Biological Invasions (2006) 8: 231–240
DOI 10.1007/s10530-004-5163-9

Facilitation and inhibition of seedlings of an invasive tree (*Acer platanoides*) by different tree species in a mountain ecosystem

K. O. Reinhart[1,2,*], Fernando T. Maestre[3,4] & Ragan M. Callaway[1]
[1]Division of Biological Sciences, The University of Montana, Missoula, MT 59812, USA; [2]Present Address: Department of Biology, Indiana University, Jordan Hall RM 127, 1001 East Third Street, Bloomington, IN 47405-3700, USA; [3]Departamento de Ecología, Universidad de Alicante, Apartado de correos 99, 03080 Alicante, Spain; [4]Present Address: Department of Biology, Duke University, Phytotron Building, Science Drive, Box 90340, Durham, NC 27708-0340, USA; [*]Author for correspondence (e-mail: kureinha@indiana.edu)

Received 11 February 2004; accepted in revised form 21 October 2004

Key words: *Acer platanoides*, ecosystem-level changes, facilitation, invasion resistance, *Pseudotsuga menziesii*

Abstract

Facilitation is known to be an important process structuring natural plant communities. However, much less is known about its role in facilitating the invasion of ecosystems by non-native plant species. In this study we evaluated the effects of invasive (*Acer platanoides*) and native (*Pseudotsuga menziesii*) forest types on the performance of *A. platanoides* seedlings, and related these effects to structural and functional properties associated with the two forest types, in a native *P. menziesii* forest that is being invaded by *A. platanoides*. *Acer platanoides* seedlings had higher densities, recruitment, and survival, and experienced less photoinhibition and water stress when beneath conspecific canopies than in the adjacent *P. menziesii* forest. Soil moisture and canopy cover were greater in the invaded patch than the native forest. There was no difference in soil fertility or understory light levels between locations. These demographic (i.e. seedling survival), physiological, and environmental differences appeared to be due to the effects of *A. platanoides* and *P. menziesii* trees. Thus, *Acer* trees appear to produce a more mesic environment by modifying the structure and phenology of the forest canopy and by altering the timing of transpirational water loss relative to *P. menziesii*. Environmental modification by invaders that lead to positive effects on conspecifics may help us to understand the dramatic success and lag periods of some invasive species.

Biological invasions are a serious threat to natural systems (Usher 1988; Vitousek et al. 1996). Invasive non-native plants may reduce the diversity of native species, disrupt nutrient and hydrologic cycles, and modify the disturbance regimes and geomorphology of invaded ecosystems (Gordon 1999; Mack et al. 2000; Pimentel et al. 2000). Therefore, understanding the mechanisms underlying biological invasions is crucial to understanding and predicting invasions and will contribute to the management and restoration of invaded and natural ecosystems (Mack et al. 2000; Levine et al. 2003).

Successful invasion by non-native species has been linked to the functional traits of invaders and the invasibility of the native plant community (Mack et al. 2000). The absence of natural enemies such as herbivores and pathogens (Keane and Crawley 2002), fluctuating resources (Davis et al. 2000), resistance to particular root exudates (Callaway and Aschehoug 2000), and empty niches (Elton 1958) have been proposed to affect the invasibility of communities. Ecosystem-scale factors such as anthropogenic or stochastic forms of disturbance (Hobbs and Huenneke 1992) may also contribute to the success of invaders. Recently, facilitative interactions among non-native species have been proposed as important drivers of invasion (Simberloff and Von Holle 1999). Positive interactions between plants are common in natural plant communities (Callaway 1995, 1998), but there have been few empirical studies of facilitation as a process affecting the invasion of plant communities (Maron and Connors 1996).

A. platanoides (Linn.) is a late-successional tree occurring naturally in mesic deciduous forests throughout much of Eurasia (Schmucker 1942). It has invaded mixed-deciduous forests in riparian bottomlands (Reinhart 2003), coniferous forests in Montana and Idaho (K. O. Reinhart, personal observation), and deciduous hardwood forests throughout the northeastern USA (Nowak and Rowntree 1990) and eastern Canada (Dunster 1990). *A. platanoides* invasion in the northern Rocky Mountains appears to be moderate at the present time (K. O. Reinhart, personal observation). However, virtual monocultures of the invader can develop in floodplains (Reinhart 2003), its recruitment in deciduous forests can far outpace native recruitment (Wyckoff and Webb 1996; Martin 1999), and models of recruitment indicate that future population growth of this species will be very rapid in the area (E. Greene, unpublished data).

Invaders with unique structural and functional attributes relative to resident native species are predicted to have a stronger impact on the composition, succession, and productivity of the invaded community than invaders that are similar to the native plant species (Levine and D'Antonio 1999). However by attaining dominance in a foreign system, an invasive species that is a functional analog to species already present in the recipient community can also impact ecosystem-level processes by homogenizing the system (Levine et al. 2003). Within deciduous hardwood forests of eastern North America, *A. platanoides* appears to be functionally (i.e. deciduous tree, late-successional, and shade adapted) similar to two native species, *Acer saccharum* Marsh. and *Fagus grandifolia* Ehrb. (Lei and Lechowicz 1997; Delcourt and Delcourt 2000). Since *A. platanoides* is a late-successional deciduous tree species, it represents a functionally unique species in relatively mesic evergreen coniferous forests dominated by *P. menziesii* Mirbel Franco and *Thuja plicata* Donn. in the northern Rocky Mountain region (Peet 2000).

Here we evaluated the effects of *A. platanoides* and *P. menziesii* forest types on *A. platanoides* seedlings and related these effects to functional properties associated with the two forest types. Based upon general observations and the results from previous empirical studies (Wyckoff and Webb 1996; Martin 1999; Reinhart 2003), we hypothesized that *A. platanoides* seedlings are facilitated by the effects of conspecifics on the environment, and that these effects will increase their performance. We examined this hypothesis by comparing demographic patterns and ecophysiology of *A. platanoides* seedlings beneath the canopies of *A. platanoides* and *P. menziesii*.

Materials and methods

Site description

Our study site is located ~600 m NE of Bonner, Montana (N 46°52.497′ W 113°51.460′) at an elevation of 1030 m. The site is located near the bottom of a hillside with a north-facing slope of 25–32°. The average annual precipitation is 340 mm, with 140 mm falling from May to August, and the mean annual temperature is 6.7 °C. In 2000, the initial year of this study, the region experienced an intense summer drought and received only 71 mm of precipitation from May to August. In the following years, the area received 153 and 144 mm of summer precipitation in 2001 and 2002, respectively. Soils are deep, well drained gravely loam (USDA 1995). The natural community is dominated by *P. menziesii* trees, with mixed *Acer glabrum* Torr. and *Betula occidentalis* Hook. trees, and understory shrubs such as *Amelanchier alnifolia* Nutt and *Symphoricarpos albus* Hook. Two patches of invading *A. platanoides* were identified at the study site. The patches differ in size. The larger patch is of approximately 250 m^2 in area and contains 15 *A. platanoides* trees, and the smaller patch is 60 m^2 in area and contains 3 *A. platanoides* trees. Seedlings of

A. platanoides were found in and around the patches, while seedlings of *P. menziesii* were uncommon. The majority of our research was conducted in the large patch of *A. platanoides* and the adjacent *P. menziesii* forest on the same slope and aspect to the north, which had no *A. platanoides* trees. The "*soil experiment*" described below was the only experiment that utilized both patches of *A. platanoides*. There were no apparent differences in either landscape positioning or geomorphology between the large invaded patch and the adjacent *P. menziesii* forest.

Seedling demography

In July of 2000, we established a 42-m transect at a constant elevation and starting in the large *A. platanoides* patch and extending into the *P. menziesii* forest. Eight 15-m parallel transects, separated by 6 m, were run perpendicular to and down slope from the 42-m transect. The first 15-m transect was placed in the large patch. The second 15-m transect was placed on the interface between the invaded patch and adjacent intact forest, and the remaining six, 15-m transects were placed at 6-m intervals away from the invaded patch and parallel to the previous two 15-m transects. Five 1-m^2 permanent plots were randomly placed along each of the 15-m transects. All *A. platanoides* seedlings in each plot were counted and tagged. In June, 2001 and 2002, we measured survival of tagged seedlings and counted and tagged new seedlings. From these data, we estimated total seedling density for all three years and quantified survival and recruitment of seedlings between the following years; 2000–2001 and 2001–2002. The effect of distance from the *A. platanoides* patch on total seedling density was analyzed with repeated measures ANOVA (ANOVAR), with distance and time as factors. The data were transformed with a square-root function ($\sqrt{[X + 0.5]}$) to maintain equality of the covariance matrix. The effect of distance from the *A. platanoides* patch and year on survival and seedling density was analyzed with two-way ANOVA. The variances were heterogeneous, but we still used ANOVA because it is robust to heterogeneity of variances (Underwood 2002). All of the analyses were performed with SPSS version 10 (SPSS Inc., Chicago, IL, USA).

Seedling physiology

We compared the physiology of *A. platanoides* seedlings in the conspecific patch to those in neighboring *P. menziesii* forest. Seven random points were selected at each location, and five *A. platanoides* seedlings were selected in close proximity to each point. We randomly selected one seedling out of five from each of seven points ($n = 7$) in each location on July 11 and August 2 and 17, 2000. On each sampling date, we recorded water potentials and chlorophyll fluorescence of selected seedlings. These measures provide estimates of water stress and photosystem stress, respectively. Predawn and midday (14:00 h MST) water potentials were measured *in situ* on small leaves using a pressure bomb (PMS Instrument Co., Corvallis, OR, USA). Chlorophyll fluorescence was measured by using a portable, pulse-modulated fluorometer (OS-100, Opti-Sciences Inc., Tyngsboro, MA, USA). Predawn and midday (14:30 h MST) measures of maximal (F_m) and minimal (F_0) fluorescence were used to calculate maximum efficiency of the photosynthetic energy conversion of PSII ($F_v/F_m = [F_m - F_0]/\ F_m$). Predawn measurements were performed before sunrise; midday measurements were made after 30 min dark adaptation. We tested the effect of forest type on F_v/F_m and leaf water potentials of *A. platanoides* seedlings with two-way ANOVA (location and sampling date), with both factors being fixed. To maintain homogeneity of variances for these analyses, we transformed predawn F_v/F_m data with a power function (x^2), midday F_v/F_m data with a power function (x^3), and midday and predawn water potentials with a natural log function ($\ln x$). Even after transformation, the predawn water potential and the midday F_v/F_m data continued to violate the homogeneity of variances assumption. Analysis of variance was still used, because it is robust to heterogeneity of variances (Underwood 2002).

Canopy characteristics

We accompanied the midday fluorescence measurements with measurements of photosynthetically active radiation (PAR) within the understory ($n = 7$) during cloudless conditions using a light meter and quantum sensor (LI-250, LI-COR, Lincoln, NE, USA). We also characterized the canopy cover of the *A. platanoides* patch ($n = 10$) and of the neighboring *P. menziesii* forest ($n = 15$) by measuring leaf area index (LAI), with a LAI-2000 Plant Canopy Analyzer (LI-COR, Lincoln, NE, USA). LAI measurements were taken from random points on September 6, 2001 during overcast conditions. Canopy measurements were compared with a reference location in the open. Measurements were taken 1 m above the ground, using a 45° view cap on the sensor head. We tested the effect of forest type on LAI and PAR with two sample *t*-tests.

Soil moisture

Gravimetric soil moisture was measured on August 2 and 17, 2000. We collected soil at midday from random points in the invaded patch and native forest ($n = 10$). We cored soil to a depth of 10 cm and used the −5 to −10 cm portion of the core for moisture analysis. Differences between forest types (*A. platanoides* vs *P. menziesii*) were tested with two-way ANOVA (location and sampling date as fixed factors). Data were transformed with a log function ($\log [x + 1]$) prior to analysis to maintain homogenous variances.

During 2001, we measured soil moisture in the two forest types (*A. platanoides* [$n = 6$] and *P. menziesii* [$n = 15$]) using frequency domain reflectometry. Measurements were taken on May 16, June 19, and July 25, with a Sentry 200-AP soil moisture probe (Troxler Electronic Laboratories, Inc., Research Triangle Park, NC, USA) at three depths (−10, −20, and −30 cm from the surface). The effect of forest type on soil moisture was analyzed with repeated measures ANOVA; location, time, and soil depth were factors with time and soil depth as repeated measures and location as a fixed factor.

Soil experiment

In this experiment, we evaluated the effect of soil from the two forest types (*A. platanoides* and *P. menziesii*) and two sites (two *A. platanoides* patches and adjacent *P. menziesii* forest) on the growth of *A. platanoides* seedlings. On August 27, 2001, we collected field soil (0–10 cm in depth) from six and four randomly selected points within the large and small *A. platanoides* patches, respectively. Soil was also collected from six and four randomly selected points within the *P. menziesii* forest adjacent to the large and small *A. platanoides* patches, respectively. The soil was then mixed to a 1:1 ratio with commercial silica sand averaging 0.60–0.85 mm in diameter (20/30 grit, Lane, MT, USA), and this mixture was used to fill individual plastic pots (16.5 cm wide and 17.5 cm tall). *A. platanoides* seedlings of the same approximate size, which germinated in 2001, were collected from the large patch on August 30, 2001. Immediately after field collection, seedling roots were surface sterilized in order to avoid transplanting rhizosphere biota from the field soil into the experimental units. Surface sterilization was accomplished by placing seedling roots in a 10% solution of commercial NaOCl for 10 min followed by rinsing with deionized water. After root sterilization, one *A. platanoides* seedling was planted into each pot. The initial basal diameter, leaf number, and stem height of each seedling was measured. Plants were kept in the University of Montana greenhouse and watered 3–4 times a week. Supplemental light was added to prevent senescence in the autumn and winter. After nine months in the greenhouse, each seedling was measured for final basal diameter, leaf number, and height, and the plants were harvested thereafter and divided into roots, stems, and leaves. All harvested material was dried at 65 °C until constant weight. The effect of soil location on the total biomass, root mass ratio (root biomass: total biomass), and the relative change in seedling height ([(final height − initial height)/ initial height] * 100) were tested with two-way ANOVA in which soil type and site were fixed factors.

Results

A. platanoides seedlings were found far from the parental patch, but the density of *A. platanoides* seedlings was ≥ 3 times higher within or near the parental patch than away from the patch (Figure 1a; ANOVAR; $F_{\mathrm{Distance}} = 83.2$, $\mathrm{df} = 7$, $P < 0.0005$). Seedling density was greater in 2000 than the other two years (ANOVAR;

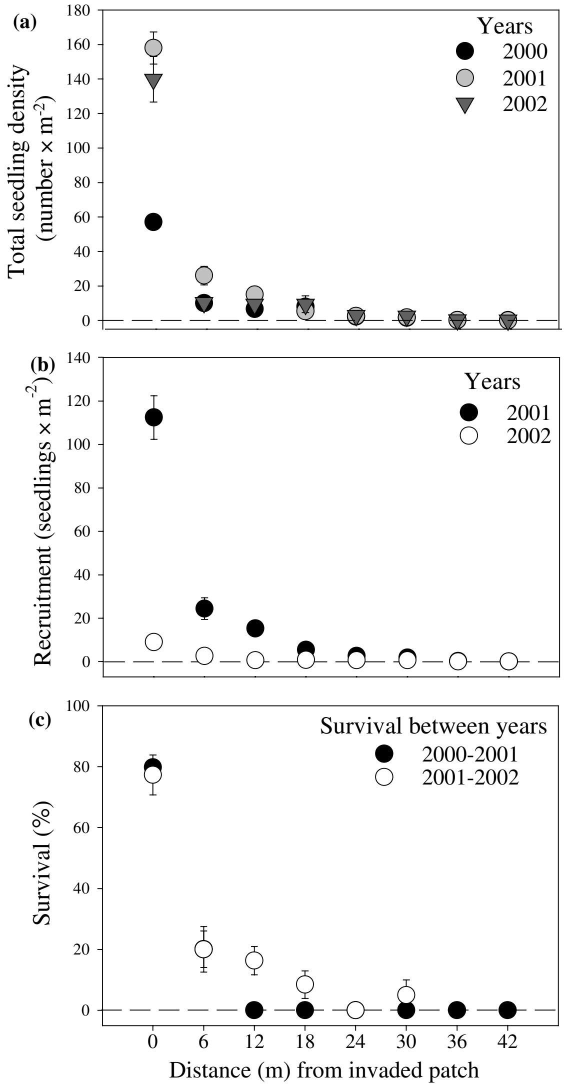

Figure 1. Total density (a), recruitment (b), and survival (c) of *Acer platanoides* seedlings with increasing distance from the parental patch. The effect of distance from the patch on seedling densities per plot over three years was tested using repeated measures ANOVA with sphericity assumed. Effect of distance from the *Acer* patch on the recruitment and survival for separate years was tested with two-way ANOVA. Error bars represent 1 S.E. ($n = 5$ at each distance).

$F_{\text{Year}} = 60.3$, df = 2, $P < 0.0005$), and the variation in distance was greatest in close proximity to the invaded patch (ANOVAR; $F_{\text{Distance} \times \text{Year}} = 29.3$, df = 14, $P < 0.0005$). We also found ≥ 3.3 times higher seedling recruitment in the invaded patch than the *P. menziesii* forest (Figure 1b; ANOVA; $F_{\text{Distance}} = 95.0$, df = 7, $P < 0.0005$). Recruitment was higher in 2001 than 2002 (ANOVA; $F_{\text{Year}} = 152.7$, df = 1, $P < 0.0005$), and the variation between years was greater in close proximity to the invaded patch than away from the patch (ANOVA; $F_{\text{Distance} \times \text{Year}} = 69.3$, df = 7, $P < 0.0005$). Seedling survival was ≥ 2.8 times higher in the conspecific patch than in surrounding natural forest (Figure 1c; ANOVA; $F_{\text{Distance}} = 70.7$, df = 7, $P < 0.0005$). Seedlings had greater survival between 2001 and 2002 than 2000 and 2001 (ANOVA; $F_{\text{Year}} = 14.3$, df = 1, $P < 0.0005$). Additionally, there was an interactive effect of Year and Distance on seedling survival (ANOVA; $F_{\text{Distance} \times \text{Year}} = 3.04$, df = 6, $P = 0.015$).

We also found a strong effect of the forest type on the physiological performance of *A. platanoides* seedlings (Figure 2). Seedlings in the conspecific patch had greater water potentials than seedlings in the *P. menziesii* forest at both predawn (ANOVA; $F_{\text{Location}} = 81.6$, df = 1, $P < 0.0005$) and midday (ANOVA; $F_{\text{Location}} = 56.2$, df = 1, $P < 0.0005$). Similarly, seedlings in the conspecific patch had higher F_v/F_m values at both predawn (ANOVA; $F_{\text{Location}} = 138.8$, df = 1, $P < 0.0005$) and midday (ANOVA; $F_{\text{Location}} = 90.2$, df = 1, $P < 0.0005$). Predawn and midday water potentials values were greater in early July than late-July and August ($F_{\text{Location}} = 145.8$, df = 2, $P < 0.0005$; $F_{\text{Location}} = 104.8$, df = 2, $P < 0.0005$, respectively), and predawn and midday F_v/F_m values were greater in early July than late-July and August ($F_{\text{Location}} = 34.9$, df = 2, $P < 0.0005$; and $F_{\text{Location}} = 57.9$, df = 2, $P < 0.0005$, respectively). Moreover, the seasonal differences in F_v/F_m values between locations were greater in August and late-July than early-July (predawn data, $F_{\text{Location} \times \text{Time}} = 12.2$, df = 2, $P < 0.0005$; midday data, $F_{\text{Location} \times \text{Time}} = 13.1$, df = 2, $P < 0.0005$).

Canopy cover (LAI) was 55% greater in the invaded patch than in the adjacent native forest (Figure 3; two sample *t*-test, $t = 6.44$, df = 23, $P < 0.0005$). These structural differences did not correspond with a difference in understory light quantity (PAR; $t = 1.07$, df = 40, $P = 0.292$). The soil was more moist in the *A. platanoides* patch (12.7 ± 1.3 and 11.0 ± 0.7; means ± 1 SE) than in the *P. menziesii* forest (5.1 ± 0.4 and 6.7 ± 0.9) on August 2 and 17, 2000, respectively (ANOVA; $F_{\text{Location}} = 59.2$, df = 1, $P < 0.0005$).

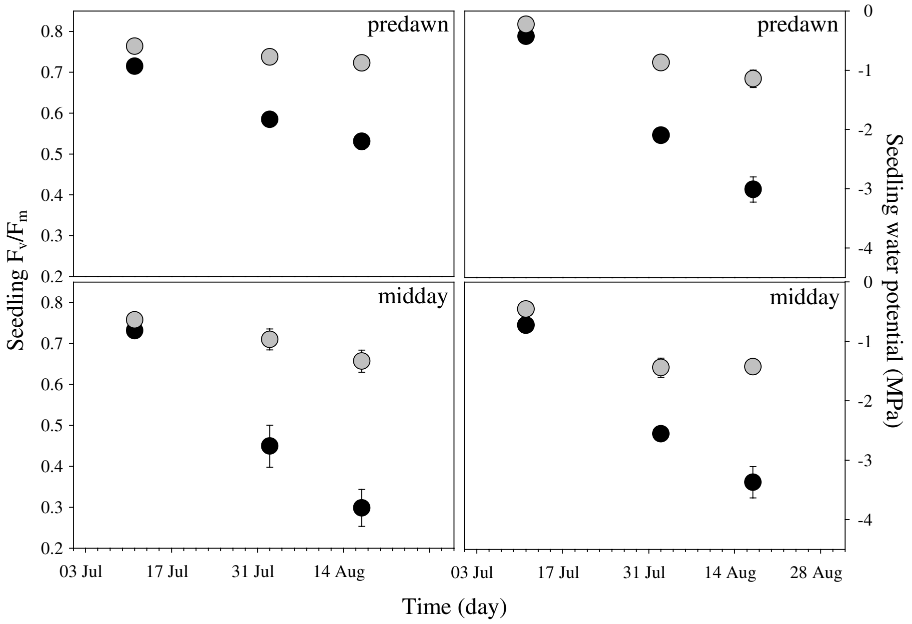

Figure 2. Effect of location on leaf water potential and maximum efficiency of photosystem II (F_v/F_m) of *A. platanoides* seedlings ($n = 7$ per treatment) during summer 2000. Seedlings were located either in a patch invaded by *Acer* (gray circles) or in the neighboring *P. menziesii* forest (black circles). Error bars represent 1 S.E. ($n = 7$ per treatment).

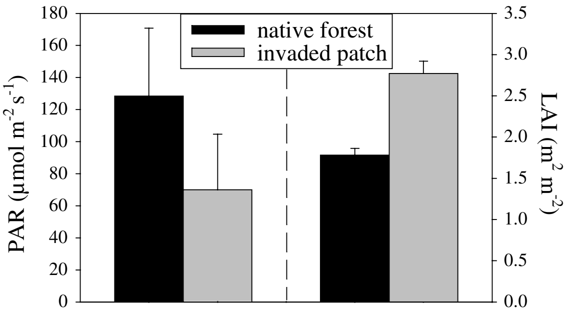

Figure 3. Effect of forest type (invasive *A. platanoides* vs native *P. menziesii*) on PAR in the understory and LAI. Error bars represent 1 S.E.

There was no effect of sampling date (ANOVA; $F_{\mathrm{Time}} = 0.2$, df = 1, $P = 0.62$) and no significant interaction between sampling date and location on soil moisture ($F_{\mathrm{Location\ \times\ Time}} = 3.6$, df = 1, $P = 0.07$). In 2001, soil moisture was also greater in the *A. platanoides* patch than in the *P. menziesii* forest (Table 1a and Figure 4). Deeper soils had greater soil moister than surface soils, and soil moisture varied seasonally (Table 1b and Figure 4).

Soil from the different forest types did not affect the growth of *A. platanoides* seedlings. There was no effect of forest type on total biomass, root mass ratio, or relative change in seedling height (Table 2).

Discussion

A. platanoides seedlings had higher densities, recruitment rates, and survival rates, and experienced less photoinhibition and water stress, beneath conspecifics than beneath adjacent *P. menziesii* trees. Moreover, the increased physiological stress associated with *Acer* seedlings growing in *P. menziesii* forest relative to the *A. platanoides* patch in 2000 corresponded with a dramatic difference in seedling survival between the two forest types during the period with the lowest overall seedling survival (between 2000 and 2001). These patterns (i.e. survival and ecophysiological data) suggest that mature *A. platanoides* trees may facilitate conspecific seedlings, and that conditions existing beneath *P. menziesii* canopies resist the spread of *A. platanoides*. These results

Table 1. Summary of repeated measures ANOVA with the effect of forest location (*A. platanoides* vs *P. menziesii* forest), sampling time, and soil depth. *P*-values ≤ 0.05 are in bold.

Source of variation	df	MS	*F*	*P*
(a) Between-subjects effects				
Intercept	1.0	14982.9	357.3	**< 0.0005**
Location	1.0	825.0	19.7	**< 0.0005**
Error	15.0	41.9		
(b) Within-subjects effects				
Time	1.2	647.0	23.5	**< 0.0005**
Time × Location	1.2	8.6	0.3	0.63
Error (Time)	18.3	27.5		
Depth	1.5	315.2	33.7	**< 0.0005**
Depth × Location	1.5	8.9	1.0	0.38
Error (Depth)	22.3	9.4		
Time × Depth	2.0	1.7	0.4	0.66
Time × Depth × Location	2.0	3.2	0.8	0.45
Error (Time × Depth)	30.1	4.0		

Tests were performed using the type four sums of squares from SPSS version 10 (SPSS Inc., Chicago, IL, USA). Between-subject effects of the model tested Location. Within-subject effects of the model tested Location × Time × Depth and all combinations of factors. The error covariance matrix was not proportional to the identity matrix so the df were adjusted with the Greenhouse–Geisser test.

correspond with patterns of higher *A. platanoides* seedling densities beneath conspecific adults than beneath natives in deciduous forests in the northeastern USA (Wyckoff and Webb 1996; Martin 1999) and riparian forests in Montana (Reinhart 2003). We hypothesize that the greater seedling densities associated with the invading *A. platanoides* reported here and in other studies is driven partly by differences in seedling survival. However, this pattern is also influenced by the increased seed rain beneath conspecifics relative to heterospecifics.

Increased performance (i.e. increased survival and less physiological stress) of *A. platanoides* seedlings was closely related to changes in forest structure and environmental conditions promoted by conspecific trees, which were primarily increased soil moisture in the *A. platanoides* patch relative to the *P. menziesii*-dominated forest. These differences may be confounded by subtle differences in geomorphology and landscape position and the lack of replication. However, the apparent homogeneity of the landscape suggests that differences in LAI, soil moisture, and seedling responses were due to modification of the environment by the overstory canopy.

P. menziesii is physiologically active earlier in the spring (Lewis et al. 1999) than *A. platanoides*, which must produce leaves before transpirational water loss is possible. Full-size leaves are not

Table 2. Summary of two-way ANOVA of effects of soil source (*A. platanoides* vs *P. menziesii*) and site on the total biomass, root mass ratio (root mass × total biomass^{-1}), and relative change in height of *A. platanoides* seedlings.

Dependent variable	Factor	df	MS	*F*	*P*
Total biomass	Soil	1	2.86	0.16	0.69
	Site	1	2.97	0.17	0.69
	Soil × Site	1	20.50	1.18	0.29
	Error	16	17.42		
Root mass ratio	Soil	1	0.0005	0.11	0.74
	Site	1	0.0087	1.91	0.19
	Soil × Site	1	0.0029	0.63	0.44
	Error	16	0.0046		
Relative change in height	Soil	1	10113.0	0.97	0.34
	Site	1	54.0	0.01	0.94
	Soil × Site	1	9440.0	0.90	0.36
	Error	16	10476.0		

Tests were performed using the type three sums of squares from SPSS version 10 (SPSS Inc., Chicago, IL, USA).

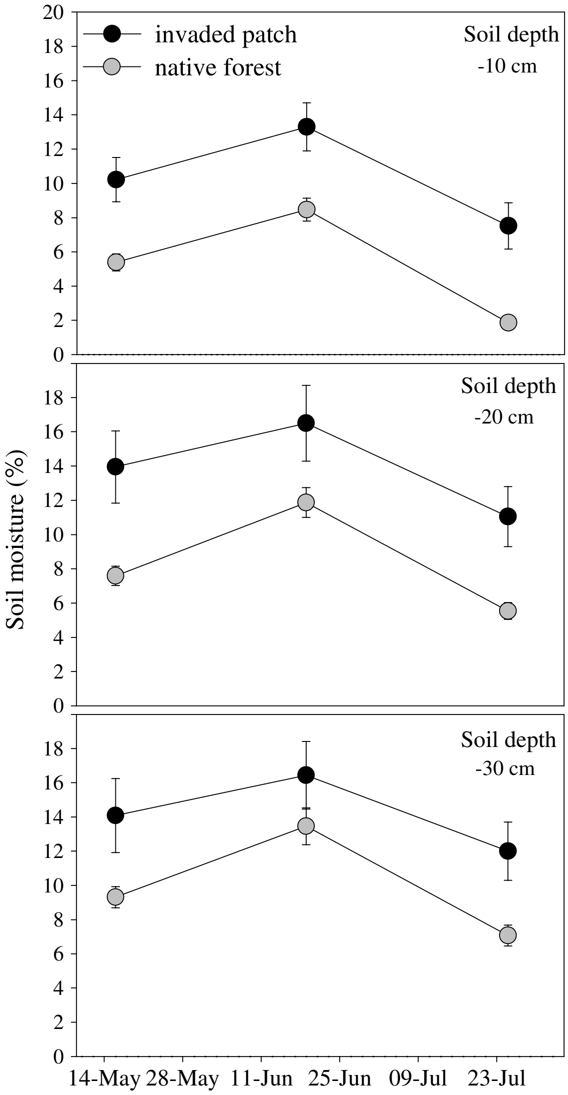

Figure 4. Effect of forest type (invaded patch of *A. platanoides* [$n = 6$] vs native forest of *P. menziesii* [$n = 15$]) on soil moisture on different days and at different depths below the soil surface. Refer to Table 1 for repeated-measures ANOVA results. Error bars represent 1 S.E.

developed until mid- to late-May in Montana (Reinhart, unpublished data). Thus, the initial differences in soil moisture between locations in mid-May of 2001 appear to be due to early transpiration by *P. menziesii*. Invasive plants with different phenologies than natives have been shown to impact the hydrology in other ecosystems (Mueller-Dombois 1973). The reduced soil moisture in the *P. menziesii* forest relative to the *Acer* understory may also have been affected by temporal variation in canopy cover (i.e. evergreen vs deciduous; Iroumé and Huder 2002). The evergreen canopy will intercept greater amounts of winter and spring precipitation than a deciduous canopy which will reduce water infiltration into the soil below the evergreen canopy relative to the deciduous canopy. *P. menziesii* is also known to negatively effect the water use and growth of other native conifer species by aggressively using water resources and reducing the moisture content of the soil in other areas of western Montana (A. Sala, unpublished data).

Soil moisture may have also been affected by differences in canopy cover. During the growing season, *A. platanoides* canopy cover (LAI) was greater than that of *P. menziesii*. In contrast, we did not detect a difference in understory light quantity between forest types, which may have resulted from small sample size and high variability in PAR measurements associated with the mixture of sun flecks and deep shade. Increased shade may suppress some species, but shade can benefit others by reducing leaf temperatures, transpiration and evaporation rates, and light damage (see Egerton et al. 2000; Shumway 2000). Many studies have found that soil in understories is more mesic than in neighboring open areas (McLeod and Murphy 1977; Belsky and Amundson 1989; Ko and Reich 1993). This canopy effect may result from decreased evaporation rates or through hydraulic lift of water through the roots of plants (Horton and Hart 1998).

Our results indicate that the effect of the different overstory trees on soil (structure, fertility, and biota) neither facilitates nor inhibits invasion of *A. platanoides*. Research in the northeastern USA also found no effect of soil from invaded and uninvaded sites on the growth of conspecifics (Howard et al. 2000). Thus, differences in soil moisture, rather than differences in soil fertility, appear to be the primary factors affecting the invasion of *A. platanoides* in upland ecosystems in the northern Rocky Mountains.

In conclusion, our results suggest that *A. platanoides* facilitates conspecific seedlings by creating a more mesic environment than produced by the natural upland coniferous forest. *P. menziesii* forests appear to be relatively resistant to invasion by

A. platanoides, because they produce, or are associated with, environments that are too stressful for *Acer* to proliferate. The primary limiting resource for *A. platanoides* invasion into this forest type appears to be water. Natural and anthropogenic gaps or years with increased precipitation may initiate colonization of *A. platanoides* in conifer forests, and transformation of the ecosystem by colonists may start a form of "invasional meltdown" (Simberloff and Von Holle 1999) in which positive feedback between invader and environment drives exponential population increase as described for many successful exotic species.

Acknowledgements

We thank Maureen S. O'Mara for her assistance in the field and Anna Sala for her insightful comments and friendly discussions. We thank Plum Creek Timber Company, Inc. (Missoula, MT) for allowing access to their property. We thank two anonymous reviewers for their helpful comments. The work of F. T. Maestre was supported by a FPU fellowship of the Spanish Ministerio de Educación, Cultura y Deporte. This research was supported in part by funding to R. M. Callaway by the Andrew W. Mellon Foundation and NSF, DEB-9726829 and in part by funding to K. O. Reinhart by USDA-NRI Grant 2003-02047.

References

Belsky AJ and Amundson RG (1989) The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya. Journal of Applied Ecology 26: 1005–1024

Callaway RM (1995) Positive interactions among plants. The Botanical Review 61: 306–349

Callaway RM (1998) Are positive interactions species-specific? Oikos 82: 202–207

Callaway RM and Aschehoug ET (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. Science 290: 521–523

Davis MA, Grime JP and Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88: 528–534

Delcourt HR and Delcourt PA (2000) Eastern Deciduous Forests. In: Barbour MG and Billings WD (eds) North American Terrestrial Vegetation, pp 357–395. Cambridge University Press, Cambridge

Dunster K (1990) Exotic plant species management plan, Point Pelee National Park, Report prepared for Parks Cananda, Ontario Region

Egerton JJG, Banks JCG, Gibson A, Cunningham RB and Ball MC (2000) Facilitation of seedling establishment: reduction in irradiance enhances winter growth of *Eucalyptus pauciflora*. Ecology 81: 1437–1449

Elton CS (1958) The Ecology of Invasions by Animals and Plants. Methuen, London, UK

Gordon DR (1999) Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. Ecological Applications 8: 975–989

Hobbs RJ and Huenneke LF (1992) Disturbance, diversity, and invasion: implications for conservation. Conservation Biology 6: 324–337

Horton JL and Hart SC (1998) Hydraulic lift: a potentially important ecosystem process. Trends in Ecology and Evolution 13: 232–235

Howard TG, Gurevitch JK, Brown K and Fang W (2000) The differential influence of site and soil characteristics on invasibility of forest communities. The Ecological Society of America 85th Annual Meeting

Iroumé A and Huder A (2002) Comparison of interception losses in a broadleaved native forest and a *Pseudotsuga menziesii* (Douglas fir) plantation in the Andes Mountains of southern Chile. Hydrological Processes 16: 2347–2361

Keane RM and Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution 17: 164–170

Ko LJ and Reich PB (1993) Oak tree effects on soil and herbaceous vegetation of savannas and pastures in Wisconsin. American Midland Naturalist 130: 31–42

Lei TT and Lechowicz MJ (1997) The photosynthetic response of eight species of *Acer* to simulated light regimes from the centre and edges of gaps. Functional Ecology 11: 16–23

Levine JM and D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87: 15–26

Levine JM, Vilà M, D'Antonio CM, Dukes JS, Grigulis K and Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society of London 270: 775–781

Lewis JD, Olszyk D and Tingey DT (1999) Seasonal patterns of photosynthetic light response in Douglas-fir seedlings subjected to elevated atmospheric CO_2 and temperature. Tree Physiology 19: 243–252

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M and Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10: 689–710

Maron JL and Connors PG (1996) A native nitrogen-fixing shrub facilitates weed invasion. Oecologia 105: 302–312

Martin PH (1999) Norway maple (*Acer platanoides*) invasion of a natural forest stand: understory consequence and regeneration pattern. Biological Invasions 1: 215–222

McLeod KW and Murphy PG (1977) Establishment of *Ptelea trifoliata* on Lake Michigan sand dunes. American Midland Naturalist 97: 350–362

Mueller-Dombois D (1973) A non-adapted vegetation interferes with water removal in a tropical rain forest area in Hawaii. Tropical Ecology 14: 1–18

Nowak DJ and Rowntree RA (1990) History and range of Norway maple. Journal of Arboriculture 16: 291–296

Peet RK (2000) Forests and meadows of the rocky mountains. In: Barbour MG and Billings WD (eds) North American Terrestrial Vegetation, pp 75–121. Cambridge University Press, Cambridge

Pimentel D, Lach L, Zuniga R and Morrison D (2000) Environmental and economic costs of nonindigenous species in the United States. Bioscience 50: 53–65

Reinhart KO (2003) Mechanisms for invasion by non-native trees — facilitation, ecosystem engineering, and escape from belowground enemies. PhD Dissertation, The University of Montana, USA, 122 pp

Schmucker T (1942) The tree species of the northern Temperate Zone and their distribution. Silvae Orbis 4: 406

Shumway SW (2000) Facilitative interactions between a sand dune shrub and species growing beneath the shrub canopy. Oecologia 124: 138–148

Simberloff D and Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biological Invasions 1: 21–32

Underwood AJ (2002) Experiments in Ecology. Cambridge University Press, Cambridge, 504 pp

USDA (1995) Soil Survey of Missoula County Area, Montana Part 1, United States Department of Agriculture, Natural Resources Conservation Service and Forest Service

Usher MB (1988) Biological invasions of nature reserves: a search for generalizations. Biological Conservation 44: 119–135

Vitousek PM, D'Antonio CM, Loope LL and Westbrooks R (1996) Biological invasions as global environmental change. American Scientist 84: 468–478

Wyckoff PH and Webb SL (1996) Understory influence of the invasive Norway maple (*Acer platanoides*). Bulletin of the Torrey Botanical Club 123: 197–205