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BIODIVERSITY RESEARCH

The fate of alien conifers in long-term plantings in the USA

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ABSTRACT

For more than 100 years, non-native conifers have been introduced into habitats in the USA that already support native conifers. These introductions have yielded few naturalizations and even less evidence of invasions. We investigated the specific fates of nine non-native conifers in an array of introduction sites across the USA (Priest River, Idaho, Wind River, Washington, Cedar Creek, Minnesota, and Nantucket Is. and Martha's Vineyard, Massachusetts) through tree-ring analyses, comparisons of growth with adjacent native conifer populations, and surveys for regeneration and spread. Most of the original non-native tree plantings have died (e.g. *Abies veitchii*, *Pinus densiflora*, and *Pinus halepensis* at Wind River, WA); a few have survived but display low vigour and are not regenerating (e.g. *Larix decidua*, *Pinus mugo*, and *Picea abies* stands at Priest River, ID). *Pinus sylvestris* recruitment is apparent at all sites examined. *Pinus thunbergii* appears to be invasive on Nantucket Is., although the native *Bursaphelenchus xylophilus* (pinewood nematode) causes high mortality in mature trees. Non-native *Pinus* spp. at the Eddy Arboretum, California and Pack Forest, Washington also experienced high mortality. Dendroclimatic analyses revealed no difference in the effect of climate on the annual growth of native and non-native conifers. Plantations of introduced conifers in the south-eastern USA have died *en masse* (e.g. Harrison Experimental Forest, Mississippi, Olustee Arboretum, Florida). Such widespread extirpations are in sharp contrast to the fate of native conifers in adjacent stands as well as the multiple cases of large-scale conifer invasions in the Southern Hemisphere. Given the diversity of alien plant species that have invaded the USA, the circumstances surrounding the lack of persistence of introduced conifers becomes an important line of inquiry for understanding the factors and circumstances that facilitate or thwart biological invasions.

Keywords

Alien conifers, biological invasions, forest plantations, invader, *Pinus sylvestris*, *Pinus thunbergii.*

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INTRODUCTION

Conifers dominate enormous swaths of the Earth's vegetation, principally in the Northern Hemisphere (Dallimore & Jackson, 1967). The collective ecological amplitude of conifers is so great that native conifers are represented in environments that range from arctic (e.g. *Picea abies, Pinus sibirica*) to tropical (e.g. *Pinus kesiya*, *Pinus merkusii*) and from arid (e.g. *Pinus ponderosa*, *Pinus pinea*) to those with perennially moisture-saturated soils (e.g. *Picea mariana*, *Taxodium distichum*) (Polunin, 1960; Critchfield & Little, 1966). Such enormous diversity within the group's environmental tolerances or requirements, coupled with their universal use as sources for pulp, timber, and resin (Le Maitre, 1998), has long meant that conifers have been deliberately introduced into new habitats, even habitats far beyond their native range (Richardson & Bond, 1991). Such deliberate attempts at range extension circumvent dispersal barriers and create the opportunity for these plant immigrants to persist without cultivation (Richardson & Rejmánek, 2004).

Immense areas in the Southern Hemisphere have been converted to plantations and now often serve as the source for invasions into adjacent natural communities (Richardson & Higgins, 1998). Subsequently, approximately two dozen species of conifers (e.g. *Pseudotsuga menziesii*, *Larix decidua*, *Pinus pinaster*, and *Pinus radiata*) have become invasive (*sensu* Mack *et al.*, 2000) across the Southern Hemisphere (Richardson & Rejmánek, 2004). Invasive conifers escape from cultivation and reduce native species diversity, decrease available water by increasing evapotranspiration, and alter other aspects of ecosystem function (Richardson & Higgins, 1998).

In sharp contrast, few conifer invasions have been reported in the Northern Hemisphere, particularly when compared to the

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scope and species diversity of invasive angiosperms (White *et al*., 1993; Cox, 1999; Kowarik, 2003). *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Larix kaempferi* regenerate in Britain (Clement & Foster, 1994), while *Pinus contorta* and *Pseudotsuga menziesii* grow at rates similar to the growth rates for native conifers in Finland (Nikkanen & Silander, 2003). Among 49 species of alien conifers planted in the Białowieża Forest on the border of Poland and Belarussia in the early 20th century, two species (*Pinus strobus* and *Pinus banksiana*) are naturalized, but no alien conifers have become invasive (Adamowski, 2004). *Pinus strobus* invades native *Pinus sylvestris* forests in the Czech Republic (Hanzélyová, 1998), and *Pinus nigra* is invasive around Lake Michigan in the USA (Leege & Murphy, 2001). *Pinus sylvestris* spreads through the peatlands of Ontario, Canada (Ripmeester, 1996). Considering the aerial extent and environmental heterogeneity of the Northern Hemisphere, these isolated examples appear anomalous in comparison to the varied conifer invasions in the Southern Hemisphere (Richardson *et al*., 1994).

Native conifers in the USA display much species diversity and collective geographical extent, and most are merchantable; these features have seemingly minimized incentive to import alien species. However, non-native conifers were introduced into the USA as early as 1846 (Graves, 1900) and probably much earlier (Mack, 1991 and references therein) by private landowners. Graves (1900) matter-of-factly explained that many American planters 'began with imported trees', such as *Pinus sylvestris* and *Picea abies*, in establishing their plantations. The USDA both encouraged the creation of these private plantations (USDAFS, 1907; Peck, 1910) and began establishing plantations in the event alien conifers would be needed to replace native timber species (Fairchild, 1898). This bet-hedging against unspecific threats to the future of forestry led to the establishment of a network of small, widely scattered US Forest Service (USFS) plantations of alien conifers (USDAFS, 1923).

In the 1950s the USFS resumed nationwide forestry trials with non-native trees as potential replacements for parasitized native species (K. Outcalt, pers. comm.). In addition, non-native conifers were used to stabilize dunes along shorelines (Littlefield, 1942; Leege & Murphy, 2000). Many non-native species are still cultivated in the USA for ornamentation and as Christmas trees (e.g. *Pinus sylvestris*, *Picea abies*) (Koelling & Heiligmann, 1993).

Few alien conifers derived from plantations appear to have persisted in the USA, much less spread. *Pinus sylvestris*, which was planted between 1870 and 1883 in Oneida County, New York, was naturalized and spreading through abandoned fields and along roadsides as early as 1925 (York & Littlefield, 1942). Also in New York, row plantings of *Larix decidua* in 1867 yielded progeny distributed throughout approximately 1 km^2 by 1939 (Cook, 1939). In Michigan, *Pinus nigra*, *Pinus sylvestris*, and *Picea abies* have also become naturalized (Leege & Murphy, 2000; Kilgore & Telewski, 2004a).

Anecdotal accounts have long suggested that non-native conifer naturalizations (*sensu* Mack *et al*., 2000) are conspicuously rare across North America, but comprehensive documentation has been lacking. Do these observations reflect the continental status for non-native conifers or are naturalized alien conifers actually common across the USA? The need for a clear, quantitative picture of these species in the USA sparked our investigation. The outcome of field trials, some initiated more than 100 years ago, provides an ideal experimental opportunity to investigate this general question. Consequently, assessing the fate of these trials allowed us to compare the response and predict the future of native and non-native conifers across the northern tier of the USA.

METHODS

Field sites and species of interest

We investigated the fates of non-native conifers at introduction sites across the USA (Priest River Experimental Forest, Idaho (PREF), Wind River Experimental Forest, Washington (WREF), Cedar Creek Natural History Area, Minnesota (CCNHA), Nantucket Island, Massachusetts, and Correllus State Forest, Massachusetts (MFCSF)) (Table 1). Non-native conifers were introduced to these sites for silvicultural trials (PREF, WREF, and MFCSF), as windbreaks (CCNHA), or for reforestation and landscaping (Nantucket Is.). We selected sites based on the reported survival of non-native conifers, the initial time of planting (before 1970), and limited alteration of the habitat (i.e. no recurrent mowing, logging, removal of seedlings, or irrigation). These selection criteria limited field sites to the northern USA; searches for sites in the south-eastern and south-western USA revealed no large stands of non-indigenous conifers that met these requirements. Although sites with substantial disturbance capable of destroying (mowing) or fostering (irrigation) were avoided because such disturbance would have introduced variables into the design for which their specific character, intensity, and frequency were unknown, an array of minor disturbances (e.g. routine removal of dead trees and trail maintenance, pocket gopher activity, and storm damage) had occurred at all sites.

From July to August 2005, we sampled five stands of alien species (*Pinus sylvestris*, *Picea abies*, *Larix decidua*, *Pinus mugo*, and *Pinus nigra*) at the PREF arboretum and a stand of the native *Larix occidentalis* growing directly south of the arboretum. We examined stands of *Abies alba*, *Larix decidua*, *Picea abies*, *Picea orientalis*, *Pinus mugo*, *Pinus nigra*, *Pinus peuce*, and *Pinus sylvestris* between July and August 2004 at WREF. Silen & Olson (1992) reported the history of conifer introductions at the Wind River Arboretum (Table 2). At the CCNHA in September 2004, we investigated the reported spread of *Pinus sylvestris* from a windbreak (J. Knops, pers. comm.) and sampled a stand of *Pinus strobus*, a native pine that plays an early mid-successional role (Curtis, 1959). Since 1895 *Pinus thunbergii* has been planted extensively on Nantucket Island in recognition of the pine's high salt tolerance (Littlefield, 1942). In October 2004, we investigated the status of *Pinus thunbergii* on Nantucket Is. and sampled one stand in the maritime shrublands community on the island's south-western coast. We also searched for *Pinus thunbergii* in the maritime shrublands of Martha's Vineyard. At the MFCSF on Martha's Vineyard, we compared patterns in annual growth of a *Pinus sylvestris* stand with a native *Pinus rigida* stand and also sampled small stands of *Picea abies* and *Picea glauca*.

Table 1 Physical characteristics for the five sites analysed for conifer survival, health, and vigour in this study

	PREF, ID	WREF, WA	CCNHA, MN	Nantucket Is., MA	MFCSF, MA
Latitude	48°21′ N	45°49′ N	45°24′ N	41°28′ N	41°23′ N
Longitude	116°50′ W	121°57′ W	93°16′ W	70°10′ W	70°35′ W
Elevation (m)	715	350	280	10	20
Mean Jan min. temp. (°C)	−7.72*	−3.56*	−17†	−3.83‡	−5.33‡
Mean July max. temp. (°C)	28.11*	27.06*	27.83†	24.11‡	26.00‡
Annual min. precip. (cm)	40.64*	144.27*	35.86†	64.29‡	76.40‡
Annual max. precip. (cm)	119.89*	361.95*	116.31†	153.39‡	166.07‡
Total area of planting (ha)	80**	4.45§	*c.* 0.1	*c.* 638	445¶

Site descriptions:

PREF, ID, Priest River Experimental Forest, Idaho; WREF, WA, Wind River Experimental Forest, Washington; CCNHA, MN, Cedar Creek Natural History Area, Minnesota; MFCSF, MA, Manuel F. Correllus State Forest, Massachusetts. (Nomenclature for conifers follows Farjon & Page,1990).

Sources: *Western Regional Climate Center, 2005; †Minnesota Department of Natural Resources, 2004; ‡North-east Regional Climate Center, 2005; **Wellner *et al*. (1951); §Silen & Olson (1992); ¶Foster & Motzkin (1999).

Table 2 Non-native conifer introduction history at the five sites analysed (see Table 1 for explanation of site acronyms. Asterisk indicates species known to be invasive elsewhere (Richardson & Rejmánek, 2004))

Location	Species	Period of planting	Number planted	Provenance
PREF, ID	*Larix decidua**	1931†	Unknown	Unknown
	Picea abies	1931†	Unknown	Unknown
	*Pinus mugo**	1931†	Unknown	Unknown
	*Pinus nigra**	1931†	Unknown	Unknown
	*Pinus sylvestris**	1931†	Unknown	Unknown
WREF, WA	*Abies alba*	1927‡	20‡	Switzerland‡
	*Larix decidua**	1923; 1925‡	19‡	England; Poland‡
	Picea abies	1912; 1936‡	10‡	Prussia; Germany‡
	Picea orientalis	1919‡	21‡	Caucasus‡
	*Pinus mugo**	1929‡	20‡	Switzerland‡
	*Pinus nigra**	1936‡	20‡	Russia‡
	Pinus peuce	1928; 1936‡	17‡	Unknown‡
	*Pinus sylvestris**	1912, 1923; 1957‡	50‡	Russia; Germany‡
CCNHA, MN	*Pinus sylvestris**	1950s§	*c.* 400	Unknown
Nantucket Is., MA	*Pinus thunbergii*	1895–present¶	Thousands	Multiple origins
MFCSF, MA	*Picea abies*	*c.* 1965**	Unknown	Unknown
	*Pinus sylvestris**	1932**	*c.* 21,925**	Unknown

Sources: †R. Denner, pers. comm.; ‡Silen & Olson (1992); §J. Haarstad, pers. com.; ¶Littlefield (1942); **Foster & Motzkin (1999).

Field methods

We determined the survival, health, and reproductive capacity of the original plantings at each site as indices to the alien species establishment. Although these observations are confounded by different times of conifer introduction, number of trees planted, and numerous abiotic and biotic site factors, the end result (e.g. extirpation or naturalization) of the introductions at each site is revealed through inspection of the adults and progeny.

At each site we used growth measurements (d.b.h. and tree height) and qualitative observations of tree health (e.g. apparent attack by predators, grazers, and parasites) to evaluate the vegetative response of the adult trees to their site. In all but the Nantucket site, the original planted trees had retained their tags or were still in the original planted alignment at the sites, thereby ensuring that we were not inadvertently mistaking recruits for the founder trees. Tree cores were taken at 1.3 m to compare the growth and environmental response of non-native conifers with adjacent, native congeners. We searched for seedlings of introduced conifers along transects (30 m or 60 m long depending on the size of the plot) placed 8 m apart and immediately outside the planted area at each site to detect tree regeneration. (We omitted the *Pinus peuce* stand where seedling identification was uncertain.) If many saplings occurred outside the introduction site, we measured the distance from the original trees to the furthest progeny. We excluded from our measurements *Pinus*

Table 3 Survival, vigour, and regeneration for non-native conifers at the five sites analysed (see Table 1 for explanation of site acronyms)

Site	Species	Survival and vigour	Mean height (m)/ d.b.h. (cm) (sample size)	Regeneration; distance from parent
PREF, ID	*Larix decidua*	~150 adults; nodding crowns	18.90/25.36 (84)	None detected
	Picea abies	~75 adults	17.54/20.00 (57)	None detected
	Pinus mugo	4 adults	3.75/7.87 (4)	None detected
	Pinus nigra	4 adults	16.08/43.05 (4)	None detected
	Pinus sylvestris	11 adults	15.71/39.34 (9)	Various cohorts; 85 m
WREF, WA	*Abies alba*	19 adults; wooly aphid damage	11.34/20.24 (10)	None detected
	Larix decidua	6 adults; dead branches	13.98/27.90 (6)	None detected
	Picea abies	4 adults;	26.03/40.13 (4)	6 saplings; 4 m
	Picea orientalis	21 adults; bark damage	22.02/31.04 (10)	2 saplings; 2 m
	Pinus mugo	8 adults	13.69/19.92 (7)	2 unidentified saplings
	Pinus nigra	9 adults	17.38/33.05 (9)	None detected
	Pinus peuce	8 adults; white pine blister rust	13.69/20.83 (8)	Not investigated
	Pinus sylvestris	19 adults; dead branches	14.06/21.84 (20)	3 seedlings; 5 saplings; 60 m
CCNHA, MN	*Pinus sylvestris*	~300 adults	15.61/32.05 (46)	Various cohorts; 206 m
Nantucket Is., MA	*Pinus thunbergii*	Many adults; diseased; spreading	5.42/13.49 (29)	Various cohorts
MFCSF, MA	*Picea abies*	35 adults	16.11/42.04 (8)	Many seedlings; 46 m
	Pinus sylvestris	Many adults; wind and parasite damage	10.63/33.83 (15)	Various cohorts

thunbergii on Nantucket Is. and *Pinus sylvestris* at Correllus Forest where multiple introduction sites prevented identification of parent trees. Photosynthetically active radiation (PAR) measurements were taken on clear days from ground level with an AccuPAR ceptometer (Decagon Devices, Inc., Pullman, WA, USA) along the original transects at 5 m intervals (except at the WREF where measurements were taken at 3 m intervals) between 1100 h and 1400 h (pst). Above-canopy PAR measurements were documented before and after measurements below the canopy. Litter depth, aspect, and percentage of slope were also measured. Collection of these data allowed us to determine the likelihood of the species persistence at each site.

Analyses

Growth measurements were compiled and averaged. If native and non-native congeners were growing in habitats with the same aspect and slope, growth measurements of these species were contrasted by determining equal variance (*F*-test) and testing the equality of means (two-tailed Student's *t*-test). Above-canopy PAR measurements were averaged to compensate for changes in light levels during sampling, and relative PAR values (below-canopy values divided by the average of above-canopy values) were calculated for each stand. These data were arc-sin transformed for comparison with Tukey's multiple comparison test using SAS 9.1 software (SAS Institute Inc., 2002).

Tree cores were prepared according to Stokes & Smiley (1968) and measured with a Velmex Positioning System (Velmex Inc., Bloomfield, NY, USA). We used J2X software (Voortech Consulting LLC, Nolderness, NH, USA) to format measurements, and series were cross-dated using COFECHA (Holmes, 2000) when sample size and series length permitted. COFECHA removes low-frequency variance derived from tree ageing and microsite differences by smoothing, modelling, and log-transforming the ring width values (Holmes *et al.*, 1986; Schweingruber, 1988). Series that correlated with less than a 99% confidence interval with the master series were not used to build the master chronology. Series with high correlation were analysed using ARSTAN (Holmes, 2000) to create master chronologies, and index values were plotted as a function of time. Index values were calculated by dividing the mean measurement value for each year by a negative exponential regression line, which allowed comparison between species (Fritts, 1966; Holmes *et al.*, 1986). The mean sensitivity for the master series was also determined; sensitivity measures the difference between two consecutive years of growth and estimates the climatic sensitivity of species (Schweingruber, 1988).

To determine whether effective precipitation limits the growth of native, non-native species, or both, Palmer Drought Severity Index (PDSI) data were compared with each chronology using PDSI data (Cook *et al.*, 1999) as an undated series in COFECHA, which functions as an R^2 test. Palmer Drought Severity Indices are based on principle components analyses of established tree-ring chronologies with climatic variables, including precipitation and temperature (Cook *et al.*, 1999). However, PDSI do not account for the effect of snowfall and short-term weather events on tree growth (Alley, 1984). Therefore, outliers from the master chronologies were compared with extreme events (e.g. sudden drops in temperature, extreme heat, heavy snow pack) derived from 20th century meteorological data (US Environmental Data and Information Service, 1970–2000).

RESULTS

Most of the non-native conifers that were planted have not persisted; a few have survived but with low vigour (*sensu* Daubenmire, 1968) and are not regenerating (Table 3). *Abies veitchii*, *Cedrus deodara*, *Juniperus excelsa*, *Pinus halepensis*, and *Pinus pinaster* died after introduction at the WREF (Silen & Olson,

Table 4 Tree-ring analyses and dendroclimatology for non-native conifers at the five sites analysed (see Table 1 for explanation of site acronyms. Asterisk indicates non-native species)

Site	Species	Mean ring width (mm)	Standard deviation (mm)	Mean sensitivity (ARSTAN)	Correlation with PDSI (%) (R^2)
MFCSF, MA	*Pinus sylvestris**	2.18	1.19	0.274	30
	Pinus rigida	2.28	1.15	0.283	31
	*Picea abies**	5.90	2.47	0.226	0
	Picea glauca	2.83	1.72	0.229	3
PREF, ID	*Larix decidua**	2.02	1.06	0.246	35
	Larix occidentalis	1.99	1.13	0.308	33
CCNHA, MN	*Pinus sylvestris**	4.02	1.18	0.230	8
	Pinus strobus	9.94	2.36	—	0

PDSI, Palmer Drought Severity Index.

1992). Few individuals of *Pinus nigra* and *Pinus mugo* remain in stands at the PREF, and no regeneration of *Larix decidua* was detected at either site. However, a few *Picea abies* and *Picea orientalis* saplings were found at the WREF. *Picea abies* is regenerating at the MFCSF. Natural regeneration of *Pinus sylvestris* was observed at all sites, but many of the mature trees are diseased. *Pinus thunbergii* is spreading prolifically on Nantucket Is. but is parasitized by the native pinewood nematode (*Bursaphelenchus xylophilus* Steiner and Buhrer).

Many of the original plantings of *Larix decidua* and *Picea abies* remain as adults at the Priest River site. No *Larix decidua* or *Picea abies* seedlings were found, although seedlings of native species (e.g. *Abies grandis* and *Pseudotsuga menziesii*) are present. Only male strobili were observed on the four *Pinus mugo* individuals we located. No survivors remain of the original *Pinus sylvestris* adults planted in the arboretum plot at PREF. Nine apparently planted adults occur across the road from the original plot, and *Pinus sylvestris* seedlings are spreading into varied habitats (e.g. marsh, river bank, roadside) up to 80 m from the adult trees.

The majority of non-native conifer species at WREF have perished. Therefore, the focal species we selected represent the best-survival scenario. Less than 50% of *Pinus sylvestris*, *Picea abies*, *Pinus nigra*, *Pinus mugo*, *Larix decidua*, and *Pinus peuce*, but 95% of *Abies alba* and 100% *Picea orientalis* remain (Table 3). Damage to the bark by red-breasted sapsuckers, woolly aphids (*Adelges piceae* Ratzeburg), and snow damage have stunted the growth of *Abies alba*. The vigour of *Larix decidua* is low and rapidly declining. Saplings of *Picea abies* and *Picea orientalis* occur near the stands bordering the trail clearing. Seed predation, sapsucker activity, and a needle parasite are apparent on the *Picea orientalis*. *Pinus nigra* displays the most vigorous growth of all alien tree species sampled at the Wind River site. *Pinus peuce* occurs in two stands; in one the alien pine exhibits progressive symptoms of white pine blister rust. *Pinus sylvestris* adults have low vigour, but saplings were detected as much as 60 m from the original planting site. The height and d.b.h. of *Pinus contorta* and *Pinus sylvestris* are not significantly different ($P = 0.55, 0.12$).

Adult *Pinus sylvestris* at CCNHA appear healthy, and the original windbreak shelters a cohort of saplings that are approximately 15 years younger than the adults, based on the number of annual rings at 1.3 m. *Pinus sylvestris* has spread 206 m from the windbreak, but these saplings are sparse and often uprooted by pocket gophers (J. Haarstad, pers. comm.). On the south-eastern side of the windbreak, *Populus* and *Quercus* spp. are becoming established in the field and are overtopping *Pinus sylvestris*. Despite their younger age, *Pinus strobus* adults have a larger diameter than *Pinus sylvestris* adults at this site ($P = 0.005$); however, their height is similar.

Pinus thunbergii is growing along the circumference of Nantucket Is. and is spreading throughout the maritime shrublands community. Isolated groups of *Pinus thunbergii* originating from ornamental plantings also surround and spread from buildings in nascent foci (*sensu* Moody & Mack, 1988). Adult trees are heavily parasitized by the pinewood nematode and induced defence mechanisms (i.e. high densities of resin ducts) are visible in over half the core samples taken. Only two native members of the maritime shrublands community (*Carex* sp. and *Toxicodendron radicans* (L.) Kuntze) colonize under *Pinus thunbergii* trees.

We located one *Pinus thunbergii* population near the south-eastern shore of Martha's Vineyard (South Beach). At the Correllus State Forest, *Picea abies* is growing vigorously, and saplings are up to 46 m from the eastern side of the plot. The d.b.h. of *Picea abies* is significantly greater than that of *Picea glauca* ($P = 0.0025$), even though the *Picea abies* trees are younger. Adult *Pinus sylvestris* at the MFCSF have many dead branches, and adults and saplings are heavily infected with *Diplodia pinea* Desm. Radial growth of *Pinus sylvestris* and *Pinus rigida* are not significantly different ($P = 0.103$).

We created master chronologies for four pairs of congeners, but the number of rings present in *Pinus strobus* cores is insufficient for analysis with ARSTAN (Table 4; Figs 1 and 2). Native species have slightly higher mean sensitivities than non-native species. The mean sensitivities of the MFCSF *Pinus* spp. and PREF *Larix* spp. are higher than the mean sensitivities of *Pinus* spp. and the *Picea* spp. at CCNHA and MFCSF, respectively. Approximately 30% of the variation in annual ring widths of *Pinus* spp. at the Correllus State Forest and *Larix* spp. at the Priest River Arboretum can be explained by climatic factors incorporated

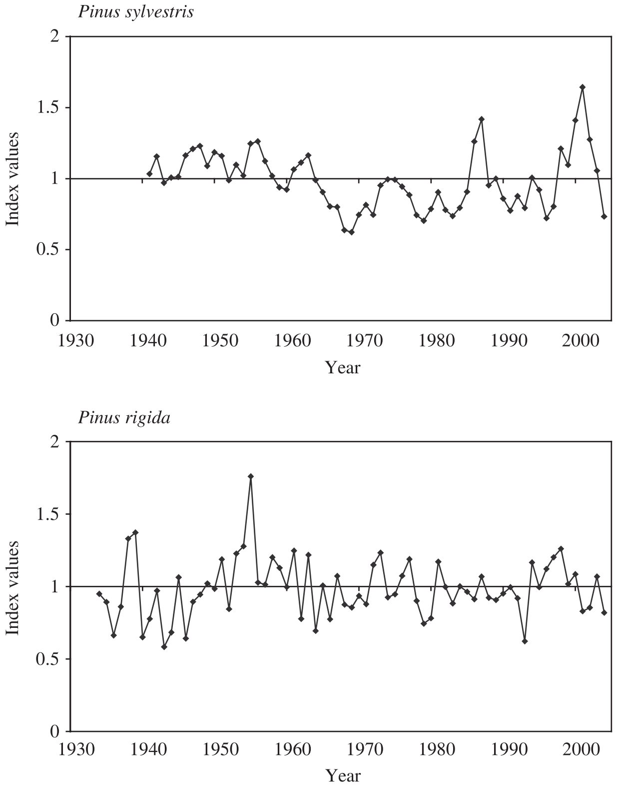

Figure 1 Master ring-width chronologies, based on ARSTAN, for native and non-native *Pinus* spp. at the Correllus State Forest, MA.

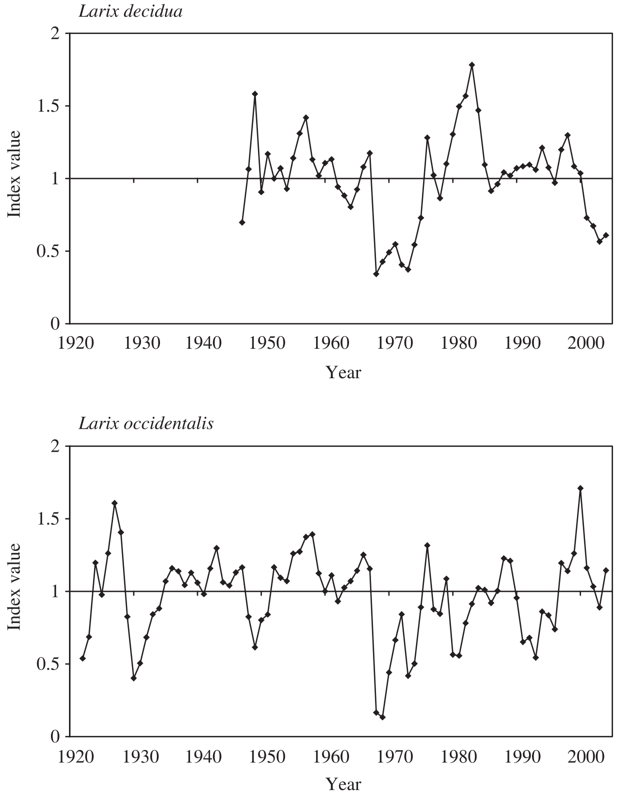

Figure 2 Master ring-width chronologies, based on ARSTAN, for native and non-native *Larix* spp. at the Priest River Experimental Forest, ID.

in PDSI, but almost none of the ring width variation in the other species is explained by PDSI. Ring measurements correlated similarly with PDSI data within native and non-native congenera, but variation among genera within sites is high.

PAR beneath *Pinus sylvestris* canopies at the sites at PREF, CCNHA, and the MFCSF is significantly greater ($P = 0.05$) than that at other sites. Available PAR underneath all alien conifer plantings at the Wind River site, *Larix decidua* at PREF, *Picea abies* at PREF, and the Correllus Forest site is not significantly different ($P = 0.05$). The mean litter depth under *Pinus thunbergii* (2.3 cm) is greater than the litter depth outside of the stand (0.93 cm).

DISCUSSION

Analyses, including field assessments at five sites, for the introduction of alien conifers across the northern USA reveal few instances of naturalization. In addition to the few previous accounts of non-native conifer persistence (see Introduction), we confirmed the persistence for only two non-native conifers, *Pinus sylvestris* and *Pinus thunbergii*, through field determinations. Limited evidence for naturalization, much less invasion, of alien conifers raises questions as to why most non-native conifers introduced to North America have repeatedly failed to survive. Possible explanations fall into several major categories for which our results provide insight.

Conclusions regarding US sites

Natural regeneration of *Pinus sylvestris* (PREF, CCNHA, and MFCSF) occurs under the highest percentage of available PAR we measured. *Pinus thunbergii* recruitment appears unrestricted by light levels; recruitment by any other conifers is confined to canopy openings. *Pinus sylvestris* is the only alien conifer regenerating at PREF, and its wide ecological amplitude and ability to disperse (Obminski, 1970) indicate that it may persist indefinitely. However, *Pinus sylvestris* seems unlikely to become invasive at PREF, considering the superior competitive ability of *Pinus contorta* (Elfving *et al.* 2001). In contrast, *Pinus thunbergii* threatens to replace native species in maritime shrublands and sandplain heathland communities (Swain & Kearsley, 2001). The competitive ability of *Pinus thunbergii* (documented in this study by competitive exclusion of all but two native plants) and its potential alteration of soil development through high litter production may underlie its apparent invasion of the maritime shrublands of Nantucket Is.

At CCNHA, oaks and poplars are overtopping *Pinus sylvestris*, a light-demanding species (Burns & Honkala, 1990). At the Correllus Forest site, limited recruitment and parasitism threaten *Pinus sylvestris*. Moreover, native and non-native conifers in MFCSF are slated for removal (Dunlop, 2004). The small remaining populations of alien species at WREF suggest that these introductions will not persist. Furthermore, the USFS may discontinue its limited maintenance of the Wind River Arboretum (S. Greene, pers. comm.), and the encroachment of *Pseudotsuga menziesii* into the alien conifer plots may continue.

Snowfall in January 1969, was the maximum received in 94 years at PREF and the 1969 mean low temperature is also the lowest on record (Western Regional Climate Center, 2005). The native and non-native *Larix* spp. responded similarly to the heavy snowfall and consistent low temperatures in winter, 1968–69 (Fig. 2). When correlated with species chronologies, PDSI also indicate climatic adaptation (Graumlich, 1993). The annual growth response to precipitation and temperature (PDSI) does not differ between native and established non-native congeners (Table 4). Once alien tree species are established, climate is apparently not a greater mortality threat to non-native trees than to native trees. In contrast, performance of native and non-native pines at the pine barrens in lower Michigan revealed higher climate sensitivity among non-native species (Kilgore & Telewski, 2004b). Correlation of annual ring widths for *Pseudotsuga menziesii* and *Pinus ponderosa* with PDSI data (0.31; 0.30) in the southern Canadian Cordillera is similar to the response of *Pinus* spp. from the MFCSF and *Larix* spp. from PREF (0.30–0.35) (Watson & Luckman, 2002).

Fate of other alien conifer plantations in North America

Our conclusions are specific to five sites in the USA, but other plantings of alien conifers in North America have had similar outcomes. Approximately 84 pine species were planted at the Eddy Arboretum in California; these trees have experienced massive mortality (D. Johnson, pers. comm.). Forty-six pine species from the Eddy Arboretum were planted at Pack Forest near Tacoma, WA, and after a decade, *Pinus pinaster*, *Pinus halepensis*, and *Pinus canariensis* had experienced high mortality (Zumwalt, 1938). Beginning in 1892, forty-five species of non-native conifers were planted in chaparral in the San Gabriel Mountains of California: some of the larger plantings consisted of 23,000 *Cedrus deodara*, 27,000 *Pinus canariensis*, and 64,300 *Pinus halepensis* seedlings. Initial survival of the plantings was low, and none of these species have proven invasive (Burns & Sauer, 1992).

Repeated growth trials in the south-eastern USA also yielded no persistent alien conifers (Zobel *et al.*, 1956). Planting of alien conifers in Arkansas and Louisiana resulted in poor survival; less than 1% of 581 *Pinus pinaster* individuals and 419 *Pinus nigra* individuals survived 10 years (Grigsby, 1969). Forty-five native and non-native pines (25 individuals each) were planted at the Harrison Experimental Forest Arboretum in Gulfport, Mississippi, beginning in 1955 and the Olustee Arboretum in Olustee, Florida in 1954. The non-native pine species in Mississippi exhibited much slower growth than native species 10 years after planting (Schmitt & Namkoong, 1965). As of 2004, no non-indigenous species remained in the Harrison Arboretum (R. Schmidtling, pers. comm.). ‘Tests at the Olustee Arboretum confirm findings at other southern arboreta, and indicate that southern forestry problems are *not* likely to be solved by a foreign miracle tree’ (Kraus, 1963).

Causes for the fate of alien conifers in North America

Characteristics of pine species that facilitate their invasion in the Southern Hemisphere include low seed mass, short time to reproductive age, and production of frequent, large seed crops (Rejmánek & Richardson, 1996). Most of the non-indigenous species that persist in North America (e.g. *Pinus sylvestris* and *Pinus nigra*) also exhibit these characteristics, but as documented here many alien pines with these same features (e.g. *Pinus halepensis* and *Pinus pinaster* (Grotkopp *et al.*, 2002)) have not persisted in the USA. What factors may impede or prevent alien conifer persistence in North America that do not arise (or are overcome) in the Southern Hemisphere?

Time since planting (i.e. residence time)

A short lag phase preceded most pine invasions in the Southern Hemisphere. For instance, *Pinus halepensis* was spreading in South Africa 25 years after its initial introduction. In Australia, *Pinus elliottii* was invading landscapes by 1960, thirty years after large-scale planting (Richardson & Higgins, 1998). Brief lag phases have also occurred in North America. *Pinus thunbergii* was planted in the 1890s on Nantucket Is. and had produced three generations by 1930 (Jones, 1930). The invasion of *Pinus nigra* was observed near Lake Michigan 30–40 years after its introduction (Leege & Murphy, 2000). Lag phase populations that eventually proliferate are often indistinguishable from populations that fail (Cousens & Mortimer, 1995). Could alien conifers in North America still be in a lag phase but become invasive? Installation of alien conifer plantations in the USA has markedly declined, and trees in the remaining plantations show no evidence of invasion even after 50 years. Thus, it seems unlikely that these populations will yet undergo an exponential increase.

Parasites

The ‘enemy release hypothesis’ maintains that immigrant species owe their persistence to their effective release from natural enemies they encounter in their native range (Elton, 1958). But immigrants may instead acquire a new array of parasites. The degree of taxonomic unrelatedness of the immigrants to natives in the new range is one predictor of their susceptibility to parasites (Strong *et al.*, 1984). Thus, plantings of *Pinus radiata* in Chile, Africa, Australia, and New Zealand were largely disease-free from the late 1800s until mid-20th century when *Dothistroma pini* Hulbary was accidentally introduced from North America (Manion, 1991).

Alien conifers in North America probably have not had even a temporary reprieve from parasitic attack. For example, introduced pines face an extensive array of lethal native macro- and microparasites (dwarf mistletoes, nematodes, and fungi) (Harrington & Wingfield, 1998). *Pinus nigra*, *Pinus thunbergii*, and *Pinus sylvestris* are highly susceptible to infection by the native pinewood nematode (*Bursaphelenchus xylophilus*), whereas many native pines (e.g. *Pinus strobus*, *Pinus resinosa*, *Pinus elliottii*) are resistant (Mamiya, 1983; Wingfield *et al.*, 1984). Although parasites likely destroy introduced conifers in North America, there is no evidence that parasites alone account for these aliens' common failure to become naturalized.

Absence of requisite mycorrhizae

Conifers grow poorly or even die without mycorrhizal associates. As a result, the demise of alien conifers in new ranges that lack compatible mycorrhizae fungi are classic examples of range restriction (Briscoe, 1959; Mikola, 1970; Richardson *et al*., 2000). The sites we examined are well within the range of native conifers, which often reside in adjacent stands. These natives are undoubtedly infected with ectomycorrhizae (EM) fungi. Most EM fungi are considered generalists in their range of hosts and would readily infect not only alien congeners but even members of different coniferous families (Molina *et al*., 1992). Furthermore, most EM fungi are not host-specific below the genus level (< 10% in field studies in California and Montana (Horton & Bruns, 1998; Cullings *et al*., 2000)). Consequently, a mycorrhizal limitation for alien conifers, except in sites far removed from forests (Stoeckeler & Slabaugh, 1965), is unlikely but cannot be discounted outright.

Size of founder population

Small founder populations are usually driven to extinction (Mack, 2000). Conifer invasions in the Southern Hemisphere were facilitated, if not instigated, by large, commercial plantations (Richardson & Higgins, 1998; Richardson, 1998). By contrast, non-indigenous conifers have rarely been grown on a large scale in North America. If non-native conifers were as widely planted in North America as in the plantings in the Southern Hemisphere, would more conifer invasions ensue? The comparatively large founder populations employed for *Pinus nigra* on the sand dunes of Lake Michigan (26,000 seedlings between 1956 and 1972 (Leege & Murphy, 2000)) and the thousands for *Pinus thunbergii* on Nantucket Is. (Jones, 1930) likely contributed to their establishment. Interaction between the size of the founder population and the persistence strongly influences the outcome of introductions, including the conifer introductions we investigated here (Lockwood *et al*., 2004; Richardson *et al*., 2004).

CONCLUSIONS

Alien conifers have consistently failed to become naturalized, much less invasive, across the USA. This failure includes dozens of alien conifers with radically different native ranges, diverse habitats across the conterminous USA, and numerous introduction scenarios. Apparently, the combination of species, habitats, and introduction events that would yield a persistent population has rarely been assembled. We report here a quantitative record with which to begin exploring the cause(s) for these widespread extirpations. Do chance events alone explain this pattern (Mack, 2000; Drake & Lodge, 2004), as opposed to chronic, intrinsic features of the environments in North America with respect to the spread of conifers? Confirmation of the former scenario would highlight the need to monitor conifer introductions in the USA for evidence of incipient naturalization (Richardson & Rejmánek, 2004) and to conduct risk assessments (e.g. propagule pressure, character of cultivation, number of introduction attempts) for future alien conifer introductions. Confirmation of the latter scenario would be cautionary signal to future attempts to develop forestry in the USA with alien conifers. As is so often the case in explaining the distribution of species, the explanation will likely have multiple, interacting components (Goheen & Hansen, 1993; Cairns & Moen, 2004). Whatever the explanation, the fate of alien conifers in the USA from an ecological and economic standpoint warrants careful investigation and resolution.

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