



## Ecology/Écologie

Does the invasive species *Ailanthus altissima* threaten floristic diversity of temperate peri-urban forests?*Les populations invasives d'Ailanthus altissima menacent-elles la diversité floristique des forêts tempérées périurbaines ?*Eric Motard<sup>a,\*</sup>, Audrey Muratet<sup>b</sup>, Danielle Clair-Maczulajty<sup>a</sup>, Nathalie Machon<sup>b</sup><sup>a</sup> Laboratoire de physiologie de l'arbre, université Paris Diderot, 2, place Jussieu, 75005 Paris, France<sup>b</sup> Conservation des espèces, restauration et suivi des populations, UMR 7204 MNHN-CNRS-UPMC, 61, rue Buffon, 75005 Paris, France

## ARTICLE INFO

## Article history:

Received 4 February 2010

Accepted after revision 8 June 2011

Available online 15 September 2011

## Keywords:

Floristic inventories  
Understory vegetation  
Interspecific competition  
Allelopathy  
Invasion

## Mots clés :

Allélopathie  
Compétition interspécifique  
Invasion  
Inventaires floristiques  
Végétation du sous-bois

## ABSTRACT

We examined the influence of the invasive species *Ailanthus altissima* (Mill.) Swingle on the understory of the Fontainebleau forest, a peri-urban forest of Paris (France), by comparing invaded versus control plots. We performed floristic inventories in fixed plots around the base of *A. altissima* vs native trees in different habitat types of the forest. Our findings suggest that the understory vegetation is significantly poorer and more common under *A. altissima* than under the other tree species and that the floristic composition is significantly different. Furthermore, the number of *A. altissima* root suckers growing in the plots was significantly negatively correlated with floristic richness. This effect can be attributed to both interspecific competition and allelopathic properties of *A. altissima*. These results give an estimate of the threat to biodiversity ascribed to *A. altissima* in the Fontainebleau forest.

© 2011 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

## R É S U M É

Nous avons examiné l'influence des populations invasives d'*Ailanthus altissima* sur les plantes du sous-bois de la forêt de Fontainebleau, une forêt périurbaine de Paris (France), en comparant des aires envahies à des aires témoin. Les inventaires floristiques ont été effectués sur une surface constante autour de la base des troncs d'*A. altissima* et de celle des arbres autochtones. Nos résultats suggèrent que la végétation du sous-bois est nettement plus pauvre et composée d'espèces plus communes sous *A. altissima* que sous les autres espèces d'arbres et que la composition floristique est sensiblement différente. En outre, la densité de drageons d'*A. altissima* dans les aires d'inventaires est significativement négativement corrélée avec la richesse floristique. Cet effet peut être attribué à la fois à la compétition interspécifique et aux propriétés allélopathiques d'*A. altissima*. Ces résultats témoignent de la menace que fait peser *A. altissima* sur la biodiversité dans la forêt de Fontainebleau.

© 2011 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

## 1. Introduction

Deliberate or accidental introduction of plants and animals in ecosystems is considered as one of the major sources of biodiversity change. The Convention on

\* Corresponding author.

E-mail addresses: motard@biologie.ens.fr (E. Motard), muratet@mnhn.fr (A. Muratet), danielle.clair@univ-paris-diderot.fr (D. Clair-Maczulajty), machon@mnhn.fr (N. Machon).

Biological Diversity [1] regards it as one of the main factors of loss of biodiversity across the globe. There is a fairly large number of published studies on ecosystem impacts of invasive plants (*sensu* [2]) even though only few studies show evidence of negative impacts of invasive plant species on ecosystems [3–6]. Further, there can be regional differences in the impact of exotic plants (i.e. studies on *Impatiens glandulifera* in Europe: negative effects in northeast of England [7] compared to negligible effects in Czech Republic [8]). Their impact could be a reduction of local diversity [4] and changes in community composition [5]. However, other studies seem to contradict these assertions in [2].

The aim of this article is to study the threat to vegetation ascribed to an invasive plant, the tree-of-heaven (*Ailanthus altissima* (Mill.) Swingle), in a forest where it has begun to invade protected areas. This Simaroubaceae is native to China and was introduced all around the world for ornamental purposes. It was first planted in Europe in the mid-18<sup>th</sup> century. Due to its fast expansion, it is already considered as invasive in the majority of countries in which it was introduced [9,10]. It is very tolerant of urban conditions (nutrient and water deficient soil, polluted air city) and it can even grow in sidewalk cracks, parking lots and roadsides [11]. Thus, it is in full expansion in big cities [12,13]. It settles fast in agglomerations [14,15] along railways and roads, and invades more natural zones. For example, it was recorded in peri-urban forests [16] in Hungary and in Western USA [17]. Its presence is, however, also recorded in old undisturbed forests in the USA ([18,19]).

*A. altissima* develops quickly thanks to its double strategy of reproduction [20]. Firstly, its sexual reproduction leads to high production of winged fruits scattered by wind over long distances [18]. Secondly, it also reproduces vegetatively by vigorous root suckers growing from root buds [21]. These biological characteristics alone could explain the strong capacity of colonization on a larger scale of this species. At specific site, the dark shade generated by the numerous root suckers could help it to compete efficiently with other plant species. Furthermore, it also produces allelochemical phytotoxic compounds that are known to inhibit the growth of herbaceous seedlings under artificial conditions [22–26]. However, the mere presence of phytotoxins in plants did not prove the occurrence of allelopathy under natural conditions [23]. The first study that described the impact of *A. altissima* on natural vegetal communities was conducted in Mediterranean habitats [27]. It is clear that the invasion of *A. altissima* leads to a reduction in diversity and richness of native Mediterranean vegetation. In a northern American temperate forest, another study showed allelopathic effects of *A. altissima* on coexisting native tree species (*Quercus rubra*, *Acer rubrum* and *Acer saccharum*) exposed to real spatio-temporal variation of allelochemical production and activity. In these transplantation experiments, *A. altissima* seems to have important negative effects on seedling growth of American native tree species [28], but increases soil fertility in its neighbourhood [29]. To our knowledge, nothing about the effect of *A. altissima* has been undertaken considering the whole forest vegetation and its possible

regional variations. Actually, we wonder if *A. altissima* is a threat to the whole understory vegetation.

In this study, we examine the potential impact of *A. altissima* on the understory vegetation in situ in a peri-urban forest of the Parisian region known to host significant biodiversity [30]. This allowed us to observe, for the first time, the impact of *A. altissima* on the forest flora. As the Fontainebleau Forest is listed as MAB reserve and is invaded by *A. altissima* at its periphery, it was necessary to know the exact distribution of this invasive species to find out how much this forest is threatened. Our objectives were to assess:

- the distribution of *A. altissima* in the Fontainebleau forest to quantify its occurrence in different types of habitats, and particularly within the forest;
- its potential effect on floristic indices (Indigeneity, Rarity and Richness) of the shrub and herbaceous layers;
- its role in the potential change on floristic communities' composition.

We aimed to provide managers with reliable data on the threats to the forest's biodiversity caused by *A. altissima*.

## 2. Methods

### 2.1. Study area

The study area is the Fontainebleau forest, an old peri-urban forest located 65 km south of Paris, which covers an area of approximately 280 km<sup>2</sup>. It is considered as a "biogeographical crossroad" [31] because the climate is oceanic with continental, Nordic and even Mediterranean trends (mean annual temperature: 9.88 °C and annual rainfall: 700 mm). The tree layer is largely composed of Scots pine (*Pinus sylvestris*), common and Durmast oak (*Quercus robur* and *Q. petraea*) and beech (*Fagus sylvatica*). These natural conditions have allowed the development of an exceptionally rich fauna and flora: there are 6800 species of animals including more than 5000 insects and 5700 species of plants. Recently (1998), the Fontainebleau Biosphere Reserve was the 365th Reserve to be created in the world and the 10th in France. It covers 700 km<sup>2</sup>, including the forest of Fontainebleau. In this forest, *A. altissima* was reported for the first time in 1925 [32].

### 2.2. Distribution of *A. altissima* in the Fontainebleau forest

For management reasons, the forest is divided in plots (or sectors). The presence of *A. altissima* was sought in the totality of each forest sector by both managers and the authors. The distribution of *A. altissima* in the Fontainebleau forest was also assessed for each sector of the forest from the data provided by the managers and field checks. Furthermore, we carried out a broader survey to complement and update these data. We also radiated from every site where *A. altissima* had been located to precisely define the limits of the stands, i.e. where no new individual could be found. For each site, we reported all the data for presence and recorded the type of habitats: inner woods,

meadows, riverbanks, borders of forest adjoining gardens, rails and roadsides. For statistical reasons, habitats that hosted less than ten mature *A. altissima* were discarded from analysis, i.e. meadows and riverbanks. Only four habitat types were thus considered: borders of forest adjoining gardens (Gardens), borders of forest adjoining railways (Rails), borders of forest adjoining roadsides (Roads) and inner woods (Woods).

### 2.3. Floristic plots

The data were collected once, mid-April to mid-July 2006. No significant differences emerged in terms of floristic richness between spring and summer (Kruskall-Wallis tests).

In each habitat (Table 1), we completed a floristic inventory (according to official French nomenclature [33]) under every *A. altissima* mature tree (i.e. sexually reproductive, and with a trunk diameter of about 30 cm). We recorded all present wild vascular species growing in a two-meter-radius circular plot centered on the tree trunk. Only non-overlapping plots were considered.

To study the impact of *A. altissima* on the flora, we used three parameters: species richness (Richness), the total number of species observed in the site, Indigeneity, the proportion of indigenous (versus naturalized) species and Rarity. For a given species, rarity (Rasp) is the fraction of sites (including all habitats) in the department in which the species was not observed. Rasp varies between 0 (the species was observed in all sites) and 985/986 (the species was observed in a single site in the department). At the plot level, Rarity is the mean of specific rarity indices over all species observed in the plot.

To assess the impact of *A. altissima* on floristic indices, we also counted the number of its root suckers growing in the plots. Root suckers are easily recognized thanks to their particular morphology (large leaves, long internodes, brownish bark) [20]. Our aim was to explore the relationships between the number of suckers and the floristic indices in *A. altissima* plots.

For Gardens, Woods and Roads habitats, we studied an adjacent zone, for control purposes, where *A. altissima* was not present but with similar ecological conditions (shading and influences of anthropogenic factor) and 10 m distance from the invaded zones. For the Rail habitat, we were unable to find control zones in the neighbourhood of the invaded areas. In these “control zones”, we performed floristic

inventories, with the same protocol, under the native mature tree species (*Acer pseudoplatanus*, *Carpinus betulus*, *Fagus sylvatica*, *Quercus petraea* and *Quercus robur*) (Table 1). Note that we did not perform enough vegetation inventories under Scots Pine to be able to use them statistically because the spatial distributions of these two species overlap very little in this forest. The effect of the different tree species' morphology on understory vegetation was released by choosing trees whose trunks had approximately the same diameter as mature *A. altissima*. We compared understory vegetation of invaded plots (i.e. plots centered on *A. altissima* trunks) with that of control plots (i.e. centered on other tree species' trunks). We recorded the species that had contrasting frequencies in the invaded vs control plots and compared their Landolt ecological indicator values (soil humidity, soil nitrogen content, pH and light, [34]).

### 2.4. Data analysis

Statistical analyses were performed using R 2.6.1 [35] and Minitab15.1.1.0 [36]. To describe the floristic diversity of the understory mature trees, we used classical indices [37]:

- species richness (Rich) per plot;
- indigeneity (Ind), i.e. the proportion of native (vs exotic) species within a plot (according to the regional list established by the National Botanical Conservatory of the Paris Basin, [38]);
- average species rarity (Rar) per plot (species rarity given in terms of regional data, referring to the proportion of sites where a given species was not observed, across all habitats of the region [39]).

Two-way ANOVAs were performed to test for significant differences in the plots' floristic indices:

- among habitats;
- among invaded vs control zones;
- in terms of interaction.

Spearman tests assessed the relationships between root suckers density and floristic indices in invaded plots.

We used the distance-based redundancy analysis (dbRDA) [40] based on species presence/absence data to detect significant differences in the floristic composition of plots among habitat types and among invaded vs control plots in each habitat type. Finally, Wilcoxon non-parametric tests were used to compare the Landolt ecological values [34] of the species with contrasting frequencies in the invaded vs. control plots.

## 3. Results

In the Fontainebleau forest *A. altissima* was found mostly along borders of different habitats. Its distribution in 2006 is shown on the map of Fig. 1.

We inventoried 324 plots, i.e. 187 invaded plots (at the base of *A. altissima* mature trees) and 137 control plots (at the base of native mature trees). We observed a total of 241 plant species, including 209 native species (86.7%).

**Table 1**

Number of plots inventoried under different tree species in each habitat type.

Tree species	Habitat types			
	Gardens	Rails	Roads	Woods
<i>A. altissima</i>	<b>31</b>	<b>47</b>	<b>79</b>	<b>30</b>
<i>Acer pseudoplatanus</i>	–	–	<b>15</b>	1
<i>Carpinus betulus</i>	1	–	6	<b>28</b>
<i>Fagus sylvatica</i>	7	–	9	<b>10</b>
<i>Quercus petraea</i>	–	–	1	<b>10</b>
<i>Quercus robur</i>	<b>13</b>	–	<b>18</b>	<b>18</b>

Plots used for statistical analysis (when greater than ten per habitat) are in bold characters.

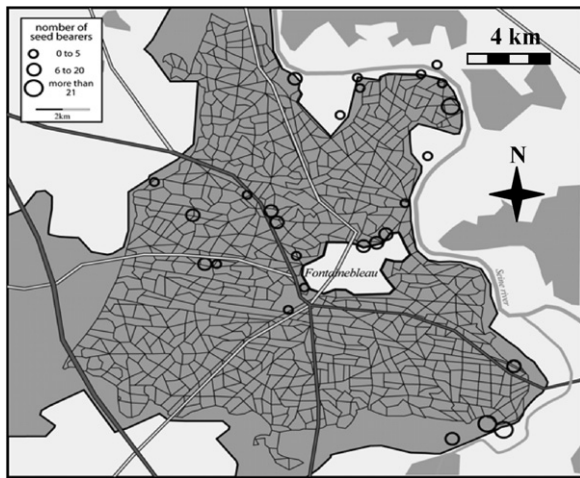


Fig. 1. Map of the Fontainebleau forest showing all the *A. altissima* sites (circles).

### 3.1. Floristic index variations

The analysis of variance indicated the existence of significant differences for indigeneity and rarity among habitats, for richness and rarity among invaded vs. control plots, and for indigeneity in a cross analysis of the two factors (Table 2). No effect of habitat on richness was observed; we found an average of 9.1 species (SD = 3.2) per invaded plot and 12.4 species (SD = 3.8) per control plot. Mean species rarity was significantly lower in *A. altissima* plots (mean rarity = 0.88 and SD = 0.03 vs. 0.89 and 0.03 respectively in control plots) and in plots located in Gardens (0.87, SD = 0.02) than in those located in Woods and Roads (0.90, SD = 0.03 for both) (Fig. 2).

### 3.2. Relationships between root sucker density and floristic indices per plot

Within the invaded plots, the number of root suckers observed ranged from 0 to 88 and was negatively correlated with species richness under *A. altissima* ( $Rich = 9.43 - 0.06 \times A. altissima \text{ root suckers}$ , Spearman test:  $r^2 = 0.11$ ;  $P$ -value < 0.0001) (Fig. 3). In contrast, neither plot indigeneity nor plot rarity was significantly correlated with sucker density (results not shown).

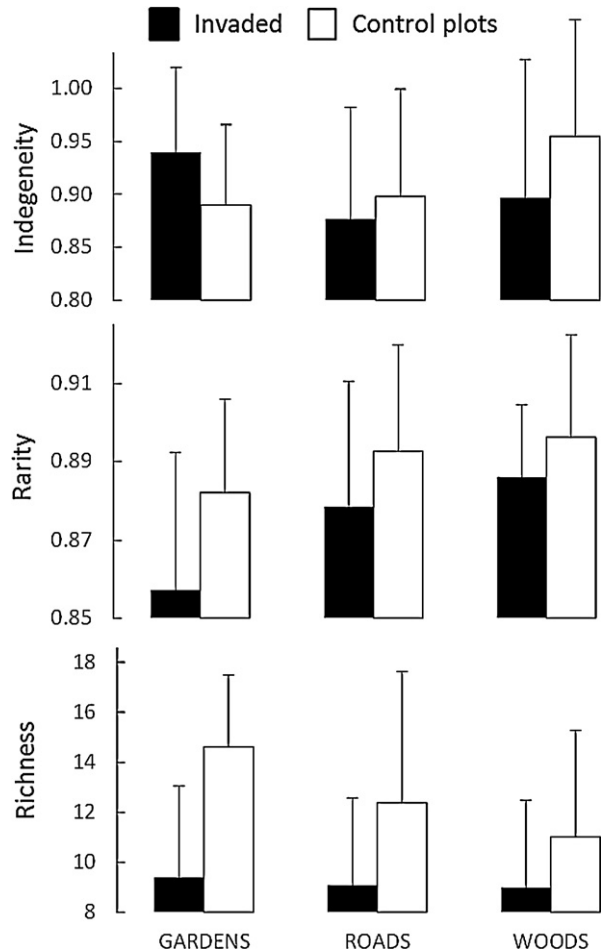


Fig. 2. Mean values for invaded vs native plots across the three habitat types and for each floristic diversity index. Error bars correspond to standard deviation.

### 3.3. Comparison of understory vegetation between invaded and control plots

In the inventories performed under *A. altissima* trees, 168 species were counted, whereas in the inventories performed under native trees, 193 species were recorded.

In each habitat type, we compared the floristic composition in *A. altissima* plots vs control plots. In Gardens, Roads and Woods species, composition differed

Table 2  
ANOVA for each floristic diversity index.

	Df	Richness		Rarity		Indigeneity	
		F value	Pr (>F)	F value	Pr (>F)	F value	Pr (>F)
Habitat	2	2.9	0.06	17	1.10E-07	6.5	1.70E-03
Invasive (vs native)	1	36.5	5.00E-09	7.7	0.01	2	0.16
Habitat*Invasive	2	2.5	0.08	0.6	0.55	3.5	0.03
Residuals	271						

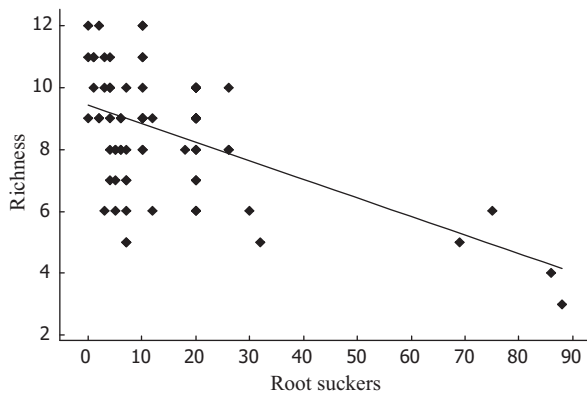


Fig. 3. Relationships between root sucker number and specific richness in invaded plots.

significantly between invaded and control plots (dbRDA test:  $P$ -value  $< 0.01$ ). Among the species the most frequently recorded under native trees, some were hardly observed under *A. altissima*, e.g. *Brachypodium sylvaticum* and *Lonicera periclymenum* (Table 3). In contrast, some common species recorded in more than 50% of *A. altissima* plots were less frequent under native trees, e.g. *Galium aparine* and *Alliaria petiolata*. The subsponaneous species *Parthenocissus quinquefolia* was only recorded under *A. altissima*. The Wilcoxon tests showed no significant difference in Landolt ecological values (Wilcoxon tests: Humidity  $P$ -value = 0.53, pH  $P$ -value = 1, Nitrogen  $P$ -value = 0.067 and Light  $P$ -value = 0.46) between these two classes of species. Nevertheless, the mean nitrogen value for the species mainly found under *A. altissima* is 4.0 (nitrogen rich), whereas those mostly found in control plots present a value of 3.2 (medium level of nitrogen) (Table 3).

Table 3

Frequency of species and their Landolt ecological values [35], in control and invaded plots. Only species whose frequency differences were highly significant ( $\chi^2$  square tests not shown) and higher than 10% are listed.

Species observed at the base of trees	Control plots (%)	Invaded plots (%)	Landolt ecological values			
			Humidity	pH	Nitrogen	Light
<i>Galium aparine</i>	18	51	3	3	5	3
<i>Alliaria petiolata</i>	30	55	3	3	5	2
<i>Ulmus minor</i>	5	20	3	4	3	3
<i>Bromus sterilis</i>	3	16	2	3	4	3
<i>Parthenocissus quinquefolia</i>	0	13	3	3	3	3
<i>Veronica hederifolia</i>	4	16	3	3	4	3
<i>Brachypodium sylvaticum</i>	32	7	4	3	4	3
<i>Lonicera periclymenum</i>	28	4	3	2	3	3
<i>Rubus fruticosus gr.</i>	59	36	3	4	4	4
<i>Melica uniflora</i>	29	9	3	2	2	2
<i>Carpinus betulus</i>	31	11	3	3	3	2
<i>Galeopsis tetrahit</i>	22	3	3	3	5	3
<i>Fagus sylvatica</i>	20	3	3	–	3	1
<i>Milium effusum</i>	15	1	3	3	3	2
<i>Poa nemoralis</i>	15	1	2	3	3	3
<i>Euphorbia cyparissias</i>	15	2	2	3	2	4
<i>Acer campestre</i>	16	4	3	4	3	3
<i>Fraxinus excelsior</i>	20	9	4	4	4	2
<i>Polygonatum multiflorum</i>	12	1	3	3	3	2
<i>Rosa arvensis</i>	12	2	3	4	3	3
<i>Anemone ymemorosa</i>	16	5	3	3	3	2

## 4. Discussion

### 4.1. *A. altissima* distribution

Our fairly complete field survey of the Fontainebleau forest showed that *A. altissima* grows essentially in edge habitats or disturbed sites, i.e. along the edge of roads, railways, gardens, meadows and river banks. This result concurs with previous observations [18,19], who noticed that this species was mainly found in disturbed open areas like forest borders from which it can spread in the underwood, where light is not a limiting factor [41–43]. We presume the *A. altissima* we found within the forest stands correspond to individuals that were favoured by temporary gaps in the canopy at least 30 years ago when these forest stands were a garden, a tree nursery or a vegetatively restored sandpit that were abandoned since (according to the managers' accounts). From that time, the trees produced a bank of root suckers and established durably forming a monospecific canopy preventing the regeneration of other tree species [20]. This species could thus be a threat particularly as open habitats or natural or anthropogenic gaps regularly occur in the canopy.

The preferred location of *A. altissima* along the lines of communication involves a special vigilance on the part of management of future outbreaks of this species in these areas for an early elimination of a potential new centre of invasion. Managers should also avoid slight thinning of forest area or at least ensure that revegetation is sufficiently rapid and complete to be sure that *A. altissima* will not install.

### 4.2. *A. altissima* and understory plant communities

The range of species able to grow in its neighbourhood is not especially low. The subtle differences in species



composition could be explained by the fact that the study focused on the plants of the woods and edges, already adapted to competition for light, water and nutrients. A feature common to these species that persist under *A. altissima*, could be the resistance to herbicide allelopathic compounds produced by the leaves, bark and roots. The species most frequently observed were very common in the region, e.g. *Hedera helix* (146 plots, Rar = 0.78), *Galium aparine* (95 plots, Rar = 0.75), or at least in the forest areas of the region, e.g. *Alliaria petiolata* (103 plots, Rar = 0.95).

In every habitat type where we were able to compare diversity under *A. altissima* and native tree species in control zones, understory vegetation under *A. altissima* was significantly poorer and more common per plot than under native trees (Table 2). The effect of *A. altissima* on indigeneity is only detected in Woods plots. Two hypotheses could be given to explain those effects:

- *A. altissima* spontaneously invades disturbed microsites hardly colonized by other species (passenger hypothesis [44]), e.g. in Roads and Gardens known as disturbed habitats;
- the presence of *A. altissima* leads to the impoverishment of diversity through competition and allelopathy (driver hypothesis [44]), e.g. in Woods, a less disturbed habitat.

Our results seem to indicate that establishment of *A. altissima* is facilitated by disturbance but once the species is established, it persists, spreads and displaces native vegetation.

The loss of diversity under *A. altissima* amounts to 15 to 30% approximately, depending on which tree species they are compared with and which habitat they grow in. A similar loss was previously observed in Mediterranean islands [27], or in a disturbed forest of Virginia [45].

The factor that seems to influence the diversity of the understory is the density of *A. altissima* suckers. We found a negative correlation between their number and the species richness recorded in the plots (even if our sample did not reveal a real gradient of density). This effect could be attributed both to interspecific competition and to allelopathic properties of *A. altissima*. Indeed, the number of 88 suckers per plot refers to about seven or eight suckers per square meter. The growth of such vigorous organisms implies high water and nutrient consumption and thick shade [20], and therefore, the elimination of the most sensitive species. Yet, allelopathy should also be mentioned since it was previously highlighted by numerous authors: [23,46–48] in ex situ conditions. In a field experiment in a temperate forest, the growth of seedlings of *Acer saccharum*, *A. rubrum* and *Q. rubra* were also affected by presence of *A. altissima* in their neighbourhood [28]. On the scale of tree bases, allelopathic effects could be produced by the root system [49] or by leaching of the foliage [20]. *A. altissima* suckers produce greater amounts of inhibitory compounds than adult trees [50]. We can suppose that allelopathy is all the more efficient as the sucker density is high (Allee effect) [51,52].

In any case, the communities of species recorded under *A. altissima* were significantly different from those found

under other tree species. This was confirmed in all habitats studied. We presume the chemicals it releases deeply modify the environmental conditions of its understory - giving rise to floristic communities characterized by resistant populations or indifferent species to these substances. For example, populations of exotic *Parthenocissus quinquefolia* are only recorded under tree-of-heaven. *A. altissima* is a very new species in Europe, and thus in this forest. We suppose it could inhibit the growth of species not adapting to its allelopathic properties, e.g. *Millium effusum*, *Poa nemoralis* and *Polygonatum multiflorum*, which we found relatively frequently under native trees but almost never under *A. altissima*. These three herbaceous plants are indeed known to be sensible to species composition of canopy trees. *Millium effusum* and *Polygonatum multiflorum* are vulnerable to compounds produced by *Fagus sylvatica* [53,54] whereas *Poa nemoralis* by *Quercus cerris* and *Q. conferta* [55].

The control plots were chosen in sites that are ecologically similar to the invaded areas and thus we did not really choose the native species we studied. Consequently, we often compared species composition in the understory of a variable number of native tree species. This induces certainly a bias in the results but our choice was to favour an ecological homogeneity among sites we compared.

Our results indeed showed that the species that mainly differed in frequency, between invaded and control plots, had the same ecological needs, with the exception of the soil's nitrogen contents that could be higher in invaded plots [29,56]. The non-significant result in Landolt ecological values could indeed be due to the low number of species taken into account (test power).

For these few species that are favoured in invaded plots (i.e. *Galium aparine*, *Alliaria petiolata*, *Bromus sterilis* and *Veronica hederifolia*) *A. altissima* could be a facilitator. There is a significant positive interaction and clear ecological significance between nitrogen in *Galium aparine* and in *Alliaria petiolata* [57] as for *Bromus sterilis* [58]. It has not been demonstrated so clearly that *Veronica hederifolia* was favoured by nitrogen [59].

## 5. Conclusion

In this study, we showed that *A. altissima* was present in the Fontainebleau forest, not only along roads and railways but also penetrating the forest due to natural or artificial gaps. Within the forest patches, once this species has invaded, it seems to settle in the long term. That settlement prevents the growth of a large number of other plant species and modifies the structure of the community through facilitation for common nitrophilous species and competition and allelopathy against sensitive forest species. In this way, in some areas of the Fontainebleau forest, *A. altissima* directly threatens flora of protected reserves. The data of this study will thus be taken into account in management plans to strictly limit its expansion in the forest.

## Disclosure of interest

The authors declare that they have no conflicts of interest concerning this article.

## Acknowledgments

We especially thank Monika Zavodna and Claire Jousseau for comments on drafts of this paper, Steve Hubert for the graphics, Claude Lagarde of the Office National des Forêts (ONF) provided helpful information. The English correction was performed by Anne Lindsey.

## References

- [1] Multilateral, Convention on Biological Diversity (with annexes). Concluded at Rio de Janeiro on 5 June 1992. United Nations – Treaty series 1992;1760:143–69.
- [2] D.M. Richardson, P. Pysěk, M. Rejmánek, M.G. Barbour, F.D. Panetta, C.J. West, Naturalization and invasion of alien plants: concepts and definition, *Divers. Distrib.* 6 (2000) 93–107.
- [3] B. Blossey, L.C. Skinner, J. Taylor, Impact and management of purple loostrie (*Lythrum salicaria*) in North America, *Biodivers. Conserv.* 10(10) (2001) 1787–1807.
- [4] A. El Kéblawy, A. Al Rawai, Impacts of the invasive exotic *Prosopis juliflora* (Sw.) D.C. on the native flora and soils of the UAE, *Plant Ecol.* 190 (1) (2007) 1573–1582.
- [5] K.O. Reinhart, E. Greene, R.M. Callaway, Effects of *Acer platanoides* invasion on understory plant communities and tree regeneration in the northern Rocky Mountains, *Ecography* 28 (5) (2005) 573–582.
- [6] R.W. Merriam, E. Feil, The potential impact of an introduced shrub on native plant diversity and forest regeneration, *Biol. Invas.* 4 (2002) 369–373.
- [7] P.E. Hulme, E. Bremner, T., Assessing the impact of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal, *J. Appl. Ecol.* 43 (2006) 43–50.
- [8] M. Hejda, P. Pysěk, What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? *Biol. Conserv.* 132 (2006) 143–152.
- [9] E. Weber, Invasive plant species of the world: a reference guide to environmental weeds, CABI International, Wallingford, 2003, 560 pp.
- [10] I. Kowarik, I. Sámuel, Biological flora of Central Europe: *A. altissima* (Mill.) Swingle, *Perspect. Plant Ecol.* 8 (2007) 207–237.
- [11] E. Newton, Arboreal ruffraff or ultimate tree? *Audubon* 88 (4) (1986) 12–19.
- [12] D. Jeanmonod, Plantes exotiques envahissantes: en savoir plus pour comprendre et agir. Royal Horticultural Society 2005; janvier/février: 4–9.
- [13] D. Brandes, Flora and vegetation of villages in northeastern Burgenland, Austria *Phytocoenologia* 16 (2) (1988) 225–258.
- [14] I. Kowarik, R. Böcker, Zur Verbreitung, Vergesellschaftung und Einbürgerung des Götterbaumes (*A. altissima altissima* (Mill.) Swingle) in Mitteleuropa, *Tuexenia* 4 (1984) 9–29.
- [15] R. Nowack, Naturalization of *Paulownia tomentosa*. Thunb. Steud. In the Rhein-Neckar region west Germany, *Floristische Rundbriefe* 21 (1) (1987) 23–32.
- [16] K. Matrai, L. Szemethy, P. Tóth, K. Katona, Székely Resource use by deer in lowland non-native forests, Hungary, *J. Wildl. Manage.* 68 (4) (2004) 879–888.
- [17] C.D. Huebner, Vulnerability of oak-dominated forests in West Virginia to invasive exotic plants: temporal and spatial patterns of nine exotic species using herbarium records and land classification data, *Castanea*. 68 (1) (2003) 1–14.
- [18] I. Kowarik, Clonal growth in *A. altissima* on a natural site in West Virginia, *J. Veg. Sci.* 6 (1995) 853–856.
- [19] L.B. Knapp, C.D. Canham, Invasion of an old growth forest in New York by *A. altissima*: sapling growth and recruitment in canopy gaps, *J. Torrey Bot. Soc.* 127 (2000) 307–315.
- [20] D. Clair-Maczulajtys, Quelques aspects de la biologie de l'*A. altissima* (Mill.) Swingle: étude de la double stratégie de reproduction par graines et par drageonnement en relation avec les métabolites de réserve PhD-Thesis. Université Paris 7, Paris, France, 1984, 441 pp.
- [21] E. Pan, N. Bassuk, Establishment and distribution of *A. altissima* in the urban environment, *J. Environ. Hort.* 4 (1) (1986) 1–4.
- [22] G. Bory, Quelques aspects de la biologie de l'*Ailanthus altissima* (Mill.) Swingle: mouvements de métabolites, croissance, développement, sécrétion et floraison chez divers types d'arbres PhD-Thesis. Université Paris 7, Paris, France, 1983, 286 pp.
- [23] R.M. Heisey, Allelopathic and herbicidal effects of extracts from tree-of-heaven (*A. altissima*), *Amer. J. Bot.* 77 (1990) 662–670.
- [24] R.M. Heisey, Identification of an allelopathic compound from *A. altissima* (Simaroubaceae) and characterization of its herbicidal activity, *Amer. J. Bot.* 83 (2) (1996) 192–200.
- [25] L.J. Lin, G. Peiser, B.P. Ying, K. Mathias, F. Karasina, Z. Wang, J. Itatani, L. Green, Y.-S. Hwang, Identification of plant growth inhibitory principles in *Ailanthus altissima* and *Castela tortuosa*, *J. Agr. Food Chem.* 43 (1995) 1708–1711.
- [26] R. Tsao, F.E. Romanchuk, C.J. Peterson, J.R. Coats, Plant growth regulatory effect and insecticidal activity of the extracts of the tree-of-heaven (*A. altissima* L.), *BMC Ecol.* 2 (2002) 1–6.
- [27] M. Vilà, M. Tessler, C.M. Suehs, G. Brundu, L. Carta, A. Galanidis, P. Lambdon, M. Manca, F. Médail, E. Moragues, A. Traveset, A.Y. Troumbis, P.E. Hulme, Local and regional assessments of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands, *J. Biogeogr.* 33 (2006) 853–861.
- [28] L. Gómez-Aparicio, C. Canham, Neighbourhood analyses of the allelopathic effects of the invasive tree *Ailanthus altissima* in temperate forests, *J. Ecol.* 96 (2008) 447–458.
- [29] L. Gómez-Aparicio, C. Canham, Neighbourhood models of the effects of invasive tree species on ecosystem processes, *Ecol. Monog.* 78 (2008) 69–86.
- [30] G. Lemée, Sur l'intérêt écologique des réserves biologiques de la forêt de Fontainebleau, *Bull. Soc. Bot. Fr.* 113 (1966) 305–323.
- [31] A.K. Iablokoff, Un carrefour biogéographique: le Massif de Fontainebleau. Écologie des réserves, Ed. Sedes, Paris, 1953, 98 pp.
- [32] L. Weil, Les essences ligneuses de la Forêt de Fontainebleau, *Bulletin de l'Association des Naturalistes de la Vallée du Loing* 8 (3) (1925) 140–148.
- [33] J. Kerguelen, Index synonymique de la flore de France. <http://www.inra.fr/flore-france/> (in French) 2003.
- [34] E. Landolt, Ökologische Zeigerwerte zur Schweizer Flora, Veröffentlichungen des Geobotanischen Institutes der ETH Stiftung Rübel 64 (1977) 1–208.
- [35] R Development Core Team. R: a language and environment for statistical computing. Vienne. R foundation for statistical Computing. 2008.
- [36] Minitab Inc., Minitab for Windows, release 15.24. 1999.
- [37] A. Muratet, E. Porcher, V. Devictor, G. Arnal, J. Moret, S. Wright, N. Machon, Evaluation of floristic diversity in urban areas as a basis for habitat management, *Appl. Veg. Sci.* 11 (2008) 451–460.
- [38] Conservatoire Botanique National du Bassin Parisien (CBNBP) 2008; <http://cbnbp.mnhn.fr/cbnbp>.
- [39] J.C. Abadie, La nature ordinaire face aux pressions humaines: le cas des plantes communes PhD-Thesis. National Museum of natural history. Paris, France, 2008, 250 pp.
- [40] P. Legendre, M.J. Anderson, Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments, *Ecol. Monogr.* 69 (1) (1999) 1–24.
- [41] G.R. Robinson, S.N. Handel, Forest restoration on a closed landfill: rapid addition of new species by bird dispersal, *Conserv. Biol.* 7 (2) (1993) 271–278.
- [42] G.R. Robinson, S.N. Handel, Directing spatial patterns of recruitment during an experimental urban woodland reclamation, *Ecol. Appl.* 10 (2000) 174–188.
- [43] L.J. Call, E.T. Nilsen, Analysis of interactions between the invasive tree-of-heaven (*A. altissima*) and the native black locust (*Robinia pseudoacacia*), *Plant Ecol.* 176 (2005) 275–285.
- [44] A.S. Mac Dougall, R. Turkington, Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecol.* 86 (1) (2005) 42–55.
- [45] J. Buck, D. Mann, C. Millsaps, M.S. Jackson, The impact of the exotic *A. altissima* on ground cover diversity in a disturbed Virginia forest ESA Annual Meeting, Poster Session #41 2002.
- [46] F. Mergen, A toxic principle in the leaves of *A. altissima*, *Bot. Gaz.* 12 (1959) 32–36.
- [47] V. De Feo, L. De Martino, E. Quaranta, C. Pizza, Isolation of phytotoxic compounds from tree-of-heaven (*A. altissima altissima* Swingle), *J. Agri. Food Chem.* 51 (5) (2003) 1177–1180.
- [48] R.M. Heisey, Evidence for allelopathy by tree-of-heaven (*A. altissima*), *J. Chem. Ecol.* 16 (1990) 2039–2055.
- [49] P.A. Davies, Root system in *A. altissima*, *Trans. Ky. Acad. Sci.* 10 (1942) 20–21.
- [50] J.G. Lawrence, A. Colwell, O.J. Sexton, The ecological impact of allelopathy in *A. altissima* (Simaroubaceae), *Amer. J. Bot.* 78 (1991) 948–958.
- [51] L.G. Perry, G.C. Thelen, W.M. Ridenour, T.L. Weir, R.M. Callaway, M.W. Paschke, J.M. Vivanco, Dual role for an allelochemical: (±)-catechin from *Centaurea maculosa* root exudates regulates conspecific seedling establishment, *J. Ecol.* 93 (6) (2005) 1126–1135.
- [52] W.L. Ridenour, R.M. Calaway, The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass, *Oecologia*. 126 (2001) 444–450.
- [53] C. Gallet, F. Pellissier, Interactions allélopathiques en milieu forestier, *Rev. For. Fr.* 6 (2002) 567–576.

- [54] A.M. Kooijman, Litter quality effects of beech and hornbeam on undergrowth species diversity in Luxembourg forests on limestone and decalcified marl, *J. Veg. Sci.* 21 (2010) 248–261.
- [55] L. Djurdjević L, M. Mitrović, A. Dinić, P. Pavlović, S. Bojović, G. Gajić, O. Kostić, Allelopathic investigations of *Quercus conferta* and *Quercus cerris* domination in oak forest at Avala Mt. (Serbia). Fourth World Congress of Allelopathy. Wagga Wagga, Australia; 2005.
- [56] R. Belote, R. Jones, Tree leaf litter composition and non-native earthworms influence plant invasion in experimental forest floor mesocosms, *Biol. Invas.* 11 (2009) 1045–1052.
- [57] C.D. Pigott, K. Taylor, The distribution of some woodland herbs in relation to the supply of nitrogen and phosphorus in the soil, *J. Anim. Ecol.* 33 (1964) 175–185.
- [58] A.J. Theaker, N.D. Boatman, R.J. Froud-Williams, The effect of nitrogen fertiliser on the growth of *Bromus sterilis* in field boundary vegetation, *Agr. Ecosyst. Environ.* 53 (1995) 185–192.
- [59] G.W.W. Wamelink, H.F. van Dobben, L.J.M. van der Eerden, Experimental calibration of Ellenberg's indicator value for nitrogen, *Environ. Pollut.* 102 (S) (1998) 371–375.