

Acer negundo invasion along a successional gradient: early direct facilitation by native pioneers and late indirect facilitation by conspecifics

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Summary

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- Here, we analysed the role of direct and indirect plant interactions in the invasion process of *Acer negundo* along a natural successional gradient in the Middle Rhone floodplain (France). We addressed two questions: What are the responses of the invasive *Acer* seedlings to native communities' effects along the successional gradient? What are the effects of the invasive *Acer* adult trees on the native communities?
- In the three communities (*Salix*, *Acer* and *Fraxinus* stands) we transplanted juveniles of the invasive and juveniles of the natives within the forest and in experimental gaps, and with and without the herb layer. We also quantified changes in understory functional composition, light, nitrogen and moisture among treatments.
- *Acer* seedlings were directly facilitated for survival in the *Salix* and *Acer* communities and indirectly facilitated for growth by adult *Acer* through the reduction of the abundance of highly competitive herbaceous competitors.
- We conclude that direct facilitation by the tree canopy of the native pioneer *Salix* is very likely the main biotic process that induced colonization of the invasive *Acer* in the floodplain and that indirect facilitation by adult conspecifics contributed to population establishment.

Introduction

Biotic interactions are major drivers of exotic plant invasions (Elton, 1958; Simberloff & Von Holle, 1999), in particular during colonization and establishment stages (Theoharides & Dukes, 2007). A large body of literature emphasizes either the biotic containment of invaders by native species ('natives') (Levine *et al.*, 2004) or the competitive effects of particularly strong invaders (Callaway & Aschehoug, 2000; Galbraith-Kent & Handel, 2008). Conversely, positive interactions between native and exotic species (Bulleri *et al.*, 2008) and between different exotic species (Simberloff, 2006) have been identified as important invasion promoters (Mitchell *et al.*, 2006).

Most studies analysing the role of biotic interactions in an invasion process have focused on a particular stage and either on the competitive responses or effects of invasive

species ('invasives'). However, a number of authors revealed changes in plant–plant interactions during an invasion process. In an Appalachian floodplain community, Von Holle (2005) found changes in native–invader interactions from facilitation in stressful riverbank to competition and biotic containment in more benign upland habitats. Suding *et al.* (2004) and Hager (2004) separated the effects and responses of the invaders *Centaurea diffusa* and *Lythrum salicaria*, respectively. Hager (2004) found that *L. salicaria* had stronger competitive effects on natives than responses to natives and thus that the disturbance of native communities was the primary mechanism driving colonization success, but that, later during succession, establishment success resulted from the competitive exclusion of natives. Furthermore, quantifying the role of biotic interactions at different stages of the invasion process may prove crucial for understanding the invasion of long-lived invasives because

developing vegetation is more likely to modify environmental conditions during the invasion process which in turn may alter the strength and direction of interactions between natives and invasives (Gomez-Aparicio *et al.*, 2008). Such environmental changes may occur through classic successional changes (Clements, 1916) or/and through ecosystem engineering effects induced by the invasive itself (Lambrinos & Bando, 2008).

In addition, White *et al.* (2006) suggested that indirect interactions should be incorporated into the study of invasives. Indeed, in the grasslands of south-western USA, Siemann & Rogers (2003) showed that the adults of the invasive *Sapium sebiferum* indirectly facilitated their own seedlings. Direct interactions between plant species may be altered by indirect interactions involving additional species. Indirect positive effects may occur in complex communities when a species decreases the negative effect of a strong competitor on other species (Connell, 1990). Levine (1999) argued that a number of positive associations of tree seedlings with adult trees might rather be caused by indirect positive effects than by direct facilitation. Pagès & Michalet (2003, 2006) experimentally tested this hypothesis and showed that indirect facilitation is rarely observed in forest communities because the decrease in competition between herbaceous species and tree seedlings (competitive release or indirect positive effect) is often overwhelmed by the direct negative effect on light of the tree canopy on the tree seedlings. However, Pagès *et al.* (2003) showed that some tree species such as maples, are good candidates for indirect facilitation as seedlings because of their high shade-tolerance and their low tolerance to herbaceous competitors. The role of indirect facilitation remains to be explored in invasion ecology, in particular because invasives have been shown to have particular combinations of traits that may be suitable for indirect facilitation to occur (Closset-Kopp *et al.*, 2007).

The aim of our study was to analyse the importance and direction of direct and indirect interactions between the invasive *Acer negundo* and native tree species along a natural successional gradient in a floodplain system. Because flooding induces a strong gradient of decreasing disturbance from the riverbank to old terraces (Blom & Voesenek, 1996; Whited *et al.*, 2007), floodplain forests represent a suitable system to analyse changes in biotic interactions between native and exotic species at a small spatial scale. Our experiment was conducted in the middle Rhône floodplain (France) where two main native community types have been described along a classic allogenic successional gradient (Clements, 1916): a softwood community dominated by *Salix alba* and *Populus alba* in the most disturbed habitats and a hardwood community dominated by *Fraxinus angustifolia* in the least disturbed habitats (Pautou *et al.*, 1992). The invasive *A. negundo* forms monodominant stands at the ecotone between the native softwood and hardwood communities (Pont, 1999). This system allowed

us to analyse both the responses of *Acer* to native communities as seedlings during the colonization stage, and the effect of *Acer* as adult on natives at the establishment stage (*sensu* Theoharides & Dukes, 2007). In order to analyse variation in responses and effects, we reciprocally transplanted seedlings of *Acer* and three native tree species (*Fraxinus*, *Populus* and *Salix*) at three positions along the flooding gradient: the most disturbed *Salix*–*Populus* community, the intermediately disturbed *Acer* community and the least disturbed *Fraxinus* community. Direct and indirect interactions were assessed in each stand through the removal of both the tree canopy and the herb layer. Finally, to show underlying processes, we measured the effects of tree canopies and of herb layers on resource availability (light, water and nitrogen) and quantified changes in herb layer biomass among treatments. We aimed answer to two main questions: What are the responses of the invasive *Acer* seedlings to native communities' effects along the successional gradient? What are the effects of the adult invasive *Acer* on the native communities?

Materials and Methods

Study area

The experiment was performed in the riparian forests of the Natural Reserve of la Platière, located in 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 (Météo-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 a dyke 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 zones close to the riverbank and are yearly flooded. *Acer* stands replace the *Salix* stands on older terraces along the riparian profile, are frequently flooded and characterized by the presence of some tall and old *Populus* individuals. The oldest terraces, rarely flooded, are dominated by *Fraxinus* stands.

Studied species

We used transplants of the four dominant species of these riparian forests, two early-successional species, *P. alba* L. and *S. alba* L., the late-successional species *F. angustifolia* (Vahl) (Rameau *et al.*, 1997) and the invasive *A. negundo* L. We used 1-yr-old seedling individuals because we wanted to

use transplantable individuals and to avoid germination problems, and because the seedling stage is determinant for the structure of floodplain forests (Richardson *et al.*, 2007). More precisely, we used 1-yr-old bare-rooted seedlings for both *Fraxinus* and *Acer* and cuttings from 1-yr-old seedlings for *Populus* and *Salix* in order 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). Seedlings were grown for 1 yr in local nurseries and were stemmed from seeds harvested in neighboring forests. At the end of the experiment, all *Acer* seedlings were uprooted 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 set-up (Fig. 1) because our transplantations were established within the natural range of propagule dispersal (the invasive *Acer* and other native species are already present at the mature stage in the landscape). We used a completely randomized split-split-split-plot design (Underwood, 1997), with community as main effect, tree canopy as second effect, herb layer (including grasses, forbs and small woody plants from the low shrub layer) as third effect and target species (species treatment) as fourth effect. The community treatment included the three successional forest types already described, that is, the *Salix*, *Acer* and *Fraxinus* communities, with four replicates per community type. The area of each of the 12 sites (three communities \times 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 \times 20 m plot in an experimental gap and another in the adjacent unmanipulated forest. The experimental gaps were created in late November 2003 to late January 2004 by removing all trees in a 40 \times 40 m area. We removed tree regrowth during the whole experiment. Each of the 24 plots (three communities \times four replicates \times two plots (one gap + one forest)) was divided into eight subplots of at least 3 m \times 3 m. The herb layer treatment consisted of removing all grasses, forbs and small woody plants monthly from four of the eight subplots in each plot by hand-pulling up. As a result, each of the four biotic interactions combinations (with and without tree canopy and with and without herb layer) was repeated four times in each of the 12 sites and represented in each site by a group of four subplots randomly separated in space. Finally, in late March 2004, the species treatment was applied by the random transplanting of three individuals (seedlings or cuttings) of each target species in the center of each of the 192 subplots with at least 50 cm-distance between individuals.

Resource measurements

In late May 2005, at least 3 d after the last precipitation event, two soil samples were randomly collected 3–10 cm deep in each biotic interaction combination within each site. The two soil samples were pooled and immediately weighed. Both NO_3^- and NH_4^+ were extracted as described in Wheatley *et al.* (1989). The NO_3^- was determined by ionic chromatography (4500i; Dionex, Sunnyvale, CA, USA) and the NH_4^+ by the blue indophenol method (Dorich & Nelson, 1983). The available soil nitrogen (N)

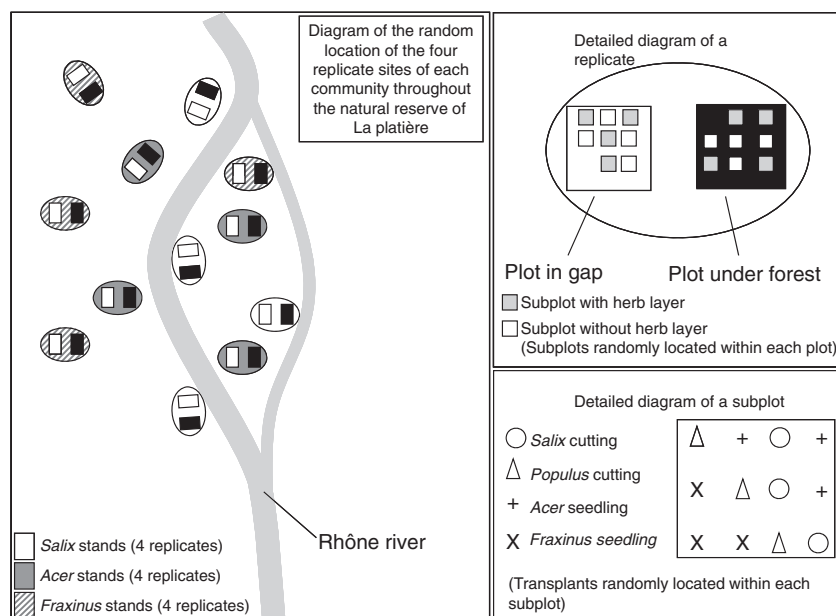


Fig. 1 Diagram of the experimental design.

content was calculated as the sum of $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$, and expressed in N mass per unit of dry soil mass (g g^{-1}). Soil samples were oven-dried at 105°C for 2 d and soil moisture was expressed in percentage of fresh soil mass. In July 2005, the fraction of photosynthetically active radiation (PAR; 400–700 nm) reaching the ground was measured at noon during a sunny day, using a portable quantum sensor (Li-188b; Li-Cor, Lincoln, NE, USA). Three PAR measurements were collected per subplot and averaged. Light availability was expressed in percentage of the mean incident PAR occurring in the four subplots of the gap without herb layer of each site.

Transplant measurements

Survival of transplants was measured in November 2005, at the end of the second growing season, and specific survival rates were calculated as the percentage of transplants alive at the end of the experiment per biotic interaction combination and per site.

We measured the basal stem diameter and the total height of each transplant at the beginning, the middle (November 2004), and the end of the experiment. For *Salix* and *Populus* cuttings, we measured the basal diameter and total height of the greatest epicormic shoot of the first growing season and the diameter of cuttings was also recorded. In November 2005, for all four species, one of the three transplants per subplot was randomly chosen to meticulously uproot and measure total biomass. However, we did not collect from subplots with null specific survival rates and this affected sample size. After oven-drying at 105°C for 3 d, we measured the total dry biomass of each individual. After different statistical tests, we found that the best allometric relation between biomass and field measurements (basal diameter, total height and cutting diameter for *Salix* and *Populus*) of each species was represented by the power function:

$$B = aX^b$$

(B , total dry weight of the individual (g); X , basal diameter of the individual (mm); a and b are estimated parameters). We linearized the model using a log–log transformation. Biomass and diameter are both subject to natural variation and measurement error, thus we used Reduced Major Axis regression (RMA, a model II regression) to estimate the parameters, using the *s.slopes* function written for implementation in R (<http://eeb37.biosci.arizona.edu/~brian/splus.html>; see Isobe *et al.*, 1990). We used these four specific allometric equations (data not shown) to convert our field measures into biomass values. We used the relative biomass increment during the second year as indicator of transplant growth to avoid bias caused by the type of individuals (seedlings or cuttings), calculated as:

$$\text{RBI} = (B_{2005} - B_{2004}) / B_{2004}$$

(RBI, relative biomass increment of each individual; B_{2004} and B_{2005} , biomass in November 2004 and in November 2005, respectively).

Biotic interactions

Tree canopy and herb layer effects on transplant performances (survival and growth) were displayed using the Relative Interaction Index (RII; Armas *et al.*, 2004):

$$\text{RII}_{\text{tree}} = (X_{\text{Fh}} - X_{\text{fh}}) / (X_{\text{Fh}} + X_{\text{fh}})$$

$$\text{RII}_{\text{herb in gaps}} = (X_{\text{FH}} - X_{\text{fh}}) / (X_{\text{FH}} + X_{\text{fh}})$$

$$\text{RII}_{\text{indirect tree}} = (X_{\text{FH}} - X_{\text{fH}}) / (X_{\text{FH}} + X_{\text{fH}})$$

$$\text{RII}_{\text{herb under forest}} = (X_{\text{FH}} - X_{\text{Fh}}) / (X_{\text{FH}} + X_{\text{Fh}})$$

(X , mean value of the transplant performance in each biotic interaction combination with (F) and without (f) tree canopy and with (H) and without (h) herb layer). The high mortality rate of *Populus* and *Salix* with tree canopy and/or herb layer did not allow us to analyse the effects of biotic interactions on their growth and impeded the calculation of some RIIs.

The RII values are symmetrical around zero and included between -1 and $+1$, with positive values indicating facilitation and negative values indicating competition. For the indirect effects of the tree canopy, we applied the calculation method of Pagès *et al.* (2003) to RII. Following Pagès *et al.* (2003), positive $\text{RII}_{\text{indirect tree}}$ values indicate indirect facilitation by trees, but only in the absence of direct facilitation from the tree canopy, and negative $\text{RII}_{\text{indirect tree}}$ values indicate additional competition.

Herb layer biomass and composition

In July 2005, two 1×1 m samples of the herbaceous aboveground biomass were randomly collected per plot. For each sample, the different species were separated, oven-dried at 105°C for 3 d and weighed. We then gathered the species in two different functional groups (see complete list in Table 1): an 'exploitative' functional group for species with high relative growth rate, size and competitive ability (e.g. *Urtica dioica* or *Renoutria japonica*) as examples of the C strategy of Grime (1979) and a 'conservative' functional group for woody species (e.g. trees seedlings and shrubs such as *Crataegus laevigata*) and short shade-tolerant herbaceous species (e.g. *Hedera helix*), which are slow-growers and bad competitors, as examples of the S strategy of Grime (1979).

Table 1 List of conservative and exploitative species identified in the herb layer of the study site

Conservative species	Exploitative species
<i>Acer negundo</i>	<i>Artemisia campestris</i>
<i>Clematis vitalba</i>	<i>Chelidonium major</i>
<i>Cornus mas</i>	<i>Galium aparine</i>
<i>Crataegus laevigata</i>	<i>Heracleum sphondylium</i>
<i>Fraxinus angustifolia</i>	<i>Lactuca perennis</i>
<i>Hedera helix</i>	<i>Mentha rotundifolia</i>
<i>Ligustrum vulgare</i>	<i>Parietaria officinalis</i>
<i>Prunus spinosa</i>	<i>Parthenocissus quinquefolia</i>
<i>Ulmus minor</i>	<i>Poa nemoralis</i>
	<i>Reynoutria japonica</i>
	<i>Rubus fruticosus</i>
	<i>Urtica dioica</i>
	<i>Vitis vinifera</i>

Conservative species includes conservative herb species and all woody species including tree seedlings.

Statistical analyses

Differences in species survival and growth rates were analysed using several ANOVA models on raw data (see the Supporting Information, Table S1). Overall differences in species survival rates were analysed using a split-split-split-plot model, with community as main plot effect, tree canopy as subplot effect, herb layer as sub-subplot effect and species as sub-sub-subplot effect. The effects of tree canopy and herb layer treatments on survival and growth rates were analysed per community and per species using a split-plot on randomized block model, with tree canopy as main plot effect and herb layer as subplot effect. We used the same split-plot on randomized block model, with tree canopy as main plot effect and functional group (exploitative vs conservative) as subplot effect to test differences in herb layer biomass. Moreover, we used one-way ANOVA model to test the effect of tree canopy on herb layer biomass within each community. Differences in resource levels (light availability, soil moisture and soil N content) were analysed using one-way ANOVA model with the four biotic interaction combinations (with/without tree canopy \times with/without herb layer) as four modalities of the treatment. Finally, One-sample *t*-tests were used to test significant deviations from zero of RII values and ANOVAs were followed by Tukey's HSD tests when necessary. Data sets were checked for normality and homoscedasticity and all analyses were carried out with JMP 5.0.1 (SAS Institute, Cary, NC, USA).

Results

Survival responses

Overall, results of the global split-split-split-plot ANOVA on species survival rates showed highly significant species effects, as well as single factor and in interaction with other

treatments (Table 2). Thus, we used the global ANOVA to analyse changes in species responses among species and communities and within-species-and-community analyses to more precisely explore the effects of the tree canopy and of the herb layer. Overall, transplants had higher survival rates in the *Fraxinus* community (including gap and forest conditions) than in the *Acer* and *Salix* ones (Tukey's HSD tests for the three effect types: *Fraxinus* stands, a; *Acer* and *Salix* stands, b; Table 2). Along the successional gradient, the effect of tree canopy shifted from overall negative in the *Fraxinus* stands to overall positive in the *Salix* stands (Fig. 2a, Table 2). More precisely, *Salix* and *Populus* transplants had negative responses to the tree canopy in the *Fraxinus* and *Acer* stands, whereas the survival of the invasive *Acer*, and to a lesser extent that of *Fraxinus*, were facilitated by the tree canopy of *Acer* and *Salix* stands (Fig. 2a, Table 3). Herb layer had an overall negative effect on transplants survival rates (Table 2) but this effect decreased from the *Salix* stands to the *Fraxinus* ones (Community \times Herbaceous in Table 2; Fig. 2c,d). Herb layer of the three communities significantly reduced the survival rates of *Populus* transplants (Table 3), in particular in the gaps (Fig. 2c). The same trend was observed for *Salix* survival rates (Fig. 2c), except in the *Fraxinus* stands (Table 3). By contrast, *Acer* and *Fraxinus* seedlings had negative responses to the herb layer only under the *Salix* canopy (Fig. 2d). This negative effect of the herb layer almost

Table 2 Results of split-split-split-plot ANOVA for the effects of community, tree canopy, herb layer, species treatments and their interactions on the transplants' survival rates

Source of deviation	df	F	P
Community	2	14.41	0.0016**
Error (main plot)	9		
Tree canopy	1	4.24	0.0695(*)
Community \times Tree canopy	2	7.72	0.0112*
Error (subplot)	9		
Herb layer	1	29.43	0.0004***
Tree canopy \times Herb layer	1	0.87	0.3754
Community \times Herb layer	2	5.77	0.0244*
Community \times Tree canopy \times Herb layer	2	3.32	0.0831(*)
Error (sub-sub-plot)	9		
Species	3	72.42	< 0.0001****
Species \times Herb layer	3	0.99	0.4
Species \times Tree canopy	3	26.31	< 0.0001****
Species \times Community	6	3.20	0.0061**
Species \times Tree canopy \times Herb layer	3	8.63	< 0.0001****
Species \times Community \times Herb layer	6	4.11	0.0009***
Species \times Community \times Tree canopy	6	1.60	0.1529
Species \times Community \times Tree canopy \times Herb layer	6	0.80	0.5757
Error (residual)	117		

****, $P < 0.0001$; ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; (*), $P < 0.1$.

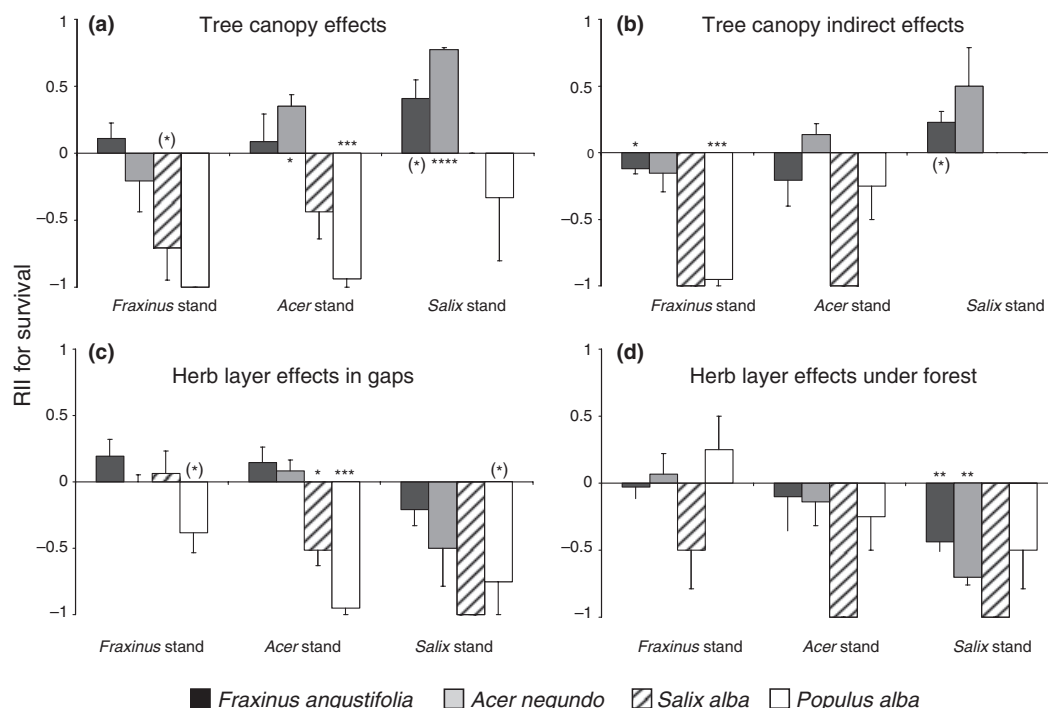


Fig. 2 (a) Direct effects of the tree canopy (mean ± 1 SE; $n = 4$), (b) indirect effects of the tree canopy (mean ± 1 SE; $n = 4$), (c) effects of the herb layer (mean ± 1 SE; $n = 4$) in the gaps and (d) under forests (mean ± 1 SE; $n = 4$) on specific survival rates in each community. Asterisks below or above bars indicate significant differences from zero (one-sample *t*-tests; ****, $P < 0.0001$; ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; (*), $P < 0.1$).

Table 3 Results of the split-plot on randomized complete block ANOVAs for the effects of tree canopy, herb layer and their interaction on the transplants' survival rates per species within each community

			<i>Fraxinus</i>		<i>Acer</i>		<i>Populus</i>		<i>Salix</i>	
Source of deviation			<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>Fraxinus</i> stand	Block	3	2.34	0.2514	0.32	0.8153	1.18	0.4481	0.89	0.5367
	Tree canopy	1	0.32	0.6134	1.35	0.3294	11.37	0.0434*	12.71	0.0377*
	Error (main plot)	3								
	Herb layer	1	0.73	0.4248	0.00	1	6.97	0.0386*	0.29	0.6122
	Tree canopy × Herb layer	1	2.24	0.1848	0.00	1	9.48	0.0217*	0.00	1
	Error (residual)	6								
<i>Acer</i> stand	Block	3	0.81	0.5674	2.68	0.2195	1.14	0.4586	0.46	0.7287
	Tree canopy	1	0.06	0.824	3.95	0.1411	13.80	0.0339*	4.45	0.1253
	Error (main plot)	3								
	Herb layer	1	0.05	0.8339	0.00	1	22.35	0.0032**	34.71	0.0011**
	Tree canopy × Herb layer	1	0.64	0.4526	0.32	0.5945	18.63	0.005**	2.33	0.1775
	Error (residual)	6								
<i>Salix</i> stand	Block	3	2.95	0.199	0.64	0.6403	0.58	0.6677	0.50	0.7082
	Tree canopy	1	21.60	0.0188*	34.91	0.0097**	1.42	0.3189	0.00	1
	Error (main plot)	3								
	Herb layer	1	27.35	0.002**	294.00	<0.0001****	9.80	0.0203*	50.00	0.0004***
	Tree canopy × Herb layer	1	6.84	0.0399*	216.00	<0.0001****	1.80	0.2283	0.00	1
	Error (residual)	6								

****, $P < 0.0001$; ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.

counterbalanced the direct positive effect of the tree canopy for these two species, as suggested by the only marginally significant indirect positive effect observed for *Fraxinus*

seedlings in the *Salix* stands (Fig. 2b). Finally, there was a strong additional competition for the two early-successional species in the *Fraxinus* and *Acer* stands (Fig. 2b).

Growth responses

Because *Salix* and *Populus* had high mortality rates in the plots with tree canopy and/or with herb layer, the analysis of the effects of the tree canopy and of the herb layer on the growth rates of these species were only limited to one-sample *t*-tests on available RII. The direct effects of both the tree canopy and the herb layer were overall negative for the growth of the four transplanted species (Fig. 3a,c,d). More precisely, the growth of *Fraxinus* seedlings was only marginally altered by the tree canopy of the *Fraxinus* and *Acer* stands, whereas that of *Acer* seedlings was significantly negatively affected by the tree canopy of the *Acer* and *Salix* stands (Table 4, Fig. 3a). In the gaps the effect of the herb layer was strongly negative for all species, and in particular for *Acer* seedlings in *Acer* stands where this effect was highly significant (Table 4, Fig. 3c). Within the forests, the negative effects of the herb layer decreased and were still significant only for *Acer* in the *Acer* stands and for *Fraxinus* in the *Salix* stands (Fig. 3d). The only significant positive indirect tree canopy effect was observed in the *Acer* stands for their own seedlings, likely because the herb layer competition strongly decreased for this species from the gaps to under the forest (Fig. 3b).

Treatment effects on resources

In the three communities the lowest light availability was observed in the plots including both the tree canopy and

the herb layer (Fig. 4). However, in the *Acer* stands, light availability was less reduced by the herb layer in the gaps than by the tree canopy, in contrast to the two other communities (within-community Tukey's HSD tests, Fig. 4a). Moreover, light availability was higher under the herb layer of the gaps of the *Acer* stands than under those of the two other communities (one-way ANOVA and Tukey's HSD test not shown). Differences in the amounts of soil resources (N content and moisture) compared among biotic interaction combinations were significant only in the *Acer* community where the herb layer of the gaps induced a decrease in soil resource compared with other biotic interaction combinations (Fig. 4b,c).

Changes in herb layer composition and biomass

There were no differences in total herb layer biomass among communities (Table 5) but there was a strong decrease in dominance of exploitative species from the *Salix* community to the *Fraxinus* community (Table 5, Fig. 5). In the *Acer* and *Salix* communities, where exploitative species were dominant, the tree canopy induced a strong decrease in their biomass, whereas there were no significant changes for conservative species (Table 5, Fig. 5). There was a significant Community \times Tree canopy \times Functional composition interaction (Table 5) because changes in understory functional composition from gaps to forest plots were different among communities. In the *Salix* community, there was an

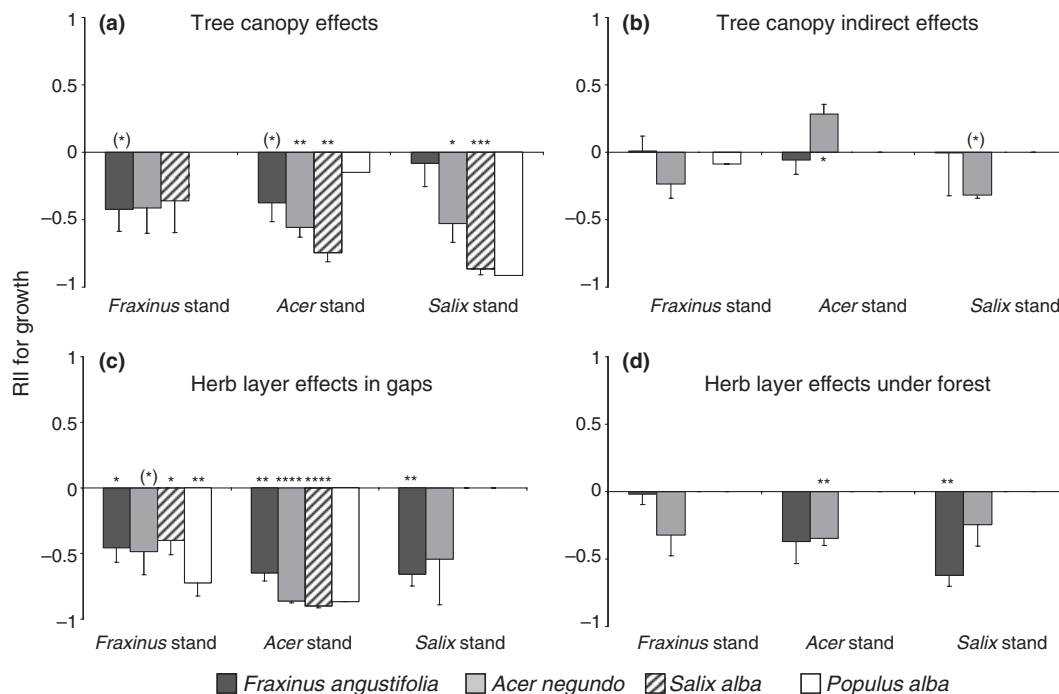


Fig. 3 (a) Direct effects of the tree canopy (mean \pm 1 SE; $n = 4$), (b) indirect effects of the tree canopy (mean \pm 1 SE; $n = 4$), (c) effects of the herb layer (mean \pm 1 SE; $n = 4$) in the gaps and (d) under forests (mean \pm 1 SE; $n = 4$) on specific growth rates in each community. Asterisks below or above bars indicate significant differences from zero (one-sample *t*-tests; ****, $P < 0.0001$; ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; (*), $P < 0.1$).

Table 4 Results of the split-plot on randomized complete block ANOVAs for the effects of tree canopy, herb layer and their interaction on the *Fraxinus* and *Acer* transplants' growth rates per species within each community

	Source of deviation	df	<i>Fraxinus</i>		<i>Acer</i>	
			<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>Fraxinus</i> stand	Block	3	0.50	0.7088	1.05	0.4858
	Tree canopy	1	4.73	0.1179	3.94	0.1414
	Error (main plot)	3				
	Herb layer	1	9.71	0.0207	4.68	0.0737
	Tree canopy \times Herb layer	1	9.51	0.0216	1.70	0.2399
	Error (residual)	6				
<i>Acer</i> stand	Block	3	0.55	0.682	1.62	0.3504
	Tree canopy	1	8.44	0.0623	16.16	0.0276*
	Error (main plot)	3				
	Herb layer	1	26.92	0.002**	49.61	0.0004***
	Tree canopy \times Herb layer	1	7.12	0.0371*	25.23	0.0024**
	Error (residual)	6				
<i>Salix</i> Stand	Block	3	0.89	0.538	0.60	0.6551
	Tree canopy	1	0.01	0.9357	24.68	0.0157*
	Error (main plot)	3				
	Herb layer	1	20.59	0.0039**	5.88	0.0515
	Tree canopy \times Herb layer	1	0.00	0.9605	2.40	0.1723
	Error (residual)	6				

***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.

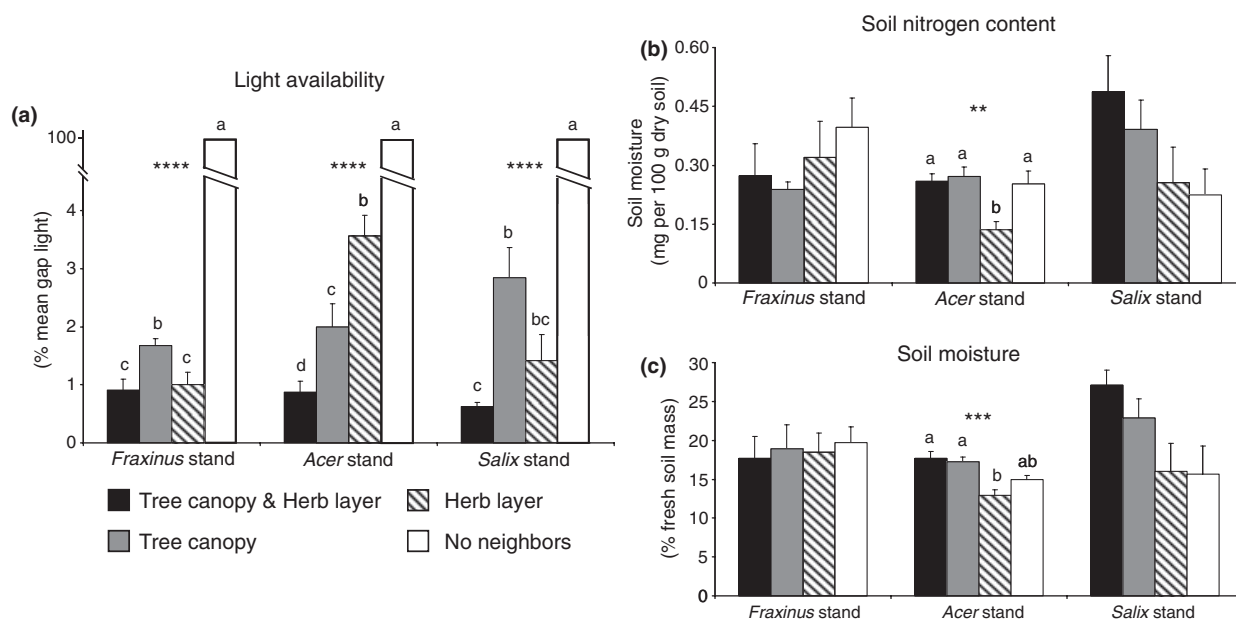


Fig. 4 Level of (a) light availability (mean \pm 1 SE; $n = 4$), (b) soil nitrogen content (mean \pm 1 SE; $n = 4$) and (c) soil moisture (mean \pm 1 SE; $n = 4$) in each treatments combination (community \times tree canopy \times herb layer). Asterisks above within community group of bars indicate significant differences between resource levels in a one-way ANOVA (****, $P < 0.0001$; ***, $P < 0.001$; **, $P < 0.01$) and letters indicate the results of the *post hoc* Tukey test ($P < 0.05$).

exclusive dominance of exploitative species and their biomass was two times greater in gaps than in forests (Fig. 5). In the *Fraxinus* community, exploitative and conservative species codominated the herb layer and there was no

difference between gap and forest conditions. By contrast, in the *Acer* community, the functional composition of the gaps was very similar to that of the *Salix* community (strong dominance of exploitative species), whereas the functional

Table 5 Results of the split-split-plot ANOVA for the effects of community, tree canopy, composition and their interaction on the herbaceous layer's biomass

Source of deviation	df	F	P
Community	2	0.84	0.4619
Error (main plot)	9		
Tree canopy	1	15.18	0.0036**
Community × Tree canopy	2	0.55	0.597
Error (sub plot)	9		
Composition	1	13.34	0.0018**
Tree canopy × Composition	1	8.06	0.0109*
Community × Composition	2	13.57	0.0003***
Community × Tree Canopy × Composition	2	4.25	0.0307*
Error (residual)	18		

***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.

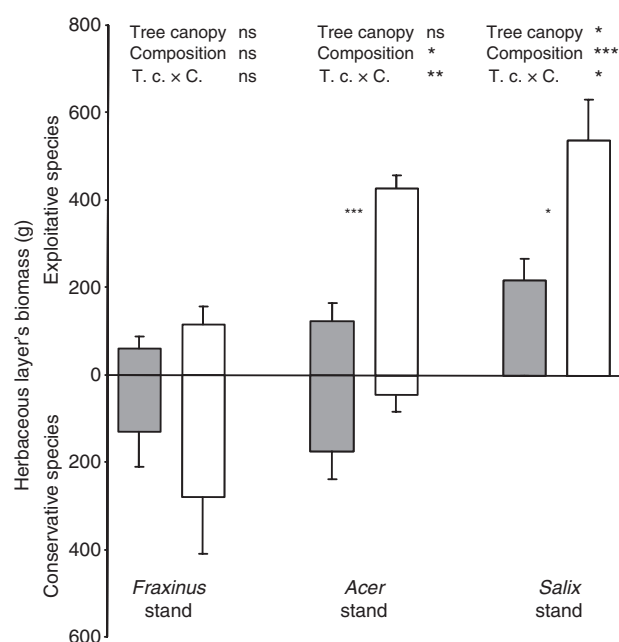


Fig. 5 Biomass (mean \pm 1 SE; $n = 4$) of exploitative (toward the top) and conservative species (towards the bottom) of the herb layer in gaps (open bars) and under tree canopy (tinted bars) for each community. Asterisks between bars indicate significant effect of tree canopy (T.c.) on herbaceous biomass per community \times functional group combination (one way ANOVAs; ***, $P < 0.001$; *, $P < 0.05$). Results of the within-community two-way ANOVAs for the effects of the tree canopy, functional composition and their interaction are displayed above each community group of bars (***, $P < 0.0001$; *, $P < 0.05$; ns, not significant).

composition of the forest plots was rather similar to that of the *Fraxinus* community (codominance of both functional groups, Fig. 5).

Discussion

The aim of our study was to explore the importance and direction of direct and indirect interactions occurring

between the invasive *A. negundo* and natives along a natural successional gradient in the middle Rhône floodplain. We wanted to tease out the driving biotic mechanisms of *Acer* invasion acting at different positions along the gradient and at different phases of the invasion process. Our results showed species-specific effects and responses to plant–plant interactions. Focusing on the invasive, we found direct positive responses of *Acer* seedlings to the *Salix* and conspecifics canopies in the most disturbed and intermediate communities, but no evidence of biotic containment of *Acer* seedlings' survival or growth by the tree canopy of the most stable community. We also found that adult *Acer* strongly altered the understory's functional composition, which is very likely to have induced an indirect facilitation of its own seedlings.

Acer seedlings' responses to native communities

The most significant result of our experiment was the strong increase in survival observed for *Acer* seedlings below the *Salix* canopy. Across all target species there was a dramatic shift in direct canopy–seedling interactions occurring for survival along the successional gradient, from positive tree canopy effects in the pioneer *Salix* community to negative effects in the late successional *Fraxinus* community. Such shifts in interactions during primary succession have been described in many systems (see for example Chapin *et al.*, 1994 for glacier chronosequences) and constitute the conceptual framework of the autogenic successional model of Clements (1916), as well as that of current facilitation models (Bertness & Callaway, 1994). Facilitation is thought to prevail at the early stages of succession where environmental severity (physical disturbance and stress, *sensu* Grime, 1979) is the highest. *Acer* was strongly facilitated in the pioneer *Salix* community and to a lesser extent in its own community, but not in the late-successional *Fraxinus* community, which is consistent with general facilitation theory; in severe environments resident species may facilitate rather than compete with invaders (Bruno *et al.*, 2003; Badano *et al.*, 2007). Our environmental measurements did not show any significant variation among communities in the tree canopy effects on both available N and soil moisture likely to suggest a mitigation of stressful conditions. In our study, as in marine ecosystems (Ceccherelli & Cinelli, 1999; Ruesink, 2007), the driving mechanism of facilitation might have been the mitigation of physical disturbance, and in particular the reduction of flooding disturbance by the web of interlocking stems in the *Salix* community (field observations). However, other mechanisms such as the mitigation of flooding stress (waterlogging in spring) might also be involved, as argued by Von Holle (2005) for the invasion of an Appalachian floodplain community.

Only *Acer* and marginally *Fraxinus* were facilitated by the *Salix* canopy and only *Salix* and *Populus* were

negatively affected by the *Fraxinus* canopy. Species responses to the effects of neighbors are known to be highly dependent on their functional strategies (Michalet *et al.*, 2006). Liancourt *et al.* (2005) have shown that the facilitative response of a target species is positively related to its competitive response and negatively related to its stress-tolerance ability. They also demonstrated that for the same species, facilitative responses were the most frequent in the most stressed part of its ecological niche and competitive responses in relatively benign environmental conditions (see also Saccone *et al.*, 2009; Forey *et al.*, 2010). Following these conclusions, the two pioneer and shade-intolerant species *Salix* and *Populus* (Niinemets & Valladares, 2006) were the poorest candidates for facilitative responses because of their very low competitive abilities, as demonstrated by their strong negative responses to the tree canopy in the highly competitive environment of the shady *Fraxinus* community. The absence of a significant facilitative response for *Fraxinus* even in the *Salix* community is not as easy to understand because this shade-tolerant species (Niinemets & Valladares, 2006; Saccone *et al.*, 2009) had a higher competitive response than *Acer* in the most shady *Fraxinus* community. If the cost of shade was similar for both species, we suggest that facilitation was observed only for the latter because the benefit of the adult *Salix* neighborhood was certainly higher than for the former. Our results for seedling survival rates in the *Salix* plots without tree canopies and without the herb layer showed that *Acer* was more negatively affected by flooding disturbance than *Fraxinus* (0.08 ± 0.1 and 0.33 ± 0.1 for *Acer* and *Fraxinus*, respectively). Consistent with Liancourt *et al.* (2005), because the abiotic environment of the *Salix* community was certainly harsher for *Acer* than for *Fraxinus*, the benefit of the *Salix* neighborhood was higher for the former, which may explain why facilitation was higher for this species.

In opposition to the tree canopy, the effect of the herb layer on seedling's survival rates ranged from null in the *Fraxinus* community to negative and affecting *Acer* and *Fraxinus* seedlings in the *Salix* community and the gap of *Acer* stands. This result is consistent with the concept of biotic containment developed by Levine *et al.* (2004). The competitive effect of the herb layer seems to have counterbalanced the facilitative effect of the tree canopy, thus impeding the colonization of the *Salix* understory by *Acer* seedlings. We suggest that there was rather a biotic containment than a real biotic resistance, because the outcome of the opposite effects of the trees and the herb layer was positive (Fig. 2b), although not significant, likely because of the high spatial variability of the cover of herb layer in the *Salix* stands (P. Saccone, pers. obs.).

Tree seedlings had also globally negative growth responses to the tree canopy and the herb layer. The mortality rates of *Salix* and *Populus* seedlings did not allow us to analyse their growth responses and we could only compare

Acer and *Fraxinus* seedling responses. The growth of the native late-successional *Fraxinus* was overall negatively affected by the tree and herb layer neighborhood, but less than that of the invasive *Acer*. *Acer* seedlings were particularly affected in the gaps of the *Acer* stands where the effect of the herb layer was stronger than in other plots.

Effect of adult *Acer* on native communities

The direct effects of adult *Acer* on survival and growth of target tree seedlings were intermediate between those of *Salix* and *Fraxinus*. By contrast, Reinhart *et al.* (2005) and Gomez-Aparicio *et al.* (2008) have shown that *Acer platanoides*, a European maple invasive in North America, suppressed native species and directly facilitated its own seedlings through understory and soil modifications, respectively. Such direct negative effects on native species were not observed in our experiment.

However, we found a significant indirect facilitation of the adult *Acer* tree canopy for the growth of its own seedlings. Although this effect was weaker than direct canopy effects, because it occurs only for this species, it is worthwhile addressing its potential role in the establishment success of *Acer*. Furthermore, weak indirect interactions might have strong community and ecosystem consequences (Berlow, 1999), and their role has been strongly neglected in invasion ecology (White *et al.*, 2006). To our knowledge, there is one study which has demonstrated that an invasive tree species, *Sapium sebiferum*, indirectly facilitates its own seedlings to the detriment of competitive prairie grasses (Siemann & Rogers, 2003).

The occurrence of indirect facilitation only for the growth of *Acer* and only in its own community may be explained by the results of previous indirect facilitation studies (Levine, 1999; Pagès & Michalet, 2003; Pagès *et al.*, 2003; Siemann & Rogers, 2003). The indirect facilitation model assumes that the direct negative effect of adult trees or shrubs on herbaceous competitors provides an indirect positive effect on tree seedlings which overrides the direct negative effect of the trees or shrubs on the seedlings (Pagès *et al.*, 2003). Levine (1999) argued that this may occur only if the different pairs of competitors involved in the system compete for different resources or have different mechanisms to acquire resources. Indeed, Siemann & Rogers (2003) showed that the seedlings of the invasive *S. sebiferum* were indirectly facilitated by the canopy of adult *S. sebiferum* through decreasing root competition between prairie grasses and the target seedlings in the shade. In addition, Pagès *et al.* (2003) stressed the importance of the functional strategy of the target seedlings; in a subalpine coniferous forest of the French Alps, they demonstrated that the shade-tolerant and nutrient-demanding species *Acer pseudoplatanus* was a much better candidate for indirect facilitation when competing with

forest weeds than shade-intolerant and nutrient conservative conifers.

In the gaps of the *Acer* stands the herb layer (dominated by two well-known exploitative competitors, *Parietaria officinale* and *Urtica dioica*, Grime, 1974) had strong negative effects on tree seedlings and in particular those of *Acer*. This negative herb effect was certainly caused by root competition, as suggested by our environmental measurements (significant decrease in N and water but not in light in these plots). In the *Acer* stands only, the tree canopy induced a shift in the herb layer functional composition with a strong decrease in exploitative species, which may have reduced root competition with tree seedlings. Thus, by reducing the belowground competitive effect of the herb layer, adult *Acer* indirectly facilitated the growth of its own seedlings, likely because this effect was not overwhelmed by the direct negative effect on light. This occurred for *Acer* seedlings but not for *Fraxinus* ones likely because the former were more sensitive to the benefit of this competitive release than the latter, as suggested by their differences in responses to the competitive effect of the herbaceous layer in the gaps of the *Acer* stands. In other words, among the four transplanted species *Acer* was the best candidate for indirect facilitation because of its high shade-tolerance associated with an exploitative strategy, consistent with the conclusion of Pagès *et al.* (2003) for *A. pseudoplatanus*.

The biotic drivers of invasion through succession

Our results stressed the importance of positive interactions for the invasion of *A. negundo* in the Middle Rhône floodplain, with a shift from direct to indirect facilitation through succession. We showed that direct facilitation by the tree canopy of the native pioneer *Salix* is the main biotic process allowing the colonization of the invasive *Acer* in the floodplain. Later in the invasion process, indirect facilitation by adult conspecifics is certainly the other biotic driver of invasion allowing the establishment of a population. These positive responses and effects were observed for the invasive but not for the natives, likely because this species had a particular combination of traits that do not have natives. In contrast to a number of other invasives, the persistence through time of *Acer* cannot be explained by higher direct competitive effects than native late-successional species. Our study adds new evidence for the importance of positive direct and indirect interactions in invasion ecology and how their roles may change along a successional gradient.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 Raw data of specific survival and growth rates by treatment combination.

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