

Effects of *Acer platanoides* invasion on understory plant communities and tree regeneration in the northern Rocky Mountains

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Quantitative studies are necessary to determine whether invasive plant species displace natives and reduce local biodiversity, or if they increase local biodiversity. Here we describe the effects of invasion by Norway maple *Acer platanoides* on riparian plant communities and tree regeneration at two different scales (individual tree vs stand scales) in western Montana, USA, using both descriptive and experimental approaches. The three stands differed in community composition with the stand most dominated by *A. platanoides* invasion being more compositionally homogenous, and less species rich (–67%), species even (–40%), and diverse (–75%) than the two other stands. This sharp decrease in community richness and diversity of the highly invaded stand, relative to the other stands, corresponded with a 28-fold increase in *A. platanoides* seedlings and saplings. The dramatic difference between stand 1 vs 2 and 3 suggests that *A. platanoides* invasion is associated with a dramatic change in community composition and local loss of species diversity; however, other unaccounted for differences between stands may be the cause. These whole-stand correlations were corroborated by community patterns under individual *A. platanoides* trees in a stand with intermediate levels of patchy invasion. At the scale of individual *A. platanoides* canopies within a matrix of native trees, diversity and richness of species beneath solitary *A. platanoides* trees declined as the size of the trees increased. These decreases in native community properties corresponded with an increase in the density of *A. platanoides* seedlings. The effect of *A. platanoides* at the stand scale was more dramatic than at the individual canopy scale; however, at this smaller scale we only collected data from the stand with intermediate levels of invasion and not from the stand with high levels of invasion. Transplant experiments with tree seedlings demonstrated that *A. platanoides* seedlings performed better when grown beneath conspecific canopies than under natives, but *Populus* and *Pinus* seedlings performed better when grown beneath *Populus* canopies, the dominant native. Our results indicate that *A. platanoides* trees suppress most native species, including the regeneration of the natural canopy dominants, but facilitate conspecifics in their understories.

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Invasive non-native plants threaten to disassemble native communities by altering their composition and reducing their biodiversity (Hobbs and Mooney 1986, Schofield 1989, Braithwaite et al. 1989, Walker and Vitousek 1991, Vivrette and Muller 1998) and pose a serious threat to

the sustained conservation of natural areas (Usher 1988). Non-native plants appear to invade successfully because of particular traits, such as high phenotypic plasticity, pollination by generalists, short-life spans, high fecundity, rapid growth rates (Bazzaz 1986,

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Rejmánek 1995), as well as the strength of their direct and indirect negative effects on native species (Vitousek et al. 1987, Gordon 1999, Marler et al. 1999, Callaway and Aschehoug 2000). Several hypotheses have been proposed to explain the remarkable vulnerability of native communities to invasion by some non-native plant species including: 1) the absence of natural enemies (Keane and Crawley 2002), 2) the existence of empty niches (Elton 1958), 3) anthropogenic disturbances (Mack 1989, Hobbs and Huenneke 1992), 4) fluctuations in resource availability (Davis et al. 2000, Mack et al. 2000), and the disproportionately strong effects of novel allelochemicals (Callaway and Aschehoug 2000, Callaway and Ridenour 2004).

Recently, Simberloff and Von Holle (1999) proposed that positive interactions among invasive non-native species might lead to an "invasional meltdown" in which invaders accelerate invasive success of additional non-natives causing the further demise of native species. Facilitation among plants (Hunter and Aarssen 1988, Callaway 1995) has the potential to rapidly accelerate invasion, but facilitation has received little attention in the context of biological invasion (but see Maron and Connors 1996).

Riparian ecosystems are particularly susceptible to plant invasion because they have been disproportionately affected by human disturbance (Patten 1998). These ecosystems are especially important in arid regions because a high percentage of animal species depend on these habitats for part or all of their life cycle (Brinson et al. 1981, Kondolf and Keller 1991).

Here we focus on the impacts of invasion by a non-native tree species on riparian plant communities in western Montana. Norway maple *Acer platanoides*, a tree native to mesic deciduous forests in Eurasia (Schmucker 1942), has invaded riparian areas in Montana. The level of invasion by *A. platanoides* in the northwestern U.S. as a whole appears to be low, but Greene (unpubl.) has modeled the rapid transformation of forests dominated by native tree species to virtual monocultures of the invader. Currently, *Acer* is invading deciduous forests throughout the northeastern U.S. (Nowak and Rowntree 1990). *Acer platanoides* is widely used throughout northern North America as a street or shade tree (Nowak and Rowntree 1990), and as for many other invasive plants, the spread of *A. platanoides* is partly due to its arboricultural use (Heywood 1989, Reichard and Hamilton 1997, Richardson 1998). In forests of the northeastern U.S., understories below *A. platanoides* canopies have reduced species richness and increased abundances of conspecific seedlings relative to nearby non-invaded areas (Wyckoff and Webb 1996, Martin 1999). In western Montana, *A. platanoides* populations are rapidly expanding and may completely exclude native tree and shrub species in some areas within decades (Greene unpubl.). However, there is little

quantitative or experimental data on the effects of *A. platanoides* on understory community composition and the regeneration of native canopy dominants.

Here we describe the effects of invasion by *A. platanoides* on riparian plant communities along a stream near Missoula, Montana, U.S. We studied the effect of *A. platanoides* invasion by 1) comparing the effect of *A. platanoides* overstories on understory species at two spatial scales: that of individual canopies and that of selected riparian stands that differed in their abundance of *A. platanoides*, 2) conducting an experiment to test the effect of different overstory tree species on the growth of the non-native, *A. platanoides* seedlings and the natives ponderosa pine *Pinus ponderosa* and black cottonwood *Populus trichocarpa*.

Methods

Study site

The study was conducted within three riparian stands along Rattlesnake Creek, Missoula, Montana, which differed in their abundance of *A. platanoides*. The high (76% *A. platanoides* canopy coverage), intermediate (11%), and low (0%) levels of *Acer* invasion correspond with *A. platanoides* canopy coverage estimated from transect data of aerial photographs. Because the invasion appears to be moving upstream (Greene unpubl.), the most heavily invaded stand was downstream of the other two stands, and the stand with the least *A. platanoides* was upstream of the two other stands. The lower stretch of Rattlesnake Creek where invasion is most intense abuts residential areas with many old *A. platanoides* trees planted along the streets and in yards. These trees likely provided the propagules for initial invasion. Based on increment cores of the largest naturalized trees, we estimate the invasion of *A. platanoides* into these stands probably started in the 1940s or 1950s. Thus, our three sites occur along an invasion gradient and possibly along an invasion front.

The three stands were located along 3.4 km of the creek, and the length of the riparian habitat where sampling occurred differed between stands. The length of riparian habitat sampled along the creek is as follows: 520 m for the most heavily invaded stand (N46°52.644', W113°58.565'), 210 m for the stand with intermediate levels of invasion (N46°53.416', W113°58.254'), and 660 m for the stand with the lowest level of invasion (N46°53.969', W113°58.345').

The climate is semi-arid and receives on average 351 mm of precipitation per yr with 150 mm falling May through August (Anon.). The soils are very deep, excessively drained Totelake gravelly loam (Anon. 1995). All stands are below a dam established in 1905, which regulates the flow of the stream. *Populus*, *Pinus*, and Rocky Mountain maple *Acer glabrum* trees dominated

the original native riparian community in areas now invaded by *A. platanoides* (Foote 1965) and continue to dominate the non-invaded areas. The native understory along the Rattlesnake Creek in 1965 was dominated by grasses, forbs, and shrubs (Foote 1965).

Overstory-understory associations

Correlations between *A. platanoides* invasion and understory community composition were made at two spatial scales: that of individual canopies and that of selected riparian stands that differed substantially in their abundance of *A. platanoides*.

1. Riparian stands

The community composition of the understory in the three stands was sampled in August and September of 1999. Ten 50-m transects were distributed throughout each stand. Plots were arranged along transects using a systematic random sampling regime. Each transect was subdivided into five intervals of 10 m. One plot was randomly positioned in each interval (total $n=50$ plots per stand). Plots consisted of 1 m² quadrats, and each quadrat was subdivided into 100 cells with 10 × 10 cm dimensions for accurate quantification of species cover (Pennings and Callaway 1992). The percent cover of all species within a quadrat was estimated by summing the number of cells in a quadrat that contained each individual species. Species were identified according to Hitchcock and Cronquist (1998) and Lackschewitz (1991) (see Appendix). The composition of the canopy (>2 m in height) directly above each plot was classified as *Acer platanoides*, native species, or open sky and canopies with both *A. platanoides* and native species were classified as *Acer platanoides*.

Understory community composition was examined at the stand scale using detrended correspondence analyses (DCA) as a multivariate ordination technique (Hill 1979) with PC-ORD software (McCune and Mefford 1995). DCA was used to determine the variation in understory community composition between stands by comparing the 2-dimensional distribution of ordinated plots for each stand. For this analysis, we incorporated all data from the transect plots into the ordination matrix.

Species richness, evenness, and the Shannon-Wiener Index of Diversity were calculated for each transect plot using PC-ORD software (McCune and Mefford 1995). Species dominance was estimated by calculating the frequency of species occurrence across all transect plots. We tested the effect of riparian stand on the diversity indices and percent cover of the 15 most dominant species for transect data across stands with 1-way ANOVA with Tukey's HSD test using SPSS software (SPSS ver. 10). Since multiple tests were performed we adjusted the alpha level using the Bonferroni method.

The scarcity of riparian stands with comparable levels of *Acer platanoides* invasion prevented replication of stands with varying levels of invasion (high, intermediate, and low). Nonetheless, we used statistical tests (DCA and ANOVA) to help illustrate the differences in community composition between riparian stands. Even though we compared adjacent stands along the lower creek drainage to minimize potentially confounding effects (geological substrate, hydrology, disturbance history, etc.), we recommend caution in relating observed differences between stands to levels of invasion because of the lack of replication. We also corroborated these stand-scale patterns with the correlative and experimental results at the tree-level.

2. Individual canopies

In August and September of 1999, the composition of the understory communities beneath 24 different *A. platanoides* trees was sampled in the riparian stand intermediate in its abundance of *A. platanoides*. Sample trees were randomly selected, but if they were located within a larger patch of conspecific trees then they were not sampled so that our measurements were as representative of one tree's effect as possible. The site with intermediate levels of invasion was sampled, because the other sites lacked a sufficient number of isolated *A. platanoides* trees. One quadrat (1 m²), placed next to the trunk of the tree but random in aspect, was used to sample each understory. Within each quadrat, the percent cover of each species was quantified as described above, and the diameter at breast height (DBH) was recorded for each tree.

Understory community composition was examined at the canopy scale using DCA. This analysis had a data matrix including quadrats from beneath randomly selected *A. platanoides* trees and quadrats from along transects described above. Samples from beneath *A. platanoides* trees were compared to all other samples within the two-dimensional distribution of all ordinated plots. A second analysis was performed by selecting only the samples from beneath *A. platanoides* trees and regressing the axis scores of these plots with the size (DBH) of the tree above the plot. The Shannon-Wiener Index of Diversity, evenness, and species richness measures were calculated for plots beneath *A. platanoides* trees using PC-ORD software (McCune and Mefford 1995). Linear regressions were used to determine whether changes in the size (DBH) of *A. platanoides* trees above plots explained changes in diversity measures within plots.

We also quantified recruitment under isolated *A. platanoides* trees by counting all seedlings and saplings under canopies. Seedling density was then regressed against the age of the overstory tree to estimate the rate of seedling recruitment.

Seedling transplant experiment

Seedlings of *A. platanoides*, *P. trichocarpa*, and *P. ponderosa* were planted 1 m from individual trunks of 20 *Acer* and 20 *Populus* canopy trees within the stand with intermediate levels of *A. platanoides* invasion in June, 1998. One seedling of each species was planted at each of the 40 sites. Transplanted seedlings were initially watered and then allowed to grow until September 1999 when they were harvested. At the time of planting, the height was measured for *Acer*, *Populus*, and *Pinus* seedlings. At the harvest, stem height was re-measured. After drying at 60°C until constant weight, we measured the total biomass of *Acer* seedlings, the biomass of green leaves for *Pinus* seedlings, and the biomass of living stems for *Populus* seedlings (there were no leaves on the *Populus*). The biomass and change in height measurements for each species were analyzed separately with a two sample t-test.

Results

Overstory-understory associations

1. Riparian stands

The plant communities in the three riparian stands were compositionally different based on DCA analysis. In stand 1, which was highly invaded, plots were more tightly aggregated in ordination space than plots from the two other stands (Fig. 1). The plots were aggregated around the species ordination coordinate for *A. platanoides*, illustrating the strong homogenizing effect of *A. platanoides* seedlings and saplings in all of these plots. The plots for stand 2 were dispersed through more ordination space than stand 1 but less than stand 3 suggesting this community may have been beginning to move towards *A. platanoides* dominance. Plots from stand 3, the uninvaded stand, were highly dispersed in ordination space illustrating a high degree of heterogeneity in understory community composition. However, the sample area of this stand (660 m of reach versus 520 m for stand 1 and 210 m for stand 2) was greater, possibly confounding these differences. Plots with overstories of *Acer platanoides* (mostly plots in stand 1) were more closely grouped in ordination space suggesting a strong homogenizing effect of *A. platanoides* trees on understory species composition (Fig. 1). Plots associated with native overstories and no canopy cover (i.e. "open sky") were much more widely dispersed in ordination space indicating a large amount of variability in the composition of these understory communities. However, relating the distribution of ordinated plots to canopy type within a stand is hindered by the tendency for stands to have canopies dominated by either *A. platanoides* (stand 1) or natives (stands 2 and 3), which makes it difficult to identify any divergence in understory

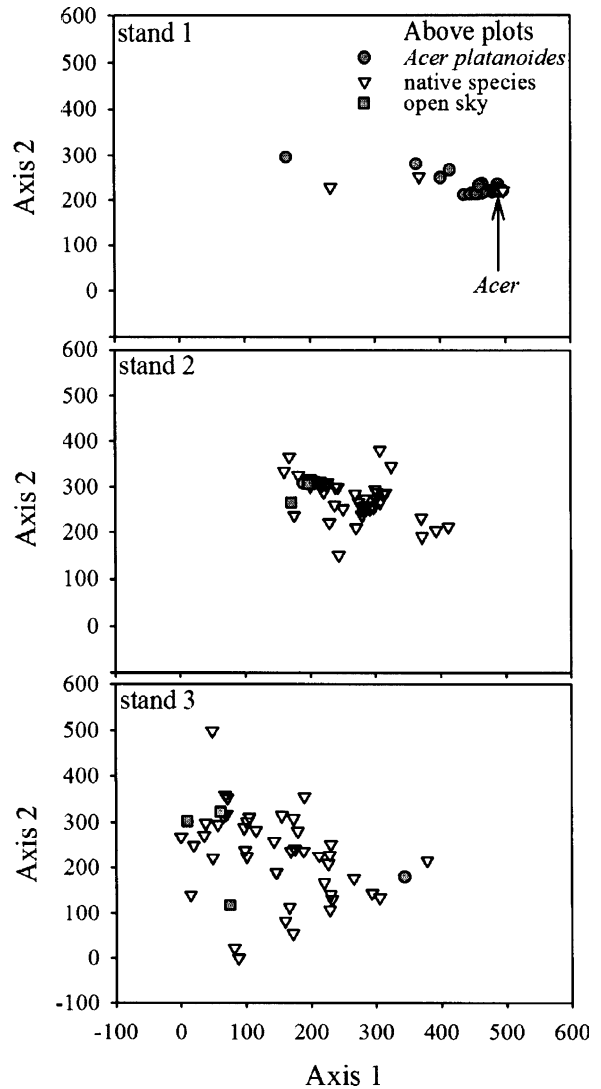


Fig. 1. Detrended Correspondence Analysis (DCA) of percent cover data from 1 m² plots. Ordinated plots are partitioned by riparian stand. The three neighboring riparian stands have three different levels of *Acer platanoides* invasion. Stand 1 has the greatest level of *A. platanoides* invasion, stand 2 has an intermediate level of invasion, and stand 3 has the lowest level of *A. platanoides* invasion. Variability in how plots are aggregated in 2 dimensional space between sites provides insight into the general differences in plant community composition between stands. Eigenvalues for axis 1 = 0.856 and for axis 2 = 0.545 for all the data combined. Each symbol represents a single plot ordinated in two dimensional space, and symbol shapes and colors distinguish between overstories with *Acer platanoides* (and possibly native species), native species without *Acer platanoides*, and open sky. The *Acer* label is the ordinated point for *A. platanoides* across all plots.

community composition within a stand that can be directly related to canopy types (*Acer platanoides* versus native species). Corresponding with the ordination results, species richness (−67%), evenness (−40%), and diversity (−75%) were lower in stand 1 than in

stands 2 and 3 (Table 1). The dramatic difference between stand 1 vs 2 and 3 suggests that *A. platanoides* invasion is associated with a dramatic change in community composition and local loss of species diversity; however, these patterns are correlative and other unaccounted for differences between stands may be the cause.

The abundance of many dominant species in the understory also differed between stands (Table 1). Stand 1 had more (>28 times) *A. platanoides* seedlings and saplings in the understory than the two other stands. Stand 2 had higher covers of two non-native herbs (*Arctium lappa* and *Cynoglossum officinale*) than stands 1 and 3 and higher cover of the non-native herb *Solanum dulcamara* than stand 1. Stand 3 had intermediate amounts of *C. officinale* and the highest cover of the native grass *Elymus glaucus*. Stands 2 and 3 had greater covers of the native shrubs *Symphoricarpos albus* and *Amelanchier alnifolia* and herb *Galium triflorum* than stand 1.

2. Individual canopy scale patterns

Within the stand with intermediate abundances of *A. platanoides*, the composition of understory communities under solitary *A. platanoides* canopies only differed from under other canopies along axis 2 but not axis 1 (Fig. 2). Specifically, the 95% CI for centroids for the two canopy types overlapped along axis 1 while there was no overlap in centroid confidence intervals along axis 2. Further-

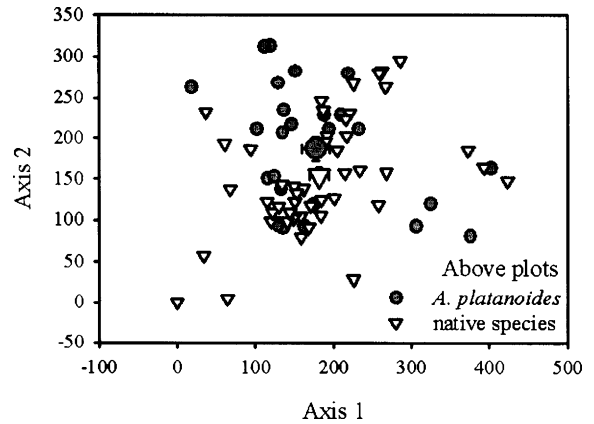


Fig. 2. Detrended Correspondence Analysis of 1 m² plots with and without *Acer platanoides* canopy cover. Plots in this analysis include 26 collected under randomly chosen *Acer* trees in the stand with an intermediate level of *A. platanoides* invasion, and 48 plots collected along randomly located transects in the same stand. Each symbol represents a single plot. Large symbols represent centroids for the smaller symbols of the same shape and show \leq 95% confidence intervals. Eigenvalues for axis 1 = 0.6742 and for axis 2 = 0.4441.

more, we found no relationship between the size of overstory *A. platanoides* trees and the composition of understory communities (linear regression for Axis 1 and tree DBH, $F = 0.11$, $p = 0.75$; linear regression for Axis 2 and tree DBH, $F = 0.18$, $p = 0.68$).

Table 1. Variation in species richness, evenness, diversity, and the percent cover of 15 most abundant species between sites ($n = 1$) located along the Rattlesnake Creek, Montana. Stand 1 has the greatest level of *A. platanoides* invasion, stand 2 has an intermediate level of invasion, and stand 3 has the lowest level of *A. platanoides* invasion. The statistical tests in this table are used to identify differences between stands and not the effects of *A. platanoides* invasion, which may be confounded by underlying variation between stands.

Variables	Riparian stands		
	1	2	3
Log(richness)	0.31 ± 0.03 ^a	0.84 ± 0.02 ^b	0.96 ± 0.02 ^c
(evenness + 1) ³	2.93 ± 0.29 ^a	4.85 ± 0.18 ^b	4.76 ± 0.14 ^b
diversity	0.37 ± 0.06 ^a	1.33 ± 0.06 ^b	1.49 ± 0.05 ^b
Dominant species	1	2	3
1 <i>Symphoricarpos albus</i> ¹	3.6 ± 2.1 ^a	31.7 ± 4.8 ^b	21.9 ± 3.4 ^b
2 <i>Acer platanoides</i> ²	65.9 ± 4.4 ^a	1.8 ± 0.4 ^b	2.3 ± 1.2 ^b
3 <i>Cynoglossum officinale</i> ²	0 ^a	13.0 ± 2.7 ^b	7.1 ± 1.7 ^c
4 <i>Populus trichocarpa</i> ¹	2.1 ± 0.6 ^a	0.9 ± 0.3 ^a	1.1 ± 0.4 ^a
5 <i>Osmorhiza chilensis</i> ¹	2.3 ± 2.0 ^{ab}	3.8 ± 0.9 ^a	0.6 ± 0.2 ^b
6 <i>Elymus glaucus</i> ¹	0 ^a	4.3 ± 1.6 ^b	22.4 ± 5.1 ^c
7 <i>Amelanchier alnifolia</i> ¹	0.04 ± 0.04 ^a	0.7 ± 0.3 ^b	2.2 ± 0.7 ^b
8 <i>Sorbus aucuparia</i> ²	0.2 ± 0.2 ^a	0.9 ± 0.3 ^a	1.0 ± 0.3 ^a
9 <i>Galium triflorum</i> ¹	0 ^a	1.5 ± 0.5 ^b	5.8 ± 2.5 ^b
10 <i>Acer glabrum</i> ¹	0.3 ± 0.1 ^a	1.4 ± 0.6 ^a	0.7 ± 0.3 ^a
11 <i>Rosa nutkana</i> ¹	1.3 ± 1.3 ^a	0.6 ± 0.3 ^a	1.3 ± 0.4 ^a
12 <i>Prunus virginiana</i> ¹	0.7 ± 0.1 ^a	0.8 ± 0.5 ^a	1.8 ± 1.1 ^a
13 <i>Solanum dulcamara</i> ²	0.1 ± 0.1 ^a	2.0 ± 0.6 ^b	0.8 ± 0.4 ^{ab}
14 <i>Arctium lappa</i> ²	0 ^a	11.0 ± 3.1 ^b	0.2 ± 0.1 ^a
15 <i>Equisetum hyemale</i> ¹	11.5 ± 3.8 ^a	7.1 ± 3.1 ^a	2.0 ± 2.0 ^a

Dominance based on the presence of species in each plot summing across all stands. ¹ = native species, ² = non-native species. Tests were performed using 1-way ANOVA and Tukey HSD post-hoc analyses with SPSS software (SPSS ver. 10). The Bonferroni method was used to correct the alpha value and test the effect of stand on diversity indices ($\alpha = 0.01695$) and on the percent cover of the 15 most dominant species ($\alpha = 0.0033$). Significant differences between stands are delineated by different letter superscripts.

However, the DBH of overstory *A. platanoides* trees was negatively correlated with the species richness of the understory (linear regression of richness and tree DBH, $F=4.47$, $p<0.05$; Fig. 3b). Corresponding with this effect, Shannon-Wiener Index of Diversity measurements were generally lower beneath large *A. platanoides* trees than smaller trees (linear regression for diversity and tree DBH, $F=3.9$, $p=0.06$; Fig. 3a). No relationship was observed between species evenness and *A. platanoides* DBH (linear regression, $F=0.42$, $p=0.52$). These results suggest a trend for decreasing species richness and diversity of the understory with the increasing size of neighboring *A. platanoides* trees. Conversely, the density of *A. platanoides* seedlings increased with the age of the overstory *A. platanoides* trees (linear regression, $F=35$, $p<0.0005$; Fig. 4).

Seedling transplant experiment

Acer platanoides seedlings had more biomass ($t=3.05$; $DF=1, 24$; $p=0.014$; Fig. 5a) and were taller ($t=4.11$; $DF=1, 24$; $p=0.004$; Fig. 5b) when planted beneath

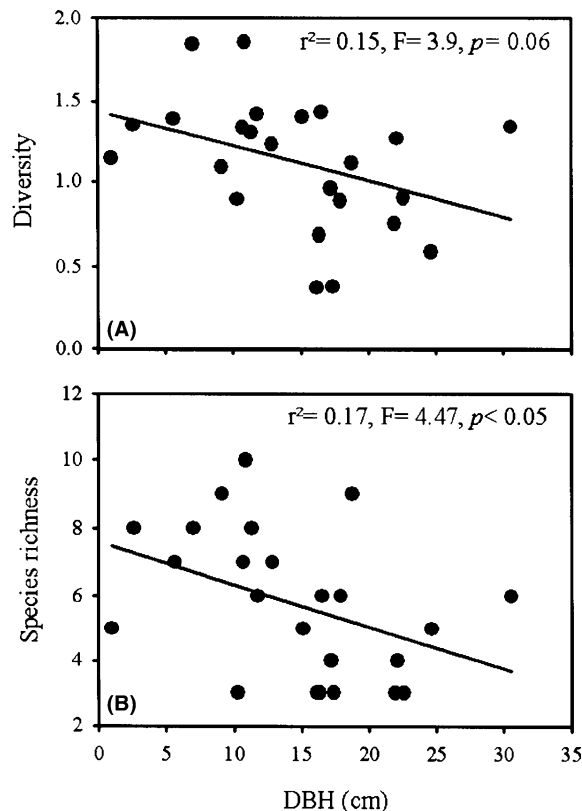


Fig. 3. Regression relationships between the diameter at breast height (DBH) of *Acer platanoides* trees and (A) the Shannon-Wiener Index of Diversity and (B) species richness in 1 m^2 plots beneath *A. platanoides* trees.

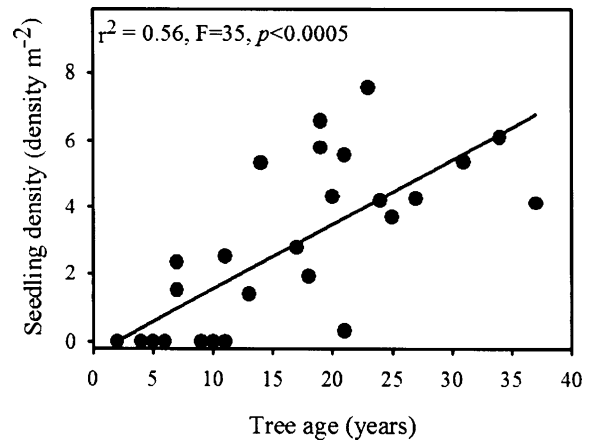


Fig. 4. Regression relationship between the age of nearest *Acer platanoides* tree and the density of *A. platanoides* seedlings in 1 m^2 plots beneath conspecific trees.

mature *A. platanoides* canopies than *Populus* canopies indicating a positive conspecific relationship. In contrast, *Populus* and *Pinus* seedlings were taller when planted beneath *Populus* trees than beneath *A. platanoides* trees indicating a negative effect of the invader on native recruitment ($t_{\text{Pinus}}=4.55$; $DF=1, 21$; $p<0.001$; $t_{\text{Populus}}=2.09$; $DF=1, 19$; $p=0.044$; Fig. 5b). *Pinus* needle mass was much greater when grown beneath *Populus* trees than under *A. platanoides* trees ($t=11.66$; $DF=1, 18$; $p<0.001$; Fig. 5a).

Discussion

Our results indicate that *Acer platanoides* causes large shifts in the community of understory plants, suppresses the recruitment of native canopy dominants, and facilitates recruitment of conspecifics. Community shifts were much more apparent at the stand scale, which is also the scale at which the effects of *A. platanoides* could be most confounded by physical differences between the stands. The level of *A. platanoides* invasion may have been influenced by differences between neighboring sites (e.g. geological substrate, hydrology, disturbance history, etc.), which are probably minor because the sites all occur along the same stream and within a couple of km of one another. Additionally, we found no difference in soil nitrogen or moisture associated with *A. platanoides* versus *Populus trichocarpa* trees and found no fertilization effect of the soil associated with stand 1 (heavily invaded) relative to stand 2 (intermediate level of invasion) suggesting that differences in soil fertility are not limiting the spread of *A. platanoides* invasion in our stands (Reinhart unpubl.). Thus, it is not likely that these factors account for the dramatic changes in the understory community that were observed.

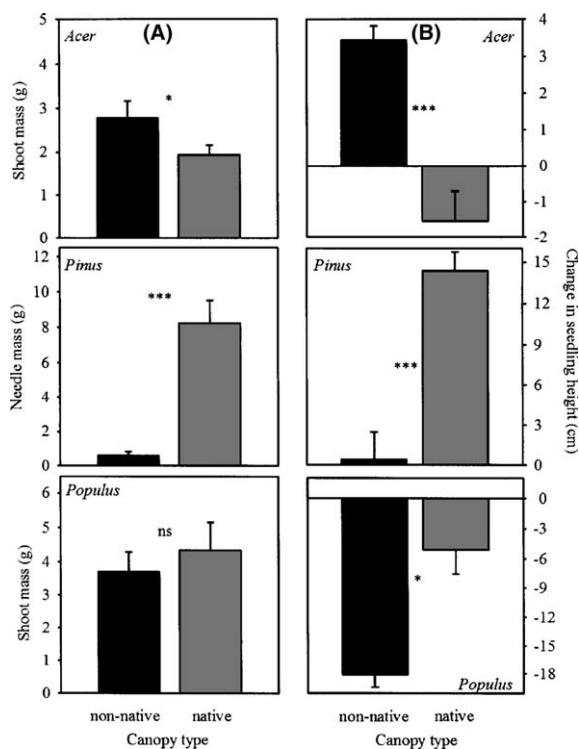


Fig. 5. Effect of overstory canopy type on transplanted seedlings. (A) Final leaf or needle biomass of three species (*Acer platanoides*, *Pinus ponderosa*, and *Populus trichocarpa*) of understory seedlings planted beneath either native, *Populus* or non-native canopies, *Acer*. (B) Change in height of three species of understory seedlings planted beneath either native, *Populus* or non-native canopies, *Acer*. A negative change in height indicates that the plants died back after planting and did not grow enough to equal or exceed their starting height. Asterisks (*, **, and ***) indicate a significant ($p < 0.05$, $p < 0.005$, and $p < 0.0005$, respectively) difference and "ns" indicates a statistically insignificant ($p > 0.05$) difference between canopy species according to t-test with homogeneity of variances not assumed (separate-variances) with SPSS software (SPSS ver. 10). Error bars represent ± 1 SE.

In contrast to the strong differences observed at the stand scale, individual canopies had relatively minor effects on community composition of the understory, but these changes generally corroborated patterns at the stand scale. The comparatively weak effects of *A. platanoides* may have resulted from the individual canopy data having been collected from a site with individual trees scattered throughout a natural matrix of vegetation. Many of these *A. platanoides* trees were younger, and apparently in the initial phase of colonization, than in the highly invaded stand. Even though *A. platanoides* did not have a large effect on the composition of understory communities in the stand with intermediate levels of invasion, declining understory diversity and species richness with *A. platanoides* size indicate that *A. platanoides*-driven shifts were beginning.

The success of *A. platanoides* at our study site may have been promoted by damming on Rattlesnake Creek. Management of rivers reduces natural disturbance within riparian areas and allows late-successional species to become more abundant. Native riparian communities are typically dominated by early- to mid-successional species with many species that are adapted to hydrologic disturbance (Hansen et al. 1995). Damming Rattlesnake Creek may have reduced the frequency and severity of floods, favoring *A. platanoides*, which is a mid- to late-successional tree species in its native communities (Schmucker 1942).

Acer platanoides canopies may suppress native vegetation by altering the quantity of light in the understory. In support of this, photosynthetically active radiation (PAR) was reduced by 95% beneath *A. platanoides* canopies ($PAR = 17.2 \pm 4 \times \text{mol} \times \text{m}^{-2} \times \text{s}^{-1}$, ± 1 SE) in the heavily invaded stand relative to the understory light levels from the stand with the lowest level of *A. platanoides* invasion ($397.5 \pm 47 \times \text{mol} \times \text{m}^{-2} \times \text{s}^{-1}$) (Reinhart 2003). If most native species are adapted to the much higher light levels that occur in native understories, and that are more typical of early- to mid-successional riparian communities, then deep shade may have devastating effects on mal-adapted native species (Baker 1949, Bazzaz 1979, Catovsky and Bazzaz 2000). In contrast, seedlings and saplings of *A. platanoides* are exceptionally shade-tolerant (Niinemets 1997) which would allow them to survive in the shade of conspecific adults. However, *A. platanoides* seedlings do not appear to just tolerate conspecific canopies. Our experimental data indicate that *A. platanoides* seedlings are facilitated by conspecific adults while *Populus* and *Pinus* seedlings are facilitated by *Populus* trees, the native dominant. However, we do not know if there is a direct beneficial effect of conspecifics (possible canopy, soil, or humidity effects), or if seedlings benefited indirectly from the suppression of native species in the understory (Li and Wilson 1998, Pagès et al. 2003). The invasion of multiple community types may require multiple mechanisms. Thus, the successful invasion, impact of the invader, and mechanisms of impact may be context specific. For example, shade and shade adaptations may be an important mechanism for invasion in riparian areas in the northern Rocky Mountains but not in deciduous hardwood forests in northeastern North America where other shade adapted species co-exist (e.g. *Acer saccharum* and *Fagus grandifolia*). Other studies have indicated that *A. platanoides* foliage produces water-soluble antifungal chemicals (Dix 1974), which may alter the soil-borne mycorrhizae, pathogenic fungi, and decomposer fungi in ways that favor conspecific seedlings (Vivanco et al. 2004). Altered soilborne fungal communities also may play a role in the disruption of native riparian communities.

After initial introduction, non-native species often appear to undergo a lag phase where population growth and spread increases slowly (Kowarik 1995). After this lag phase population size may increase exponentially. The duration of these lag phases is variable, but lag periods can be very long depending on the life history traits of the individual species and the characteristics of the invaded environment. Average lag phases have been estimated at 131 yr for shrubs and 170 yr for trees that escaped from the Royal Botanical Gardens of the Netherlands (Kowarik 1995). Perhaps because of the long lag period, few invasions by large trees have been shown to have severe impacts (but Van Wilgen and Richardson 1985, Ewel 1986, Vitousek et al. 1987, Richardson 1998). Lag phases may result from the time required to attain sexual maturity, selection processes within the invading population, a slow breakdown in the resistance of the natural recipient community, or because invaders have slowly accelerating positive feedback effects on their environment. These mechanisms are by no means mutually exclusive. The positive relationship between the density of *A. platanoides* seedlings and the age of conspecific trees in the overstory suggests that a lag phase or Allee effect (reduced reproductive success at low densities) (Stephens et al. 1999) may occur for *A. platanoides* between its establishment and rapid expansion.

The successful invasion of one species may lead to an “invasional meltdown” by facilitating the invasion of additional species (Simberloff and Von Holle 1999). This did not appear to occur in our study because other non-native species, at least those that have made it to western Montana, were as highly suppressed by *A. platanoides* as native species (Table 1). Our results; however, indicate that *A. platanoides* is gradually modifying habitat in ways that favor itself and negatively impact native species, and this may open the door to gradual invasion by non-native species that have not yet arrived.

In conclusion, we found a dramatic decline in the abundance and richness of understory plant species associated with high levels of *A. platanoides* invasion. Furthermore, *A. platanoides* canopies enhanced the growth of experimentally transplanted conspecific seedlings and suppressed the growth of transplanted seedlings of native canopy trees. Collectively, these results are similar to those documented in the northeastern U.S. that reported a decrease in the richness of native species in the understory and an increased density of *A. platanoides* seedlings in invaded areas relative to non-invaded areas (Webb and Kaunzinger 1993, Wyckoff and Webb 1996, Martin 1999). The widespread cultivation of *A. platanoides* in the northeastern U.S., eastern Canada (Dunster 1990), and northern Rocky Mountains (Nowak and Rowntree 1990) ensures that this species will continue to have many opportunities to escape and

naturalize. It is likely that the threat of *A. platanoides* will increase as invaded areas mature and alter habitats in ways that amplify both their negative effects on native species and positive effects on themselves.

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Appendix. Species list of the understory community composition from Rattlesnake Creek, Montana.

<i>Acer glabrum</i> ¹	<i>Dryopteris expansa</i> ¹	<i>Ranunculus macounii</i> ¹
<i>Acer platanoides</i> ²	<i>Elymus glaucus</i> ¹	<i>Ranunculus uncinatus</i> ¹
<i>Achillea millefolium</i> ¹	<i>Elymus</i> spp. ¹	<i>Rhamnus cathartica</i> ²
<i>Agastache urticifolia</i> ¹	<i>Epilobium</i> spp. ¹	<i>Rhamnus</i> spp. ¹
<i>Agropyron repens</i> ²	<i>Equisetum arvense</i> ¹	<i>Ribes klamathense</i> ¹
<i>Agrostis alba</i> ²	<i>Equisetum hyemale</i> ¹	<i>Ribes oxyacanthoides</i> ¹
<i>Allium cernuum</i> ¹	<i>Erigeron speciosus</i> ¹	<i>Rosa nutkana</i> ¹
<i>Alnus incana</i> ¹	<i>Fragaria virginiana</i> ¹	<i>Rubus idaeus</i> ¹
<i>Amelanchier alnifolia</i> ¹	<i>Galium boreale</i> ¹	<i>Rubus parviflorus</i> ¹
<i>Arctium lappa</i> ²	<i>Galium triflorum</i> ¹	<i>Rumex obtusifolius</i> ²
<i>Arctostaphylos uva-ursi</i> ¹	<i>Geranium robertianum</i> ²	<i>Rumex pulcher</i> ²
<i>Aster laevis</i> ¹	<i>Geum macrocarpum</i> ¹	<i>Salix</i> spp. ¹
<i>Aster occidentalis</i> ¹	<i>Heracleum lanatum</i> ¹	<i>Sambucus cerulea</i> ¹
<i>Berberis aquifolium</i> ¹	<i>Hypericum perforatum</i> ²	<i>Saxifrage arguta</i> ¹
<i>Berberis repens</i> ¹	<i>Leonurus cardiaca</i> ²	<i>Senecio triangularis</i> ¹
<i>Betula occidentalis</i> ¹	<i>Lonicera</i> spp. ¹	<i>Silene menziesii</i> ¹
<i>Bromus inermis</i> ²	<i>Lychnis alba</i> ²	<i>Solanum dulcamara</i> ²
<i>Bryonia alba</i> ²	<i>Mentha arvensis</i> ¹	<i>Solidago canadensis</i> ¹
<i>Calamagrostis inexpansa</i> ¹	<i>Mitella nuda</i> ¹	<i>Sorbus aucuparia</i> ²
<i>Calamagrostis</i> spp. ¹	<i>Myosotis scorpioides</i> ²	<i>Spiraea betulifolia</i> ¹
<i>Carex</i> spp. ¹	<i>Nepeta cataria</i> ²	<i>Streptopus</i> spp. ¹
<i>Centaurea maculosa</i> ²	<i>Osmorhiza chilensis</i> ¹	<i>Symphoricarpos albus</i> ¹
<i>Cerastium vulgatum</i> ¹	<i>Philadelphus lewisii</i> ¹	<i>Tanacetum</i> spp. ¹
<i>Chenopodium alba</i> ²	<i>Phleum pratense</i> ²	<i>Taraxacum officinale</i> ²
<i>Chenopodium</i> spp. ¹	<i>Physocarpus malvaceus</i> ¹	<i>Thalictrum occidentale</i> ¹
<i>Cirsium arvense</i> ²	<i>Pinus ponderosa</i> ¹	<i>Trifolium pratense</i> ²
<i>Cirsium vulgare</i> ²	<i>Poa</i> spp. ¹	<i>Trifolium repens</i> ²
<i>Clematis columbiana</i> ¹	<i>Populus tremuloides</i> ¹	<i>Urtica dioica</i> ¹
<i>Clematis ligusticifolia</i> ¹	<i>Populus trichocarpa</i> ¹	<i>Verbascum thapsus</i> ²
<i>Cornus stolonifera</i> ¹	<i>Prunella vulgaris</i> ²	<i>Viburnum opulus</i> ¹
<i>Crataegus douglasii</i> ¹	<i>Prunus cerasus</i> ²	<i>Viburnum</i> spp. ¹
<i>Crysanthium lycanthum</i> ¹	<i>Prunus mahaleb</i> ²	<i>Viola glabella</i> ¹
<i>Cynoglossum officinale</i> ²	<i>Prunus virginiana</i> ¹	<i>Viola</i> spp. ¹
<i>Dactylis glomerata</i> ²	<i>Pyrola asarifolia</i> ¹	
<i>Disporum trachycarpum</i> ¹	<i>Pyrus</i> spp. ²	

¹ = native species, ² = non-native species, according to the Montana Natural Heritage Association.