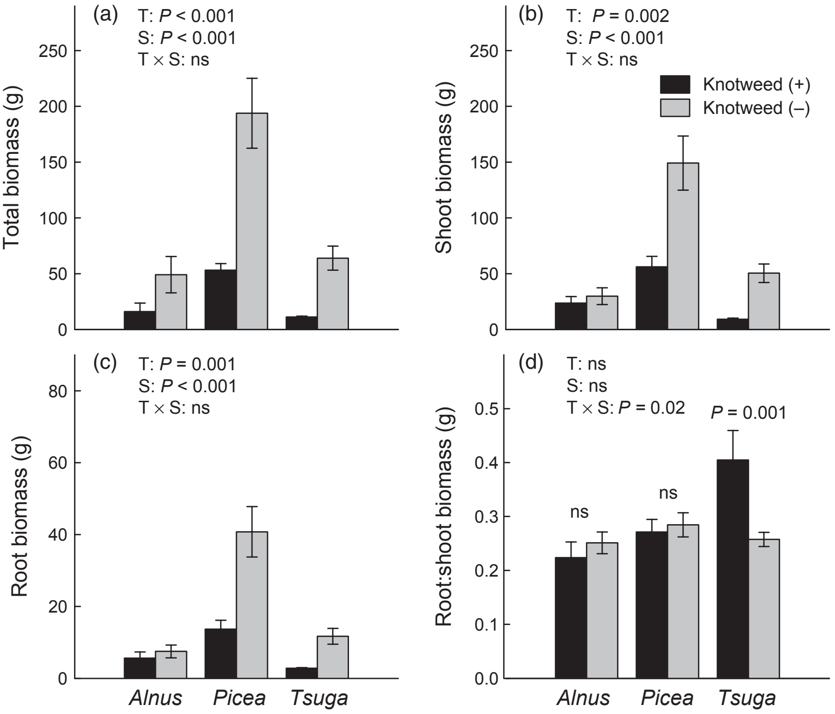

Fig. 2. Total, shoot and root biomass (a–c), and root/shoot ratio (d) for *Alnus rubra*, *Picea sitchensis* and *Tsuga heterophylla* seedlings at the end of the second growing season (2008) in the presence and absence of knotweed. Values are means (±1 SE). *P* values are from general linear mixed models (GLMM) with treatment (T), species (S) and treatment × species interaction (T × S) as fixed factors, and block as a random factor (see Table 3 for d.f. and *F* statistics). ns indicates a non-significant ($P > 0.05$) main effect or interaction. For significant treatment × species interactions, results of post hoc comparisons of means are presented above each treatment pair.

responses. In knotweed (+) plots, PAR was 79% higher above live than dead seedlings.

Tsuga heterophylla is a highly shade-tolerant, late-seral species. Similar to *Alnus* and *Picea*, survival and growth were greatly reduced by knotweed, but not in response to reduced light. In the presence of knotweed, levels of PAR did not differ above live and dead seedlings. Previous studies confirm that *Tsuga* can tolerate PAR as low as 5% (Carter & Klinka 1992),

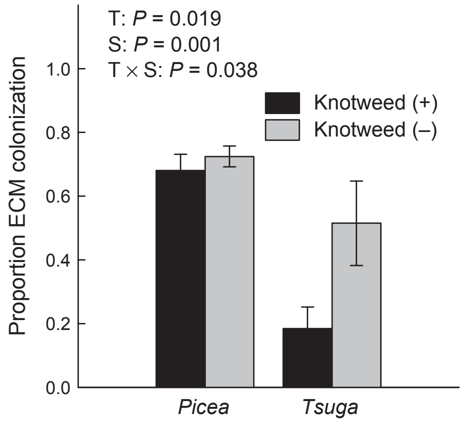

Fig. 3. Ectomycorrhizal (ECM) colonization in *Picea sitchensis* and *Tsuga heterophylla* seedlings at the end of the second growing season (2008) in the presence and absence of knotweed. Values are means (±1 SE). *P* values are from general linear mixed models (GLMM) with treatment (T), species (S) and treatment × species interaction (T × S) as fixed factors, and block as a random factor (see Table 3 for d.f. and *F* statistics).

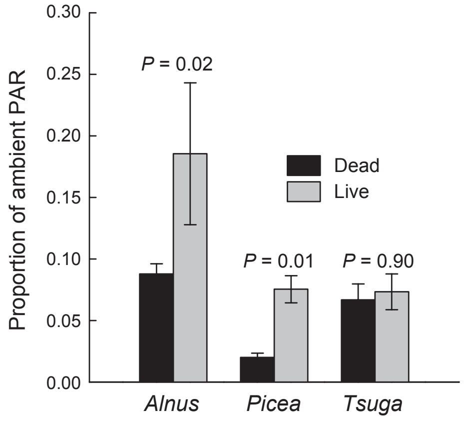

Fig. 4. Light availability [proportion of ambient photosynthetically active radiation (PAR)] above live and dead seedlings of *Alnus rubra*, *Picea sitchensis*, and *Tsuga heterophylla* in the presence of knotweed. Values are means (±1 SE). Light was measured above a total of 90 seedlings/species (10 per plot). Numbers of live seedlings are *Alnus* ($n = 8$), *Picea* ($n = 65$), Tsuga ($n = 51$). *P* values are from GLMM binary regression predicting survival of each species as a function of PAR (fixed factor), and plot (random factor); see Table 3 for d.f. and *F* statistics.

similar to (or lower than) values measured below knotweed in this experiment. On the other hand, *Tsuga* appears more sensitive to competition for below-ground resources (Christy 1986). In this study, several measures of *Tsuga* performance suggest that below-ground interactions with knotweed may be responsible for reductions in survival and growth. First, ECM colonization of surviving *Tsuga* was dramatically reduced (64% lower) in the presence of knotweed. Second, the root/shoot ratio of survivors was significantly greater in the presence of knotweed, a pattern not observed for *Alnus* or *Picea*. Greater allocation to root biomass may be a compensatory response to reductions in nutrient availability (which we did not observe) or to mycorrhizal density (Harley & Smith 1983; Perry *et al.* 1989). We assume that non-surviving seedlings (whose root systems and biomass allocation were not assessed) experienced similar, if not greater reductions in ECM colonization and growth, leading to eventual mortality. Responses in *Tsuga* thus appear to provide the first direct evidence of a reduction in mycorrhizal colonization of a native species attributable to the presence of knotweed. Although we did not test for the presence of root exudates, previous studies demonstrate that knotweed can produce antimicrobial and antifungal substances (Konstantinidou-Doltsinis & Schmit 1998; Kumagai *et al.* 2005), and suggest that chemical interference may contribute to its dominance of neighbouring species (Siemens & Blossey 2007; Vrchotová & Šerá 2008; Murrell *et al.* 2011). A similar strategy for disrupting soil mutualisms via secondary compounds has been documented in other exotic invaders (Marler, Zabinski & Callaway 1999; Stinson *et al.* 2006; Callaway *et al.* 2008). In this system, it is not clear why this effect was limited to *Tsuga*. It may be a physiological consequence of inherently slower growth in shade-tolerant *Tsuga*, particularly in the presence of knotweed. Alternatively, it may be attributable to differences in mycorrhizal morphotypes (Kropp & Trappe 1982) and their susceptibility to allelochemical or antifungal compounds produced by knotweed. Additional studies are needed to confirm the presence of these exudates and to understand the nature and specificity of their effects.

Conclusion

The success of strong invaders has often been ascribed to functional differences between invader and resident species (Elton 1958; Daehler 2003; Levine *et al.* 2003; MacDougall, Gilbert & Levine 2009). However, few, if any, studies have explicitly tested the mechanisms of interaction between strong invaders and resident species with differing functional traits (Ortega & Pearson 2005). In this study, we assessed the performance (mortality, growth and biomass allocation) of early- to late-seral tree seedlings in the presence and absence of knotweed and inferred the mechanisms of control from the correlation between species' performance and changes in light and below-ground resources.

Knotweed can impose strong controls on the growth and survival of seedlings of the dominant tree species in this riparian system; however, the mechanisms of control vary with the resource requirements of the resident species. Suppression of early- and mid-seral species with limited shade tolerance was correlated with reductions in understorey light, but suppression of a late-seral, shade-tolerant species was manifested below-ground through disruption of a critical plant mutualism that reduced ectomycorrhizal colonization of root systems. The mechanisms of interaction thus appear to reflect the breadth of resource or biotic alteration by the invader and the resources that are most limiting to species with differing functional traits.

In this system, the success of knotweed appears to reflect it dual abilities to compete for light and disrupt mycorrhizal mutualisms. Theory typically attributes successful invasions to species' abilities to competitively exploit (Tilman 1988; Levine *et al.* 2003; Maron & Marler 2008) or interfere with limiting resources through 'novel weapons' (Callaway & Aschehoug 2000; Callaway *et al.* 2008). A small, but growing body of theory (Amarasekare 2002) and empirical evidence (Human & Gordon 1996; Ridenour & Callaway 2001; Cipollini, McClain & Cipollini 2008) relates the success of strong invaders to the combined effects of resource exploitation and interference. For example, *Centaurea maculosa* can develop monotypic stands that displace native grassland species through a combination of resource competition and root-mediated allelopathy (Ridenour & Callaway 2001). Similarly, widespread invasion of forest understoreys by *Alliaria petiolata* reflects both successful competition for light and allelopathic effects (Cipollini, McClain & Cipollini 2008). The combined effect of exploitation and interference for exotic invasions has also been demonstrated in non-plant systems. Successful invasion of the Argentine ant, *Linepithema humile*, reflects its superiority in both resource exploitation and aggressive interference (Human & Gordon 1996). Ours is the first study to demonstrate the broader ecological consequences of these traits – reducing the survival and growth of co-occurring native tree species with differing resource requirements and seral roles. Additional work is needed to broaden our understanding of the ecological contexts and competitive or inhibitory mechanisms that lead to success in strong invaders.

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