Challenging growth–survival trade-off: a key for Acer negundo invasion in European floodplains?

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Abstract: We compared the performances of juvenile Acer negundo with those of native species to assess how this species has invaded intermediate habitats along European riparian successional gradients. In the middle Rhône floodplain (France), we measured survival and growth of transplants of the invasive and of three native tree species from contrasted successional status within forests and in experimental gaps and at three positions along a riparian gradient: (i) a highly disturbed Salix–Populus stand, (ii) a moderately disturbed stand dominated by the invasive Acer, and (iii) a mature Fraxinus community. Acer’s growth in the gaps was as high as that of the two native early-successional species, Salix and Populus, and higher than that of the native late-successional Fraxinus. In contrast, Acer survived as well in the shadiest understory conditions of the Fraxinus community as did Fraxinus and better than the two early-successional species. Inconsistent with the resource trade-off of succession theory, Acer showed both a high survival in the shade and a high growth in full light. This particular suite of traits shared with other invasive and native Acer species could be an example of adaptive plasticity that certainly represents an advantage to give it a competitive advantage over native species.

Résumé: Nous avons comparé les performances d’érables néguondo (Acer negundo L.) juvéniles à celles d’espèces indigènes pour évaluer comment cette espèce a envahi des habitats intermédiaires, le long de gradients successionnels riverains en Europe. Dans la plaine inondable du Rhône moyen (France), nous avons mesuré la survie et la croissance de plants de l’espèce invasive et de trois espèces indigènes provenant de différents stades successionnels et transplantés à l’intérieur de forêts et de trouées expérimentales, ainsi qu’à trois endroits le long du gradient riverain: (i) un peuplement fortement perturbé composé de Salix et de Populus, (ii) un peuplement modérément perturbé dominé par l’Acer invasif et (iii) une communauté mature de Fraxinus. La croissance de l’Acer dans les trouées était aussi élevée que celle des deux espèces indigènes de début de succession, le Salix et le Populus, et plus élevée que celle du Fraxinus indigène, une espèce de fin de succession. De plus, l’Acer survivait dans les conditions de sous-bois les plus ombragées de la communauté de Fraxinus aussi bien que le Fraxinus et mieux que les deux espèces de début de succession. Contrairement à la notion de compromis au sujet des ressources de la théorie de la succession, l’Acer avait à la fois un taux élevé de survie à l’ombre et une forte croissance en pleine lumière. Cette suite particulière de caractéristiques partagées avec d’autres espèces d’Acer invasives et indigènes pourrait être un exemple de plasticité adaptative qui contribue certainement à leur donner un avantage compétitif sur les espèces indigènes.

[Traduit par la Rédaction]

Introduction

Biological invasions by exotic species are one of the main human impacts on earth’s ecosystems and understanding the mechanisms underlying biological invasions remains a major challenge for ecologists (Mack et al. 2000). Despite the several hypotheses explaining invasive species’ success or recipient communities’ sensitivity to invasion (Richardson and Pysek 2006), no general syndromes have emerged from the literature, and the context dependency of the processes appeared as a key for understanding biological invasions (Catford et al. 2009). In other words, successful invasion likely needs an adequacy in space and time between the invader’s traits and the recipient community’s characteristics (Milbau et al. 2003). Thus, the search of such an adequacy’s print in invasion patterns should be the first step for understanding a particular invasion process.

The aim of our study was to depict the invasion process of Acer negundo L. in the riparian forests of the middle Rhône floodplain (France). This North American floodplain tree species was introduced into Europe as a garden tree at the end of the 17th century and its spread in riparian communities has been described for several European rivers (Tabacchi and Planty-Tabacchi 2003). In its native range, it is described as a fast-growing midsuccessional species with a good flood tolerance and able to dominate the understory of...
cottonwood–willow stands (Maeglin and Ohmann 1973). Floodplains are one of the most invaded landscapes because they are subjected to high propagule pressures due to the stream flow and the importance of human activities (Plantly-Tabacchi et al. 1996).

Floodplain forests are primarily structured by flood disturbance that forms a decreasing gradient from the riverbank to old terraces (van Coller et al. 2000). As a result, the riparian profile corresponds to an allogenic successional gradient with pioneer species in the most disturbed habitats and late-successional species in the least disturbed ones (Pautou et al. 1992; Battaglia and Sharitz 2006). In the middle Rhône floodplain, the invasive Acer forms monodominant stands at the ecotone between the softwood communities dominated by the early-successional species Salix alba L. and Populus alba L. and the hardwood communities of the old terraces dominated by the late-successional Fraxinus angustifolia Vahl. (Pont 1999).

Efficient sustainable management of floodplain forests needs to understand how Acer was able to outcompete native species from this midsuccessional niche. The pattern of species distribution suggests that Acer has been able to invade an empty midsuccessional niche (Elton 1958) between the soft- and hardwood native communities. Patterns of forest succession have been explained by the occurrence of trade-offs between species functional traits (Bazzaz 1979). During the juvenile stages, these trade-offs are particularly revealed by a resource trade-off (Sánchez-Gómez et al. 2006) opposing the high growth ability of exploitative early-successional species to the shade tolerance of conservative late-successional species (Kobe et al. 1995; Walters and Reich 1996). Following this model, either higher performances of Acer in the midsuccessional position or an intermediate position along the resource tradeoff could represent an advantage allowing Acer’s invasion. Thus, we performed an experiment to compare the performances of Acer with those of native species along the successional gradient. We reciprocally transplanted Acer, Salix, Populus, and Fraxinus seedlings along the riparian profile, e.g., in the Salix, Acer, and Fraxinus communities, both in the forest understories and in experimental gaps, and we measured the survival and growth of all transplants.

Methods

Study area

The experiment was performed in the riparian forests of the Natural Reserve of la Platière located on the middle Rhône floodplain near Sablons, France (45°19’N, 4°46’E). Mean annual temperature (1970–2005) is 12.3 °C and mean annual precipitation (1960–2005) is 799 mm (Meteo-France, Sablons record station). The riparian forests are located on modern alluvial deposits of a braided river. On this section, the river flow has been regulated since the 19th century by dykes upstream from the study site (Girardon rack) and more recently by the deviation of water to a hydroelectric channel. The soils are gray alluvial soils with a sandy to a loam–sandy texture and are poor in humus (Pont 1999).

Three forest community types occur in the study area with increasing distance to the river flow. Salix–Populus stands (hereafter called Salix stands) occur on old Girardon racks close to the riverbank and are flooded yearly. Acer stands occur on older terraces along the riparian profile, are frequently flooded, and are also characterized by the presence of some tall and old Populus individuals. The upper terraces, rarely flooded, are dominated by Fraxinus stands. Although Fraxinus species are overall midsuccessional species in most other habitats than fertile floodplains, in the middle Rhône floodplain forests, they represents the last stage of succession. The absence in the floodplains of more conservative species such as Quercus pubescens Willd. is due to both its competitive exclusion on fertile alluvial soils by Fraxinus (Michalet et al. 2008) and past human deforestations for agriculture (Pautou 1975).

Studied species

We used transplants of the four dominant species of these riparian forests, two early-successional species, P. alba and S. alba, the late-successional species F. angustifolia (Rameau et al. 1997), and the invasive A. negundo Seeds of the four species were harvested in neighboring forests and seedlings were grown for 1 year in local nurseries. We transplanted in the field 1-year-old bare-rooted seedlings for both Fraxinus and Acer and cuttings from 1-year-old seedlings for Populus and Salix to standardize the initial size of target individuals and to integrate the importance of the vegetative reproduction strategy for these species (Karrenberg et al. 2003). We used 1-year-old seedlings to avoid germination problems and because seedling stage is determinant for the structure of floodplain forests (Richardson et al. 2007). At the end of the experiment, all Acer seedlings were up-rooted to avoid any propagule dispersion. Regular visual inspection during the following years had confirmed that no Acer transplant had resprouted and survived.

Experimental design

The natural reserve authorities gave permission for the experiment setup because our transplantations were established within the natural range of propagule dispersal (the invasive Acer is already present at the mature stage in the landscape). We used a completely randomized split-split-plot design with community as the main effect, tree canopy as the second effect, and target species as the third effect. The community treatment included the three forest community types described above, e.g., the Salix, Acer, and Fraxinus stands, with four replicates per community type. The area of each of the 12 sites (three communities × four replicates) was 1 ha and the sites were randomly located throughout the reserve. The tree canopy treatment was applied in each site by delimiting a 20 m × 20 m plot in an experimental gap and another in the adjacent forest. The experimental gaps were created from late November 2003 to late January 2004 by removing all trees in a 40 m × 40 m area. We removed tree regrowth during the whole experiment. The initial design included eight subplots, four with and four without herbaceous species, to test the effect of herbaceous neighbors and the indirect tree canopy effects (Pagès and Michalet 2003). Preliminary analyses (not shown) revealed that overall relative seedling performances were similar with and without the herb layer. For simplification and to compare seedling performances under homogeneous light conditions (full light and tree canopy shade), we choose to present in

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this paper only the results of the subplots without the herb layer. Hereafter, we use the term “plot” for the association of the four subplots without the herb layer that were obtained by the monthly hand-pulling of all herbaceous species and shrubs. Seedlings and cuttings of the four species were transplanted in the experimental design in late March 2004 at the beginning of the growing season. Twelve individuals of each target species were randomly transplanted in each plot with at least 50 cm distance between individuals. The relative positions of all transplants (1152 individuals) were precisely mapped to allow exhaustive monitoring during the experiment.

Environmental measurements and conditions
In late May 2005, at least 3 days after the last precipitation event, two soil samples were collected 3–10 cm deep in each forest plot to characterize the nonmanipulated conditions of each site. The two soil samples were pooled and immediately weighed. NO$_3^-$ and NH$_4^+$ were extracted and NO$_3^-$ was determined by ionic chromatography (4500i; Dionex, Sunnyvale, California) and NH$_4^+$ by the blue indophenol method. Soil nitrogen content was calculated as the sum of NH$_4^+$-N and NO$_3$-N, and expressed as nitrogen mass per unit of soil dry mass (grams per gram). Soil samples were oven-dried at 105 °C for 2 days and soil moisture was expressed as a percentage of fresh soil mass. In July 2005, the fraction of photosynthetically active radiation (PAR) (400–700 nm) absorbed by the forest canopies was measured at noon during a sunny day using a portable quantum sensor (Li-188b; LI-COR, Lincoln, Nebraska). Twelve PAR measurements were collected at 10 cm above the soil in each of the 24 plots. The mean value of understory light availability of each forest plot was expressed as a percentage of the incident PAR occurring in the gap treatment of each site.

Our measures showed that light penetration and soil moisture were 50% higher in the understory of Salix stands than in the two other communities and, in contrast, that there was no significant difference in soil nitrogen content among the three communities (Table 1).

Transplant performance measurements
The survival of transplants was measured in November 2005 at the end of the second growing season and specific survival rates were calculated per plot as the percentage of targets alive at the end of the experiment. We measured the height of all individuals at the beginning (late March 2004) and end of the experiment (November 2005) and used the relative height increment as a growth rate indicator, since the duration of the experiment was the same for all transplants. The relative height increment (RHI) of each individual was calculated as

$$RHI = (H_{2005} - H_{2004})/H_{2004}$$

where $H_{2004}$ and $H_{2005}$ are the heights of individuals in late March 2004 and November 2005, respectively. The relative position of the four species along the resource tradeoff was evaluated through the graphical analysis of the specific survival rates under forest canopies (shade-tolerance indicator) on the y-axis and of the specific growth rates in full light (growth ability indicator) on the x-axis.

Statistical analyses
Differences in survival and growth were analyzed using a split-split-plot model with community as the main plot effect, tree canopy as the subplot effect, and target species as the sub-subplot effect. Within-tree canopy differences in survival and growth rates were analyzed using split-plot models with community as the main plot effect and species as the subplot effect. Because of its very low survival below forest canopies, for growth, *Populus* was excluded from several analyses. We also used one-way ANOVA models to analyze single factor effects including community effect on environmental conditions (light availability below forest canopies, soil moisture, and nutrient content) and the species effects on survival and growth responses among communities and within-tree canopy conditions. The data set was checked to confirm the assumptions of ANOVA, and we used the Shapiro–Wilcoxon test for normality and O’Brien’s test for homoscedasticity. All ANOVA models were followed by Tukey’s HSD tests when necessary. All analyses were carried out with JMP 5.0.1 (SAS Institute Inc., Cary, North Carolina).

Results
Survival rates
Among the three communities, the four species had similar survival rates in the gaps, while they showed contrasted performances in the forests, with the invasive *Acer* showing intermediate survival rates between *Fraxinus* and the two early-successional species *Salix* and *Populus* (Table 2). Tukey’s HSD test: *Fraxinus*, a; *Acer*, b; *Salix*, c; *Populus*, c; different letters indicate significant differences between means at $P < 0.05$) (see supplemental Table 3). Under the *Fraxinus* and *Salix* canopies, *Acer* had similar survival rates to *Fraxinus* and much higher ones than *Salix* and *Populus* (Tukey’s HSD tests) (Fig. 1).

In the gaps, there was also a significant community effect because, over all species, survival rates were the highest in the *Fraxinus* stand and the lowest in the *Salix* stand (Tukey’s HSD test: *Fraxinus* stand, a; *Acer* stand, ab; *Salix* stand, b; different letters indicate significant differences between means at $P < 0.05$). Finally, there was a significant community $\times$ species interaction in the gaps, certainly due to *Fraxinus* having higher survival rates than the invasive *Acer* in the *Salix* stand only (Table 2; Fig. 1).

Growth rates
Over all species and communities, seedling growth was primarily affected by the tree canopy (Fig. 2; see supplemental Table 3), with the highest growth rates occurring in the gaps. Growth rates were also species dependent (see supplemental Table 3), with species rankings significantly affected by the tree canopy (Table 2; see supplemental Table 3). In the gaps, *Fraxinus* had the lowest growth rates and *Populus* and *Acer* the highest (Table 2) (Tukey’s HSD test: *Populus*, a; *Acer*, a; *Salix*, ab; *Fraxinus*, b; different letters indicate significant differences between means at $P <$

3 Supplementary material is available on the journal Web site (http://cjfr.nrc.ca).
Species positions along the resource trade-off

The absence of community effects in the within-forests split-plot analysis on survival rates (Table 2) and in the within-gaps split-plot analysis on growth rates (Table 2) allowed us to pool species responses among communities in a global graph (Fig. 3). *Fraxinus* had the highest mean survival rate within forests and the lowest mean growth rate in the gaps, whereas the opposite result was found for both softwood species, *Salix* and *Populus*. *Acer* was not positioned on the diagonal joining these two extreme successional positions but rather in the upper right corner of the graph with a quite high mean survival rate in the forest understories. *Acer* had survival rates under forests not significantly different from those of *Fraxinus* and growth rates in full light not significantly different from those of *Salix* and *Populus* (Tukey’s HSD tests) (Fig. 3).

Discussion

The main objective of this study was to compare the performances of juveniles of the invasive *A. negundo* with those of native species along the successional gradient to identify some invasion mechanisms of *Acer* in the middle Rhône floodplain. The midsuccessional status of the invasive species in its native range and the midsuccessional position of its stands in the recipient forests suggested that its invasion success could be due to higher performances of the invasive species in this particular position along the successional gradient or to an intermediate position between native species along the resource trade-off.

*Acer* versus native performances

Results on survival showed that both *Acer* and *Fraxinus* transplants were not significantly negatively affected by the heavy shade of the *Fraxinus* and *Acer* canopies, whereas *Salix* and *Populus* had very low survival in the same conditions. The high shade tolerance of *Acer* species from mesic habitats has previously been described and in particular for *Acer saccharum* Marsh. and *Acer rubrum* L. in North America and for *Acer pseudoplatanus* L. and *Acer platanoides* L. in Europe (Lei and Lechowicz 1990; Pagès et al. 2003; Niinemets and Valladares 2006). This behavior may be explained by their high leaf size, which in turn increases their sensitivity to drought stress (Ackerly 2004; Saccone et al. 2009), as observed for *A. negundo* by Tissier et al. (2004). In its native range, *A. negundo* is considered to have an intermediate shade tolerance (Green 1934, cited in Maeglin 1995; Walters and Reich 1996) because the lowest growth rate of the early-successional species has been described across different temperate areas, in particular when compared with late-successional Fagacae or conifers from poor soils (Bazzaz 1979; Reich et al. 1997). However, because of the high nutrient availability of floodplain soils (Tabacchi et al. 1998), late-successional species from riparian areas (e.g., *Fraxinus*, *Acer*, and *Ulmus* species) are known to also have relatively high or at least intermediate growth rates between typical *r*- and *K*-strategists (Morigo et al. 2000; Schreeg et al. 2005). We found significant differences in growth rates among the three native species along the successional gradient but the midsuccesional *Acer* had a similar high growth rate as typical early-successional species.

In our experiment, the responses of the three native species were consistent with the resource trade-off (Kobe et al. 1995; Walters and Reich 1996) because the lowest growth rate in full light was observed for the most shade-tolerant and late-successional *Fraxinus*, and conversely, the early-successional and shade-intolerant *Salix* and *Populus* had the highest growth rate in the gaps. However, results for the invasive *Acer* did not fit within this resource trade-off because this midsuccesional species had an overall survival in the shade not significantly different from that of the most shade-tolerant *Fraxinus* and much higher than the shade-intolerant *Salix* and *Populus*, although both the invasive *Acer*
and the two native early-successional species had a very high growth rate in the gaps (Fig. 3).

To summarize, inconsistent with our first hypothesis, *Acer* did not show a higher survival or growth in the midsuccessional position likely to explain its invasive success. Additionally, the position of *Acer* along the resource trade-off differed from what we expected in our second hypothesis. However, these results revealed potential explanations of *Acer* invasive success.

**Trade-off and invasion**

Noble (1989) suggested that the success of a number of invasive species may be explained by their particular trade-offs in the allocation of resources. Moreover, Sanford et al. (2003) argued that the release from native constraint could lead invaders to use resources more efficiently and outperform native species in trade-offs. In their analysis of the tolerance of Northern Hemisphere trees and shrubs to drought, shade, and waterlogging, Niinemets and Valladares (2006) also found that several invasive species were moderately tol-
Fig. 2. Mean ± 1 SE (n = 4) growth rates (expressed as centimetres of increment per centimetre of initial height) of the four species in the gaps and of Fraxinus, Acer, and Salix in the forest plots of the three communities. Asterisks below the bars indicate significant differences between species in one-way ANOVAs: (*)P < 0.05, (**)P < 0.1, and ns, nonsignificant. Letters above the bars indicate the results of the within-community and canopy post hoc Tukey test at P < 0.05.

Fig. 3. Relationship between mean ± 1 SE (n = 12) survival rates within forests and mean ± 1 SE (n = 12) growth rates in the gaps (expressed as centimetres of increment per centimetre of initial height) for the four target species among the three communities. Differences between species survival rates (above the graph) and between species growth rates (on the side of the graph) are indicated by asterisks (one-way ANOVAs: ****P < 0.0001 and *P < 0.05) and letters (Tukey’s HSD test at P < 0.05). The position of the invasive Acer is in grey.

erant simultaneously to several environmental factors. The invasion success of Acer may lie in challenging the resource trade-off, i.e., associating a high growth rate in full light conditions with a high survival in the shade. Webster et al. (2005) and Closset-Kopp et al. (2007) found similar results for A. platanoides, a European invader in North America, and Prunus serotina Ehrh., a North American invader in Europe, respectively. In both studies, they described the similar r- and K-strategist traits combination, a “sit and wait” strategy, e.g., a high shade tolerance of the understory seedlings associated with a high growth rate ability in the gaps. Finally, Richards et al. (2006) analyzed this behavior through the spectrum of plasticity. Several studies indicated that phenotypic plasticity could play an important role in invasion success, and Richards et al. (2006) proposed the “Jack-and-master” scenario, which could correspond to Acer behavior in our study. They suggested a fitness norm-of-reaction characterized by robustness in stressful environments and responsiveness when conditions are more favorable.

However, the occurrence of such an association of shade tolerance and fast-growing attributes for species in their native range such as A. pseudoplatanus in Europe (Pagès et al. 2003) and A. saccharum in North America (Canham 1988; Walters and Reich 1996) suggests that challenging the resource trade-off may not be specific to invasive species or to the invasion process. Moreover, Sanford et al. (2003), who compared the performances of A. platanoides (invasive) with those of A. saccharum (native) in the Mt. Toby Forest, did not find significant differences in the resource trade-off. We suggest that if shade tolerance and nutrient acquisition are functionally independent, as suggested by Michalet et al. (2008), a number of tree species such as numerous Acer species may represent an “exploitative and shade-tolerant” strategy, which appears as a particularly efficient strategy for invading new habitats. Moreover, the fact that numerous Acer species shared this particular suite of traits could be a sign of an adaptive phenotypic plasticity. The adaptive plasticity hypothesis described the case where a plastic genotype performs better than a less plastic one across different environmental conditions with different phenotypic optima (Pigliucci 2001). Depending on the frequencies of the diverse environments, the plastic genotype may be favored by natural selection. In the case of Acer species, because they overall occupy intermediate niches in forest succession, they are subjected to changing environments (competition for resources, disturbances). Thus, an “exploitative and shade-tolerant strategy” or a “Jack-and-master” norm-of-reaction could induce over time better performances across changing environments than more specialist strategies such as pioneer or late-successional phenotypes. However, our study was not designed to test genetic hypotheses and specific studies are needed to explore it.

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**Acer invasion process**

The “exploitative and shade-tolerant” strategy of *A. negundo* is a missing combination of traits in the recipient communities from the middle Rhône floodplain representing an empty functional niche likely to have promoted *Acer* invasion (Fargione et al. 2003; Zavaleta and Hulvey 2004). However, we did not study the whole invasion process in our experiment and other factors also could potentially promote the invasion of *Acer* in the middle Rhône floodplain. For instance, Reinhart and Callaway (2004) found that, following the enemy release hypothesis, the escape from negative effects from species-specific natural enemies allowed *A. negundo* to benefit from non-species-specific mutualists from European recipient communities. The Rhône River regulation could also be a promoter of the start of the *Acer* invasion process as shown by Tabacchi and Planty-Tabacchi (2003) on the Garonne River. However, the high seedling mortality rate of the four species including the invasive in the *Salix* stands suggests that regulation by the flood disturbance regime remains strong (P. Saccone, personal observation). Furthermore, our experiment was not set up to test the relative position of the four species along the colonization–competition trade-off. However, the data from the literature (Rameau et al. 1997; Marigo et al. 2000) showed that *Acer* had similar high seed size (reversely correlated with colonization ability; Coomes and Grubb 2003) than *Fraxinus*. Moreover, the colonization success of the early-successional natives *Populus* and *Salix* is known to be primarily due to their high resprouting abilities (Karrenberg et al. 2003; Douhovnikoff et al. 2005) and *Acer* has been shown to exhibit intermediate resprouting abilities (Wilson 1970; Maeglin and Ohmann 1973). As a result, *Acer* should not challenge the colonization–competition trade-off. Our study concerned only the species performances at the seedling stage, and the understanding of the whole invasion process would need to consider factors affecting seed transport, germination rates, sapling performances, and sexual maturation.

**Conclusion**

Our results highlighted the particular strategy of *A. negundo* during its juvenile stage, which is a major filter of plant community structure and dynamics (Sánchez-Gómez et al. 2006) and in particular for riparian vegetation (Richardson et al. 2007). Crawley et al. (1996) suggested that invaders are either moreso *r*-strategists than native *r*-strategists or moreso *K*-strategists than native *K*-strategists. Our results showed that *Acer* could be as *r*-strategist as native *r*-strategists and as *K*-strategist as native *K*-strategists. We are aware that our results did not allow us to make conclusions about the expansion of *Acer* from its intermediate position to adjacent communities and in particular toward late-successional habitats naturally occupied by *Fraxinus*. However, biological inertia (Von Holle et al. 2003) and the long lifespan characterizing trees (Martin et al. 2009) may induce a time lag in the *Acer* expansion, at least in the absence of disturbance of these late-successional habitats.

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