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Light interception principally drives the understory response to boxelder invasion in riparian forests

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Abstract   Since several decades, American boxelder (*Acer negundo*) is replacing white willow (*Salix alba*) riparian forests along southern European rivers. This study aims to evaluate the consequences of boxelder invasion on understory community in riparian areas. We determined the understory species richness, composition and biomass in boxelder and white willow stands located in three riparian forests, representative of three rivers with distinct hydrological regimes. We investigated correlation of these variables to soil moisture and particle size, main soil nutrient stocks, potential nitrification and denitrification, tree canopy cover and photosynthetic active radiation (PAR) at the ground level. A greenhouse experiment was then conducted to identify the causal factors responsible for changes in the understory. The effect of soil type, PAR level and water level on the growth and the biomass production of *Urtica dioica* were examined. A lower plant species richness and biomass, and a modification of community composition were observed for boxelder understory in all sites, regardless of their environmental characteristics. The strongest modification that follows boxelder invasion was the decline in *U. dioica*, the dominant species of the white willow forest understory. These differences were mainly correlated with a lower incident PAR under boxelder canopy. The greenhouse experiment identified PAR level as the main factor responsible for the changes in *U. dioica* stem number and biomass. Our results indicate that adult boxelder acts as an ecosystem engineer that decreases light availability. The opportunistic invasion by boxelder leads to important understory changes, which could alter riparian ecosystem functioning.

Keywords   *Acer negundo* · *Salix alba* · Plant community · Canopy shading · Ecosystem engineer

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Introduction

Most studies that have compared invaded and non-invaded plant communities have revealed a lower species richness/abundance in invaded communities

(Vilà et al. 2011). Direct interactions between exotic and native plants can influence community composition in distinct vegetation strata (Gilliam and Roberts 2003; Sankey 2007). The main mechanisms identified include competition for space, nutrients and water, and allelopathy (Vilà and Sardans 1999; House et al. 2003). For example, forest invasion by grasses can result in the formation of a dense herbaceous cover that restricts seed germination and the access of tree propagules to soil (Flory and Clay 2010). When germination occurs, tree seedling growth can be limited by direct competition with grasses for nutrients, water or light (Litton et al. 2006; Hoffmann and Haridasan 2008). In some cases, the production of allelopathic compounds can also inhibit seed germination and growth (Orr et al. 2005). As a consequence, forest regeneration and/or succession can be hindered and the mature tree community is expected to be altered (Flory and Clay 2010).

Readjustment of community composition due to the reciprocal influence of vegetation from different strata can also occur indirectly, through the modification of the abiotic environment. Alterations to the quality and the quantity of standing biomass, leaf litter accumulation, and leaf litter breakdown of exotic species have consequences on nutrient cycling and nutrient pools, and thus nutrient availability for all plants in the ecosystem (Ehrenfeld et al. 2001; Strickland et al. 2010; Bottollier-Curtet et al. 2011). Additionally, some exotic species can act as ecological engineers by modifying the nature and the availability of physical resources (Jones et al. 1994; Crooks 2002). In accordance with this, light availability is a major factor mediating both exotic species invasiveness (e.g. Maule et al. 1995; Meekins and McCarthy 2001) and invasion consequences (Levine et al. 2003; Siemens and Blossey 2007) in plant communities. For example, light interception by the tree canopy indirectly influences the composition of the associated herbaceous strata. Indeed, some exotic trees deeply reduce the abundance and species richness of the herbaceous layer (Reinhart et al. 2005; Chabrerie et al. 2010) and/or woody seedlings (Reinhart et al. 2006; Galbraith-Kent and Handel 2008) by decreasing light availability for the understory. In the case of shade-tolerant tree seedlings, the new environmental conditions under the canopy cover can then facilitate the invasion process (Siemann and Rogers 2003; Reinhart et al. 2006).

Along temperate riparian areas, exotic species can represent more than 20% of the total riparian plant species richness (Planty-Tabacchi et al. 1996; Stohlgren et al. 1998; Hood and Naiman 2000). There is strong evidence that river regulation and management can induce a shift towards dominance by invasive woody species (e.g. Aguiar and Ferreira 2005; Stromberg et al. 2007; Mortenson and Weisberg 2010). *Acer negundo* L. (boxelder) is a native tree of the northeastern USA, introduced in Europe at the end of the 17th century (Maeglin and Ohmann 1973; Krivanek et al. 2006). Since then, boxelder has spread widely in southern Europe, mainly along rivers where it is now considered to be invasive (DAISIE 2011). In southwestern France, hydrological and geomorphological changes, due to river regulation and lowering of the water table, have induced both a dieback of mature *Salix alba* L. (white willow) forest and a deficiency in willow seedling recruitment (James 1996; Steiger et al. 1998; Barsoum 2002). Furthermore, severe droughts and recurrent invasions of willow stands by a destructive moth (Torossian and Roques 1989) have weakened willow populations and accelerated their decline. In contrast, boxelder can be favoured by the decrease in flood magnitude and frequency (Friedman and Auble 1999). These field observations suggest that boxelder behaves as an ecological passenger (sensu Didham et al. 2005), thereby taking advantage of white willow decline to colonize riparian forests rather than excluding white willow by competition. Currently, the ecological impacts of boxelder invasion in Europe remain unclear. A possible alteration of dead wood processing along river systems has been raised (Tabacchi and Planty-Tabacchi 2003) and the boxelder understory functional composition seems to differ from that of the native white willow (Saccone et al. 2010b).

In this study, our goal was to understand how boxelder colonisation impacts the riparian forest understory. First, we compared understory floristic composition of boxelder and native white willow stands in three riparian forests, along three rivers with distinct hydrological regimes. The modulation of individual production and species abundance, instead of species exclusion, are the first and sometimes only signals of community changes following exotic and native species interactions (e.g. Tabacchi and Planty-Tabacchi 2005; Hejda and Pysek 2006). Thus, we measured understory standing biomass and species richness. Additionally, we searched for an association between these two variables and environmental

characteristics, main soil nutrient pools and main soil nitrogen related process. Next, we conducted a greenhouse experiment to determine the effects of soil quality, water table depth, and light availability as putative causal factors of the observed understory changes. We addressed two questions: (1) Does boxelder modify understory community in comparison to white willow, regardless of the associated river hydrological regime? (2) Which of the environmental factors modified by boxelder development are associated to the observed differences?

Materials and methods

Studied species

In Europe as in its native range, boxelder is primarily found in wet or swampy habitats (Tabacchi and Planty-Tabacchi 2003; Hrázský 2005). Along lowland riparian areas, it mainly occupies the same habitat as mature white willow, a characteristic riparian pioneer tree in Europe (Tabacchi and Planty-Tabacchi 2003). In mid-successional stands at higher altitudes, boxelder occupies the same habitat as *Fraxinus* spp. (Saccone et al. 2010a, b). The recruitment of white willow seedlings in the floodplain is restricted to the open habitats of sites prone to inundation, where fine sediments are deposited and can retain high levels of moisture (Barsoum 2002; Mosner et al. 2011). In contrast, boxelder seedlings are shade-tolerant and can be found in the understory of riparian forests (Saccone et al. 2010a, b).

Selected sites

From February to November 2009, we studied three riparian forests composed of mature white willow and boxelder within the Adour-Garonne river basin, SW France (Table 1, Online Resource 1). We selected sites with differing hydrological regimes to take into account the diversity of white willow habitats. The Lamarquèze site, located on the Adour River, corresponds to a swampy forest of ca. 22 ha. This forest exhibits an advanced stage of boxelder invasion, which has developed intensively since the early 1970s (E. Tabacchi, unpublished data). In addition, the site is characterized by the occurrence of *Fraxinus angustifolia* L., *Gleditsia triacanthos* L. and residual white willow and *Alnus glutinosa* (L.) Gaertn. This site

includes a network of narrow channels connected to the main river channel, and its hydrological regime is marked by a tidal influence with a 1 m mean daily variation in water level. Seasonal floods usually occur in autumn as a consequence of storm events. The Peyrehorade site, located on the Gave-de-Pau River, corresponds to a ca. 1.3 ha residual riparian forest co-dominated by *Populus nigra* L., white willow, and boxelder. As the Gave-de-Pau River runs straight from the Pyrénées Mountains before entering its floodplain, the studied stretch is highly influenced by snowmelt events in late spring, culminating in flooding of the whole forest. The Portet site, located on the Garonne River, corresponds to a complex riparian area whose forests are dominated by white willow and *P. nigra*. The studied *S. alba*-dominated forest is poorly colonised by boxelder and covers ca. 3 ha. This site sustains the most violent floods during spring snowmelt and rainfall events. From each site, we selected a white willow and a boxelder stand of 0.10–0.15 ha with similar topography patterns to ensure that they are subjected to a similar water submersion regime. During site selection, we observed that the abundance of *Urtica dioica* (stinging nettle) was lower under boxelder canopy, than found under white willow canopy.

Plant community composition and biomass

In the understory of each boxelder and white willow stand, we assessed species richness and percentage of herbaceous species cover in six replicates consisting of 50×50 cm quadrats in April, late August, and November (Braun-Blanquet 1932). We collected aboveground plant biomass from the six replicates in April and August; these dates correspond to the peak productivity of vernal plants and *U. dioica*, respectively. Plants were subsequently divided into three categories: *U. dioica*, vernal species (*Cardamine flexuosa* With., *Cardamine pratensis* L., *Oenanthe crocata* L., *Ranunculus ficaria* L.) and the remaining other species. Biomass for each category was then weighed to the nearest 0.01 g, after drying at 105°C until constant weight.

Environmental factors

We determined percentage of tree canopy cover from six vertical wide-angle photographs (Canon EOS 450D) taken in each stand in early July, a date that

Table 1 Main characteristics of the selected sites

Name of the studied site	Lamarquèze	Peyrhorade	Portet
River			
Strahler's stream order	8	8	6
Water regime	Tide-influenced	Fluvial*	Fluvial
Site			
Longitude	01°13′32″W	01°05′08″W	01°24′49″E
Latitude	43°37′42″N	43°32′27″N	43°31′14″N
Elevation (m a.s.l.)	4	7	148
Mean monthly min air T° (°C)	8.0	10.7	9.1
Mean monthly max air T° (°C)	19.0	18.1	18.2
Annual/Summer rainfall (mm)	608/131	961/177	454/110
Site surface (ha)	39	4.6	61
Forest surface (ha)	22	1.3	3
Tree species covers in the forest (% of white willow/boxelder/others)	10/80/10	35/35/30	80/10/10
Distance between tree stands (m)	9	19	15
Elevation from the base flow line (m)	0.6	4	4
Submersion frequency	At least twice a year	Once a year	Every 3 years
Flood disturbance intensity	Low	High	Intermediate

Strahler's stream order defines stream size based on a hierarchy of tributaries. Water regime refers to the duration and timing of flooding. *Sources*: Ministère de l'Ecologie, du Développement Durable, des Transports et du Logement (2011); Météo France (2011)

* The tidal variations (< 0.5 m daily variation of water level) do not influence the selected site due to its high elevation from the base flow line

corresponds to the maximum development of the tree canopy. Coloured images were transformed into binary format, and the proportion of black pixels (which corresponds to canopy) was calculated (ImageJ 1.42q, national Institute of Health, USA). We measured the fraction of photosynthetically active radiation reaching the ground under the canopy of each stand, using a PAR quantum sensor (JYP 1000, SDEC, France; PAR, 400–700 nm). During a sunny day in July, we made 50 measurements within each stand at the solar noon. PAR availability was expressed as the percentage of the mean incident PAR measured in four open areas (1,540, 1,680 and 1,700 µmol m^{-2} s^{-1} for Lamarquèze, Peyrehorade and Portet, respectively).

From each stand, we collected eight soil samples within the upper 10 cm of substrate after litter was discarded, during February, June, July and November. Subsamples of fresh soil were then rapidly analysed to determine soil moisture, major nutrient concentration, and potential nitrification and denitrification (see below).

The soil moisture and soil organic matter content were estimated after drying at 105°C for 72 h, and ignition at 600°C for 6 h, respectively. For the soil sampled in June, we determined soil particle size distribution (Mastersizer Micro, Malvern) using four particle size classes: clays (0–2 µm), silt (2–50 µm), fine sand (50–200 µm), and coarse sand (200–2,000 µm). Fine particle proportion was calculated as the ratio of the sum of clay and silt mass divided by the total mass of particles.

Soil chemistry and bacterial activity

For four of the eight soil samples per stand, a fresh 60 g soil subsample was stirred with 300 mL of 0.5 M KCl for 2 h, and then filtered. For one part of the filtered extract, we determined NH_4^+–N concentration by spectrometry at 660 nm by means of the Berthelot colour reaction (Searle 1984). To determine NO_3^-–N, we transferred a second part of the filtered extract on a cadmium column to reduce NO_3^- into NO_2^-. The formed nitrites reacted with sulfamilamid to give a dinitrogen, which produced a pink colour in the presence of 2,4-dinitrophenylhydrazine. We analysed the coloured solution by spectrometry at 540 nm for

NO_2^-–N. Beside, a 2.5 g subsample of air-dried crushed soil was extracted according to Olsen (1954) and stirred with 50 mL of 0.5 M $NaHCO_3$ for 2 h, and then filtered. We determined PO_4^{3-}–P content by spectrometry at 825 nm (NFISO11263 1995) after colourisation (Duval 1963).

For the eight soil samples per stand, we used twenty grams (equivalent dry soil) of homogenous fresh soil to measure denitrifying enzyme activity (DEA, i.e. denitrification potential) with the acetylene inhibition method, according to Patra et al. (2005) modified from Smith and Tiedje (1979). We used three grams (equivalent dry soil) of homogenous fresh soil to measure nitrifying enzyme activity (NEA, i.e. nitrification potential), according to Dassonville et al. (2011). We were unable to measure bacterial potential activity on soils sampled in June due to technical problems.

Greenhouse experiment

During February and March 2010, we tested the effects of soil type, PAR availability and water level on *U. dioica* growth and biomass production in a greenhouse pot experiment (Online Resource 2). We tested the effect of three soils, four PAR values and two water levels. To search for additive or synergistic effects between the factors, we fully crossed the three factors with 10 replicates per combination of factors. Each replicate corresponded to one pot (16 × 16 × 23 cm, l × w × h) containing one *U. dioica* rhizome piece. The 10 replicates were placed in a 80 × 60 × 40 cm (l × w × h) container (total of 240 pots in 24 containers). The homogeneity of moisture and temperature within the greenhouse were maintained by air circulation. Temperature (mean = 19.6°C, max. = 30.3°C, min. = 2.5°C) was monitored with data loggers (Gemini-Orion, Chichester, UK).

Four days before the experiment began, we collected the top 20 cm of white willow and boxelder soils from the field at the Portet site. Soil blocks were broken up by hand into 5–8 mm aggregates, and plant roots and rhizomes were removed, before we homogenized the soils. We used compost (Proveen substrate, NF U44-551, Soprimex, France) as control soil to evaluate the viability of *U. dioica* rhizomes. Both boxelder and white willow soil types were silty-sandy soils with very close particle-size characteristics, and similar organic

matter content (7.4 ± 0.4 and 8.0 ± 0.5%, respectively). Soil nutrient analysis indicated higher PO_4^{3-}–P and NO_3^-–N concentrations in white willow soil (PO_4^{3-}–P = 83.0 ± 0.6 g kg^{-1}; NO_3^-–N = 19.3 ± 1.2 mg kg^{-1}) than in boxelder soil (PO_4^{3-}–P = 57.3 ± 6.6 g kg^{-1}; NO_3^-–N = 7.5 ± 1.1 mg kg^{-1}) (Mann–Whitney, $p < 0.05$). Ammonium-N was not statistically different between the two soil types (5.2 ± 1.3 and 3.4 ± 0.6 mg kg^{-1} for white willow and boxelder soils, respectively).

PAR levels were determined from field measurements (Fig. 1A; see "Data analysis" for details). We selected the highest occurrence of daily PAR level observed under white willow and boxelder on sunny days that corresponds to 8 (PAR 8) and 48 (PAR 48) μmol m^{-2} s^{-1}, respectively; we chose an intermediate PAR level of 16 μmol m^{-2} s^{-1} (PAR 16) to encompass the overlap between the two distributions. For a control level to evaluate the potential growth of *U. dioica* rhizomes, we used greenhouse lighting, 200–300 μmol m^{-2} s^{-1} (PAR > 200). Selected PAR levels were obtained by using neutral density filters (shade cloth). Homogeneity of PAR was verified by measuring PAR every 20 cm in two perpendicular directions in the horizontal plane.

To mimic riparian field conditions, we tested low (drained soil) and high (water-logged soil) water levels. We set one water condition with the water level below pot floors (low water level, LWL; Online Resource 2). We set a second water condition with the water level above pot floors (high water level, HWL), at a distance of 20 cm from the *U. doica* rhizome during the first month of the experiment (high water level 1, HWL1), and 3 cm during the second month (high water level 2, HWL2). We installed an independent and closed-circuit irrigation system for each container with deionised water and we covered the space between the pots with black foil. During the first month, each container held 13.6 L of water, regardless of water level condition. We irrigated each pot with 400 mL of water twice a day with a drip system and water level was adjusted every 2 days.

We took *U. dioica* rhizomes from a stand at the Portet site, 3 days before the beginning of the experiment. Rhizomes from the last growing season were selected (4–5 mm in diameter), cut into 14–15 cm-long pieces that included 3 vegetative nodes and we planted one rhizome piece per pot. Out of the 80 planted rhizome pieces, only two pieces
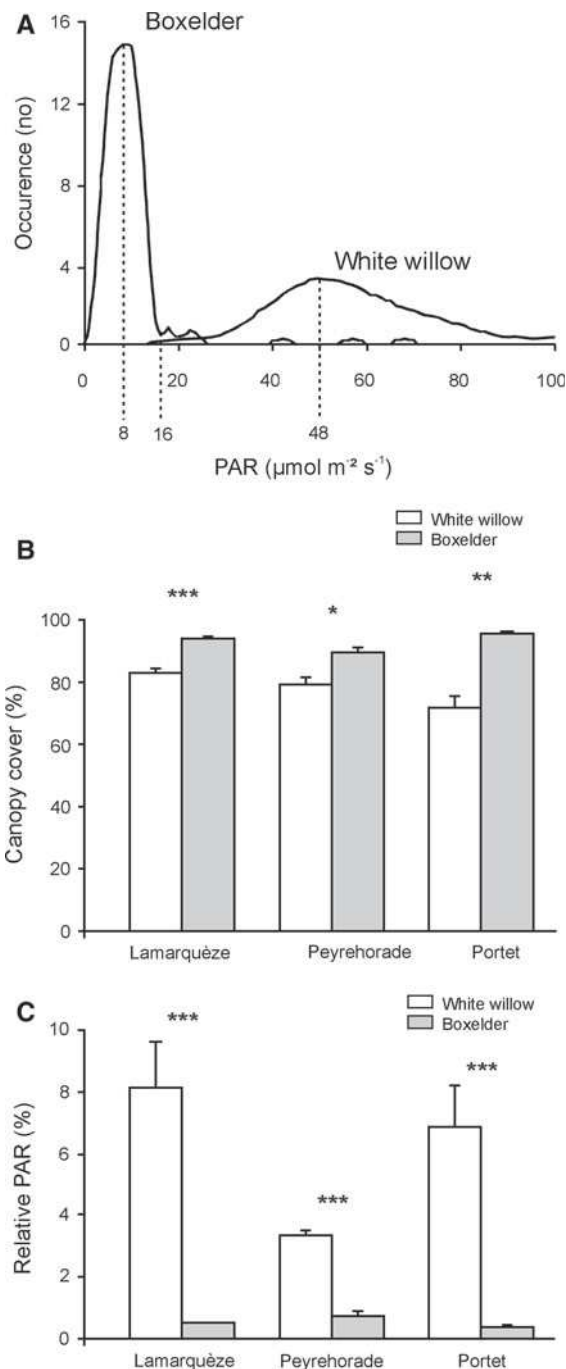
Fig. 1 PAR value frequency distribution, pooled for the three sites following Stavisky-Golay smoothing (**A**), percentage of tree canopy cover (**B**, mean ± SE), and relative PAR at the ground level (**C**, mean ± SE) in the white willow and the boxelder stand at the three sites. The absolute PAR values selected for the greenhouse experiment are indicated (**A**). The mean relative PAR is expressed as a percentage of the incident PAR in open areas (**C**). Results for Tukey's tests are given: $*p < 0.05$; $**p < 0.01$; $***p < 0.001$

were unable to produce stems during the experiment in the control soil type (compost), indicating that *U. dioica* rhizomes were highly tolerant of their cutting and transplantation. We weekly recorded the number of *U. dioica* stems per pot. At the end of the experiment, we collected the aboveground and belowground (rhizomes and roots) biomass. The belowground parts of *U. dioica* were gently rinsed to remove sediments. Aboveground and belowground parts were weighed to the nearest 0.01 g after drying at 105°C until constant weight. The mean initial mass of rhizome pieces was 335–465 mg, as estimated by weighing to the nearest 0.01 g after drying at 105°C until constant weight.

Data analysis

For the field study, differences in plant species richness, plant biomass and soil parameters between stands were assessed by a three-way analysis of variance (ANOVA). We used stand type (white willow vs. boxelder) and sampling date as fixed factors, and site as the random factor. We log-transformed plant biomass and DEA data to approach normal distribution and homogeneity of variance. Understory plant compositions were compared using analysis of similarity with plant species cover data (ANOSIM, 1,000 permutations). The number of replicates did not allow performing ANOSIM among sites and stand types for each sampling date, because of the low number of possible permutations. To circumvent this issue, we pooled all the dates for each site to test differences among stand types. When ANOSIM indicated significant differences between white willow stands and boxelder stands, we used the IndVal method and related ecological indicator values (I.V.) (I.V., Dufrêne and Legendre 1997) to refine which species were responsible for these differences. We tested the significance of individual I.V. to plant species associations using two distinct randomization procedures, taking into account when the two tests gave $p < 0.05$ (499 permutations; Dufrêne and Legendre 1997). Relationship between canopy cover and understory biomass (sampled in August) were tested with linear regressions.

For the greenhouse experiment, we smoothed raw PAR frequency distributions using the Savitsky-Golay filter (Stavisky and Golay 1964) to determine the absolute PAR level tested. We assessed differences

between boxelder and white willow soil with Mann–Whitney tests, because the data did not follow ANOVA assumptions. Since measurements were made on the same sampling units over time, we tested differences in *U. dioica* stem numbers using a four-way repeated measure ANOVA (Doncaster and Davey 2010). We used stem number per *U. dioica* individual (subject) as the response variable, time (8 levels) as the within-subject factor, and soil type, PAR availability and water level as the between-subjects factors. Differences in final aboveground biomass and belowground biomass were assessed using a three-way ANOVA with a fully cross-factored model in which soil type, water level and PAR availability were the three tested factors. We log-transformed aboveground biomass to allow analysis. The control soil type (compost) and the control PAR level (PAR > 200) were used to test the sole effect of soil type or water level. Data from the controls were excluded from the analyses to determine the effect of soil quality and PAR values relevant to field conditions (Table 3, Figs. 3, 4).

ANOVA was performed with Statistica (version 6.0, Statsoft, France) and ANOSIM was performed with PRIMER (version 5.2.2, Primer-E Ltd, UK). We used Tukey's post hoc tests when the overall difference tested with ANOVA was significant. We verified normality and homoscedacity assumptions with Shapiro–Wilk and Bartlett tests, respectively. We also made a graphic verification and tested if assumption can be followed when one out of range point is removed. If not, we used non-parametric Mann–Whitney test. All error measures stated in the text are standard error (SE). ANOVA tables are provided as Online Resource 3.

Results

Plant community composition and biomass

Due to persistent inundation following a flood in March, there were no understory plants in April at Portet (Fig. 2A). Plant species richness was overall twofold higher in white willow stands than in boxelder stands (Table 2, Fig. 2A; ANOVA, $F_{1,\ 90} = 52.0$, $p < 0.0001$). Understory composition differed between stand types (Table 2, ANOSIM, R = 0.3, $p = 0.001$). IndVal analysis indicated that *U. dioica* was associated consistently with white willow stands (I.V. = 71.3). *Lamium maculatum* (L.) L., *Carex pendula*

Huds. and *Hedera helix* L. were associated with white willow to a lesser extent (supported by only one significant test). No herbaceous species was associated significantly with the boxelder stands.

Total aboveground plant biomass was higher in white willow stands than in boxelder stands (Table 2, Fig. 2B; ANOVA, $F_{1,\ 60} = 42.2$, $p < 0.0001$). On average, *U. dioica* biomass was ninefold higher in white willow stands than in boxelder ($F_{1,\ 60} = 50.8$, $p < 0.0001$). The biomass produced by vernal species was not statistically different between white willow and boxelder stands ($F_{1,\ 60} = 0.6, p = 0.45$).

Environmental factors

The mean canopy cover was on average 15% higher in the boxelder stands than in the white willow stands (Fig. 1B, Table 2; ANOVA: $F_{1,\ 30} = 81.8, p < 0.0001$). Modal values of PAR smoothed distributions were 48 and 8 μmol m^{-2} s^{-1} under white willow and boxelder canopies, respectively (Fig. 1A). Mean PAR at the ground level was 10-fold higher under the white willow canopy than under the boxelder canopy (Fig. 1C, Table 2; $F_{1,\ 294} = 1006.6$, $p < 0.0001$). Total understory biomass decreased with increasing canopy cover (adj. $R^2 = 0.46$, $p < 0.0001$) (Online Resource 4).

Overall, fine soil particle proportion (Table 2, Online Resource 5; ANOVA, $F_{1,\ 42} = 4.1$, $p = 0.049$) and soil moisture ($F_{1,\ 160} = 3.0$, $p = 0.09$) were similar in the boxelder and the white willow stand. Differences in organic matter content between boxelder and white willow were significant but slight (Table 2) and varied on sampling date (Online Resource 5).

Soil chemistry and bacterial activity

Overall, PO_4^{3-}–P concentration (ANOVA, $F_{1,\ 72} = 44.9$, $p < 0.0001$), NO_3^-–N concentration ($F_{1,\ 72} = 20.9$, $p < 0.0001$), and NH_4^+-N concentration ($F_{1,\ 72} = 4.1, p = 0.04$) were lower under boxelder than under white willow (Table 2). However, the three sites individually exhibited differences in nutrient concentration that varied in sign (Online Resource 5).

DEA differences between boxelder and white willow were not significant (Table 2, Online Resource 5). Overall, NEA was lower under boxelder than under white willow (Table 2, $F_{1,\ 126} = 33.9$, $p < 0.0001$), although NEA differences were slight (Table 2) and varied according to sampling date (Online Resource 5).

Fig. 2 Understory mean plant species richness (**A**) and plant biomass produced (**B**) under boxelder (*Bx*) and white willow (*Ww*) cover. *Error bars*, SE ($n = 6$)
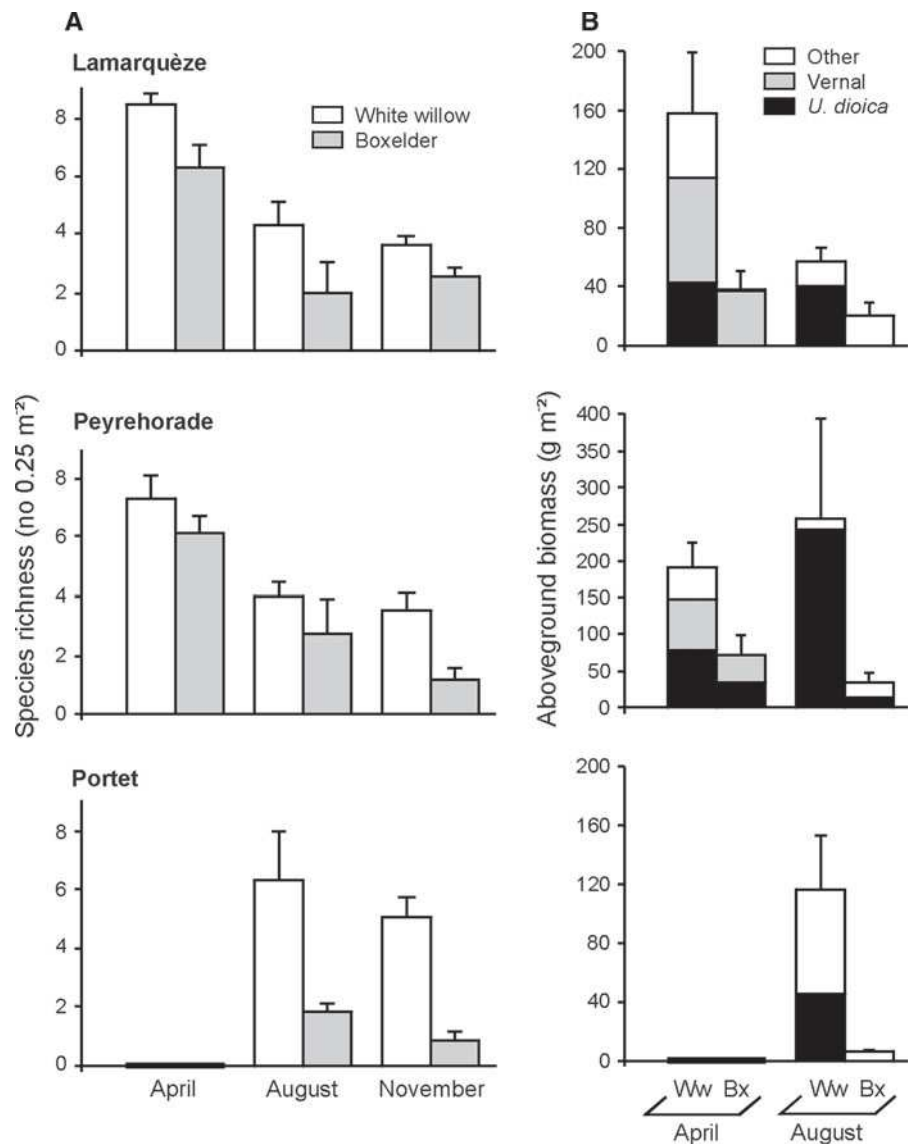
Greenhouse experiment

On average, there were fewer *U. dioica* stems in PAR 8 than in PAR 48 (Fig. 3A; repeated measures ANOVA, $F_{2, 108} = 5.7$, $p < 0.01$). Stem number remained constant throughout the experiment in PAR 48 (Fig. 3A). Conversely, stem mortality resulted in lower stem numbers from the sixth week on for PAR 16, and from the fourth week on for PAR 8, as compared to the first week ($F_{14, 756} = 14.0$, $p < 0.0001$). Stem number decrease occurred earlier in HWL than in LWL (Fig. 3B; $F_{7, 756} = 2.2$, $p = 0.03$). Stem number in HWL remained constant

after the fourth week, indicating no additional effect from a more stressful high water condition during the second month. The only significant interactions in ANOVA on stem number data were between time and the other factors.

Urtica dioica produced less aboveground (Table 3A, Fig. 4A) and belowground (Table 3B, Fig. 4B) biomass with low PAR values (Tukey, $p < 0.0001$); notably, there was ninefold lower aboveground biomass and 18-fold lower belowground biomass under PAR 8 than under PAR 48 (Table 3, Fig. 4). Under PAR 48, the final belowground biomass was higher than the initial rhizome mass; conversely, it was lower under PAR 16

Table 2 Plant community and physical–chemical characteristics (Mean $\pm$ SE) in the white willow and boxelder stands

	Sampling dates (months)	No. of replicates	White willow	Boxelder	p value
Plant community					
Species richness (no 0.25 m^{-2})	04, 08, 11	6	4.7 $\pm$ 0.4	2.6 $\pm$ 0.3	****
Composition	04, 08, 11	6	See text		***
Total biomass (g m^{-2})	04, 08	6	127.8 $\pm$ 28.8	23.8 $\pm$ 6.2	****
U. doica biomass (g m^{-2})	04, 08	6	74.7 $\pm$ 22.9	8.1 $\pm$ 3.5	****
Vernal biomass (g m^{-2})	04, 08	6	12.1 $\pm$ 6.5	6.6 $\pm$ 3.1	n.s.
Environmental factors					
Canopy cover (%)	07	6	78.4 $\pm$ 1.8	93.4 $\pm$ 0.8	****
PAR (μmol m^{-2} s^{-1})	07	50	6.1 $\pm$ 0.7	0.6 $\pm$ 0.1	****
FP proportion (%)	06	8	41.3 $\pm$ 1.5	42.4 $\pm$ 1.3	n.s.
Organic matter (%)	02, 07, 11	8	8.0 $\pm$ 0.2	7.4 $\pm$ 0.2	****
Soil moisture (%)	02, 06, 07, 11	8	32.2 $\pm$ 0.8	32.7 $\pm$ 0.6	n.s.
Soil chemistry and bacterial activity					
PO_4^{3-}–P (g kg^{-1})	02, 06, 07, 11	4	117.4 $\pm$ 3.6	95.0 $\pm$ 6.9	****
NO_3^-–N (mg kg^{-1})	02, 06, 07, 11	4	12.1 $\pm$ 1.6	8.6 $\pm$ 1.5	****
NH_4^+–N (mg kg^{-1})	02, 06, 07, 11	4	8.9 $\pm$ 0.7	7.6 $\pm$ 0.8	*
DEA (μg N_2O–N g^{-1} h^{-1})	02, 07, 11	8	2.6 $\pm$ 0.1	2.8 $\pm$ 0.1	n.s.
NEA (μg ($NO^2 + NO^3$)–N g^{-1} h^{-1})	02, 07, 11	8	1.9 $\pm$ 0.1	1.6 $\pm$ 0.1	****

ANOVA results are indicated: *n.s.* not significant

FP fine particle, *DEA* denitrifying enzyme activity, *NEA* nitrifying enzyme activity

* $p < 0.05$

*** $p < 0.001$

**** $p < 0.0001$

and PAR 8 (Fig. 4B). The interactions between PAR level and water level were significant (Table 3), and post hoc tests indicate that aboveground (Table 3A, Fig. 4A) and belowground (Table 3B, Fig. 4B) biomasses were significantly lower in HWL than in LWL only under PAR 48 (Tukey, $p < 0.0001$). It is worthwhile to notice that a significant effect of soil type was observed only under the control PAR > 200, with less aboveground (ANOVA, $F_{1, 40} = 40.6$; $p < 0.0001$) and belowground ($F_{1, 40} = 13.4$; $p < 0.001$) biomass production in boxelder soil.

Discussion

Boxelder impact on understory community

Regardless of river hydrological conditions (Table 1), the presence of boxelder in place of white willow along riparian corridors is associated with profound modifications to the understory community, including decreased species richness, lower biomass production, and the strong decline of *U. dioica*. In this study, *U. dioica* represents at least a third of the white willow aboveground understory biomass and the lower biomass produced by the boxelder understory is mainly related to the strong decline of *U. dioica*. Thus *U. dioica* appears as an indicator species of understory modification following boxelder invasion. No species was particularly associated with boxelder, suggesting that boxelder does not favour any species or species type development, as it has been observed following invasion of other exotic species (Lambdon et al. 2008; Abelleira Martinez 2010). On the contrary, our results show that species present in boxelder understory were a part of the white willow one; thus boxelder negatively affects understory species richness in riparian forest communities.
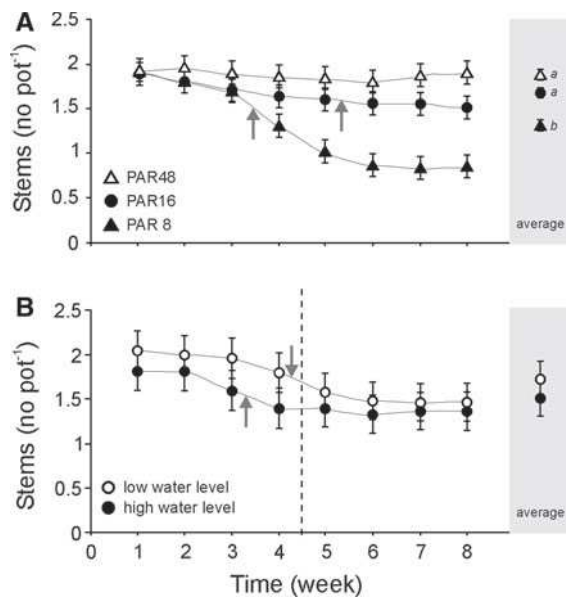
Fig. 3 Changes in the *U. dioica* stem number per pot for each selected PAR level (**A**) and each selected water level (**B**) during the 8 week-long experiment. Mean ± SE ($n = 40$ and $n = 60$ for **A** and **B**, respectively). *Arrows* indicate significant decreases in stem number (repeated ANOVA, Tukey's test $p < 0.05$). *Grey* highlighted points correspond to average stem numbers. Identical *italic letters* indicate no significant differences (ANOVA, Tukey's test $p < 0.05$). *Dashed bar* indicates the date of the shift from HWL1 to HWL2 (see "Materials and methods")

Environmental changes and understory modifications

Our field measurements indicate that variability in nutrient concentrations was larger among sites, than between boxelder and white willow stands within a given site. In addition, differences in NEA between boxelder and white willow soils were minor and depended on sampling date. This suggests that the general decline of understory under boxelder cover was not consistently affected by nutrient availability although we cannot rule out an effect on some plant species. In the greenhouse experiment, the significantly lower PO_4^{3-}–P and NO_3^-–N concentration in the boxelder soil, accounted for a very marginal source of variation (<1% SS) for *U. dioica* biomass production. Hence, nutrient availability does not appear to be a determining factor for the *U. dioca* decline observed in the field.

In riparian areas, plant development is reported to be strongly influenced by flood time and duration

(Klimešová 1994; Bendix and Hupp 2000). In our sites, the similar topography of the white willow and boxelder stands suggests that water table depth and water submersion regime were rather similar. Furthermore, a similar fine particle proportion and minor site-dependent differences in organic matter content suggest that the water retention could be quite similar in the two soil types. Results from the greenhouse experiment are consistent with those of Šrůtek (1997), who reported a decrease in biomass production of *U. dioica* accompanied by a water table depth less than 30 cm from the rhizome. However, high water level alone does not induce the death of *U. dioica* individuals, as observed both here and in Šrůtek (1997). It is thus expected that water table depth can have a negative effect on *U. dioica* growth but cannot be responsible alone for *U. dioica* decline under boxelder cover.

We observed 15% higher canopy cover and a 10-fold lower PAR under boxelder stands than under white willow stands, regardless of the field site. Since dominant tree species is the common parameter among the sites, we can suspect dominant tree species to have a principal effect on canopy cover which represents an integrated measure of the diverse parameters that can affect light interception in forests (Canham and Burbank 1994). Although *U. dioica* is a shade-tolerant species, it has been reported to be absent from areas where available light is less than 5–10% of full incident light (Olsen 1921; Taylor 2009). In the greenhouse, the most frequently observed value *in natura* under boxelder (PAR 8) induced a 50-fold reduction of *U. dioica* aboveground biomass, as compared to the value observed under white willow stands (PAR 48). Contrary to PAR 48, PAR 8 was responsible for high mortality in *U. dioica* after only a few weeks; surviving individuals were self-sustained by exploiting their rhizome reserves. Thus, *U. dioica* is expected to rely on its reserves from season to season and to finally disappear under dense boxelder cover. We are unable to dissociate the additive effects from the synergistic effect of soil type, water level, and light availability on *U. dioica* development, because soil type and water level effects were only detected in PAR 48 and PAR > 200, levels at which light is not limiting. Finally, light availability appears as the main factor controlling *U. dioica* development in the boxelder stands. Beside the difference in soil chemistry, we can suppose that the

Table 3 Summary of ANOVA on *U. dioica* aboveground (A) and belowground (B) biomasses ($n = 10$) observed in the greenhouse experiment

Source of variation	df	SS	SS (%)	MS	F	P
A.						
Soil	1	0.0	0.0	0.0	0.7	0.42
Water	1	0.1	1.7	0.1	14.7	**< 0.001**
Light	2	4.6	76.7	2.3	232.4	**< 0.0001**
Soil × water	1	0.0	0.0	0.0	0.0	0.98
Light × soil	2	0.0	0.0	0.0	0.6	0.52
Light × water	2	0.2	3.3	0.1	9.4	**< 0.001**
Light × soil × water	2	0.0	0.0	0.0	0.5	0.58
Error	108	1.1	18.3	0.0		
Total	119	6.0	100			
B.						
Soil	1	0.0	0.0	0.0	3.5	0.06
Water	1	0.1	4.8	0.1	8.7	**< 0.01**
Light	2	1.3	61.9	0.6	98.6	**< 0.0001**
Soil × water	1	0.0	0.0	0.0	2.5	0.11
Light × soil	2	0.0	0.0	0.0	1.4	0.25
Light × water	2	0.0	0.0	0.0	3.0	**0.05**
Light × soil × water	2	0.0	0.0	0.0	1.9	0.15
Error	108	0.7	33.3	0.0		
Total	119	2.1	100			

Significant results ($p < 0.05$) are in bold charcters

lower light availability under boxelder is mainly responsible for the lower understory biomass recorded under boxelder in the field.

Light availability has been suspected to facilitate invasion in numerous studies (e.g. Siemann and Rogers 2003; Reinhart et al. 2006; Galbraith-Kent and Handel 2008), but only a few studies, including this one, have focused on the understory response to changes in light availability and the resulting profound understory modifications (Reinhart et al. 2005; Chabrerie et al. 2010). The underestimated effect of light alteration in the context of tree invasion should not be neglected in future studies.

Boxelder ecology and implications for riparian ecosystems

By modifying light availability, a physical resource of the ecosystem, boxelder can be considered as an engineer species (Jones et al. 1994; Crooks 2002) in riparian forests. The resulting lower understory density and productivity under boxelder complete the results of

Saccone et al. (2010b) who showed that boxelder favours its own fitness by decreasing herbaceous competition for its seedlings. Due to this self-facilitation process that can be considered as a niche construction (Day et al. 2003), reversibility of boxelder invasion is unlikely as long as no new strong environmental change occurs in the ecosystem. In the context of white willow forest decline (James 1996; Steiger et al. 1998), boxelder is expected to continue its spread along European riparian corridors, as exemplified in southwest France. Indirect consequences of understory decline must also be considered, such as a decrease in abundance and diversity of *Urtica*-associated fauna and microflora (Taylor 2009), and intensified erosion due to decreased sediment trapping by the reduced riparian herbaceous layers (Tickner et al. 2001).

Previous field observations (Tabacchi and Planty-Tabacchi 2003) suggested that boxelder first behaves as an ecological passenger (sensu Didham et al. 2005) which takes advantage of white willow decline to colonise riparian forests, most often along regulated river systems. In this study, we have shown that
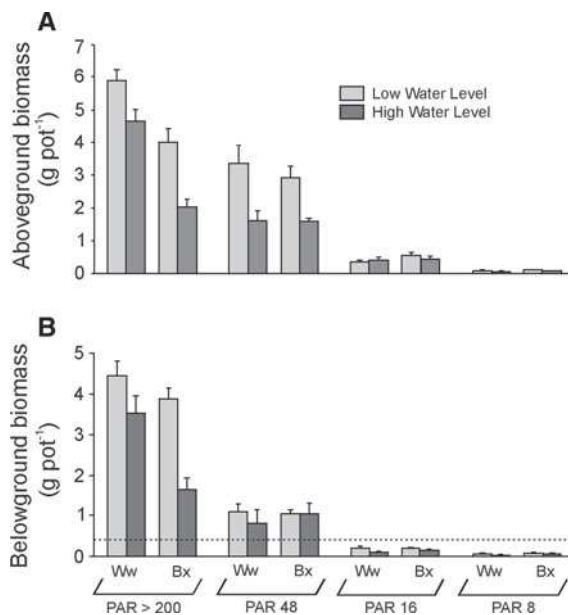
Fig. 4 Aboveground (**A**) and belowground (**B**) biomass produced by *Urtica dioica* during the experiment for each selected PAR level, according to soil type and water level. The *dashed line* indicate the mean initial weight of one rhizome piece. *Bx* boxelder soil, *Ww* white willow soil. Mean ± SE ($n = 10$)

boxelder can be considered as an engineer species that reduces available light and thus becomes an ecological driver (sensu Didham et al. 2005) that establishes a new ecological trajectory for the system. Hence, boxelder invasion is certainly both a consequence and a cause of the emergence of a novel riparian ecosystem (Hobbs et al. 2006; Richardson et al. 2007). Management strategies for invaders (Seastedt et al. 2008; Pyšek and Richardson 2010), should take into consideration the specific two-step mechanism reported here for boxelder.

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