



Impacts of the alien trees *Ailanthus altissima* (Mill.) Swingle and *Robinia pseudoacacia* L. on soil nutrients and microbial communities



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ABSTRACT

Ailanthus altissima (Mill.) Swingle and *Robinia pseudoacacia* L. are two aggressive invasive trees in riparian areas in Central Spain. We aim to test whether soil properties, nutrient mineralization rates and soil bacterial communities of riparian forest dominated by the native *Populus alba* L. can be altered by the presence of *A. altissima* or *R. pseudoacacia*. In autumn 2011 and spring 2012 we conducted a field soil sampling in three sites where invasive and native trees were paired. In addition, in a 6-month greenhouse experiment (GHE), we grew *A. altissima*, *R. pseudoacacia* and *P. alba* from seeds in a soil collected from a native area. We quantified soil organic matter (OM), nitrogen (N), phosphorous (P), nitrate (NO_3^- -N), ammonium (NH_4^+ -N), pH, potential net ammonification and nitrification rates, phosphomonoesterase (PME) activity and the composition of soil bacterial community in soils from the field study and from the GHE. Both the field and the GHE results showed the capability of *A. altissima* to decrease soil total N and of *R. pseudoacacia* to increase soil mineral N. In the field, all invaded soils had greater NO_3^- -N than *P. alba* soils. *R. pseudoacacia* field soils had greater PME activity, total N and net ammonification rates while *A. altissima* soils had lower OM, NH_4^+ -N, net nitrification and total N mineralization rates than those of *P. alba*. Differences in the composition of soil bacterial communities were only found in the field, being more evident between *A. altissima* and *P. alba* than between *R. pseudoacacia* and *P. alba* field soils. Symbiotic N_2 fixation could explain the capability of *R. pseudoacacia* to increase soil mineral N, while the potential of *A. altissima* to decrease total soil N may be attributed to changes in the balance between N input and losses from the soil. Although the GHE results indicated that the invasive trees can start changing soil conditions during early stages of establishment, more impacts found in the field study suggests that several soil properties, the composition of soil bacteria communities and microbial activities need longer time since invasion to be altered.

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1. Introduction

Invasive plants are introduced alien species able to establish viable populations and to expand to areas distant from the sites of introduction (Richardson et al., 2000). Once established, invasive plants may affect native plant communities by reducing their diversity and abundance (Vilà et al., 2011). This effect may be caused directly by allelopathy and competition for resources (Callaway and

Ridenour, 2004; Vilà and Weiner, 2004; Maron and Marler, 2008) or indirectly by modifying the environment to the detriment of native species in their own benefit (Haubensak and Parker, 2004; Niu et al., 2007). Recent reviews suggest that the overall effect of invasive plants is an increase of nutrient pools and acceleration of fluxes (Ehrenfeld, 2003; Liao et al., 2008; Vilà et al., 2011; Castro-Díez et al., 2014). The alteration of ecosystem properties by plant invaders may also increase the habitat invasibility for other plants in a process named “the invasion meltdown” (Simberloff and Von Holle, 1999; Von Holle et al., 2006). Moreover, the effects of invasive species may persist during years after the invader removal maintaining the risk of invasion and hampering the recovery of the

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ecosystem or restoration with native plants (Marchante et al., 2009; Von Holle et al., 2013).

Invasive plants may change the composition and activity of microbial communities. For instance, Hawkes et al. (2005) found that invasive grasses increased the abundance and change the composition of ammonium oxidizing bacteria, which caused greater nitrification rates in soil. Likewise, changes in soil pH caused by different plant species can alter the composition of the microbial community (Thoms and Gleixner, 2013). Greater impacts on the composition and activity of soil microbial communities can be produced by invasive species differing from natives in nitrogen use strategies (Boudsocq et al., 2012), allelochemical compounds (Callaway et al., 2008; Lorenzo et al., 2013) or the quantity and chemical composition of plant tissues and root exudates (Wolfe and Klironomos, 2005; Rodgers et al., 2008; Weidenhamer and Callaway, 2010). Moreover, the establishment of positive plant–soil–microbe feedbacks in the invaded range is considered as a cause of the invasion success of some species and a mechanism to alter microbial communities (De la Peña et al., 2010; Rodríguez-Echeverría et al., 2013). For instance, invasive species may accumulate soil pathogens, affecting native plants (e.g. the invasive weed, *Chromolaena odorata*, increased the abundance of the soil pathogenic fungi, *Fusarium semitectum* (Mangla et al., 2008)). Invasive species may also disrupt belowground mutualisms between native plants and arbuscular mycorrhizal fungi (Reinhart and Callaway, 2006) or symbiotic nitrogen-fixing bacteria (Rodríguez-Echeverría, 2010; Rodríguez-Echeverría et al., 2012). Lastly, plant invasion may also lead to the introduction of exotic soil mutualistic microorganisms (Rodríguez-Echeverría et al., 2011; Nuñez and Dickie, 2014).

Riparian forest ecosystems are highly susceptible to plant invasion due to their more buffered temperatures and moister conditions compared with surrounding ecosystems (Hood and Naiman, 2000). In addition, human activities, such as river canalization or flood regulation, cause the decline of native vegetation which forms gaps, giving exotic species a chance to be established (Zedler and Kercher, 2004). In the Iberian Peninsula, the invasive trees *Ailanthus altissima* (Mill.) Swingle (Simaroubaceae) and *Robinia pseudoacacia* L. (Fabaceae) are found colonizing riparian ecosystems (Castro-Díez et al., 2009, 2012). *A. altissima* is native to China and North Vietnam while *R. pseudoacacia* is native to Appalachian Mountains (Southeast of USA) (Kowarik and Säumel, 2007; Cierjacks et al., 2013). They are both included in the Spanish Atlas of Invasive Plants and considered among the 20 most harmful species in Spain and among the 100 worst invasive species in Europe (Sanz Elorza et al., 2004; GEIB, 2006; DAISIE, 2009). Both species have allelopathic compounds in their tissues (Kowarik and Säumel, 2007; Cierjacks et al., 2013) and they both have shown the ability to increase soil nitrate concentration and net nitrification rates in nutrient-poor soils likely due to high quality leaf litter of *A. altissima* and the ability of *R. pseudoacacia* to fix N_2 from the atmosphere (Rice et al., 2004; Gómez-Aparicio and Canham, 2008; Von Holle et al., 2013). However, the effect of both species on the composition of soil microbial communities together with soil properties and nutrient mineralization rates in riparian ecosystems remains unexplored even when soil microorganisms control important ecosystem processes, such as mineralization of soil organic matter or soil nitrate production and assimilation (Booth et al., 2005; Myrold and Posavatz, 2007).

The aim of this study was to assess the effects of the invasive trees, *A. altissima* and *R. pseudoacacia*, on soil properties and on the structure and activity of soil bacterial communities of riparian forest dominated by the native tree *Populus alba* L. (Salicaceae). We used two complementary approaches: 1) a field study comparing soil properties between invaded and paired non-invaded sites

(*A. altissima*–*P. alba* and *R. pseudoacacia*–*P. alba*) and 2) a greenhouse experiment (GHE), where the invaders *A. altissima* and *R. pseudoacacia* and the native *P. alba* were grown for six months in a native soil. It is possible that there were pre-existing soil characteristics, which contributed to invasion of the tree species (Dassonville et al., 2008). Therefore, GHE growing exotic invasive trees in non-invaded soils allow to distinguish if differences observed in the field are due to the presence of the plant invader or to the preexisting site conditions (Ehrenfeld et al., 2001).

2. Materials and methods

2.1. Field sampling

The study was conducted in the riparian zone of the Henares River (Tagus Basin, Central Spain), where *P. alba* is the dominant tree, which is accompanied by other native tree species, such as *Tamarix gallica*, *Salix alba*, *Populus nigra*, *Fraxinus angustifolia* and *Ulmus minor* (Martínez, 2000). We selected five sites (Table 1) where invaded patches by *A. altissima* or *R. pseudoacacia* were close to native patches (i.e. vegetation dominated by *P. alba*). Two sites were invaded by the exotic *A. altissima* (Chiloeches and Guadalajara), two by *R. pseudoacacia* (El Encín and Jadraque), and one invaded by both exotic trees (El Val). In this way we had three sites (replicates) per species. Geographical coordinates, a soil taxonomic classification and vegetation cover of each study site are shown in Table 1. In each patch we selected five adult dominant trees (*P. alba*, *A. altissima* or *R. pseudoacacia*), which were considered as pseudo-replicates. Below the canopy of each tree, soil samples were collected in the seasons with greatest microbial activity, i.e. autumn (12–15 December 2011) and spring (17–25 April 2012). Each soil sample consisted of the mixture of four sub-samples taken at 1 m distance around the tree trunk by means of a metallic rectangular core (11 cm depth, 7.5 cm width). Soil samples were kept in polyethylene bags and carried to the lab, spread on trays, air-dried at room temperature, sieved (1 mm mesh) (Hawkes et al., 2005; Niu et al., 2007; Lorenzo et al., 2010) and divided in two parts. One was stored at $-32\text{ }^\circ\text{C}$ for bacterial DNA analyses and the other part was conserved at $4\text{ }^\circ\text{C}$ for the analysis of soil properties (nutrients, percentage of organic matter, pH and mineralization rates). In the autumn, the litter layer (a 21 cm diameter surface) above each of the four soil subsamples was taken and pooled in a single sample. Litter samples were kept in paper bags and brought back to the lab, divided by plant part (leaf and woody), oven dried ($60\text{ }^\circ\text{C} \geq 48\text{ h}$) and weighed (Balance Sartorius BP211D, 0.0001 g) (Table 1).

In December 2011, we measured the basal perimeter of the selected trees (Table 1). In April 2012, we established a square plot ($4 \times 4\text{ m}$) containing each sampling tree in the centre. Within all square plots the canopy cover of the sampling tree species was greater than 75%. In each square plot, we registered the herbaceous and shrubs species cover (%), as well as the cover of the sampling tree seedlings and saplings (Table 1).

2.2. Greenhouse experiment

Soil from a non-invaded area dominated by *P. alba* in the Jadraque site (Table 1) was collected on 27 April 2012 to fill five 0.5 L plastic pots per species (*A. altissima*, *R. pseudoacacia* and *P. alba*). As a control, five additional pots were left without plants during the six-month experiment (named as “control t6”). In addition, an aliquot of the soil sample was taken at the beginning of the experiment (named as “control t0”). Seeds were collected in the field from at least 5 trees per species. Seeds were disinfected with 10% bleach. *R. pseudoacacia* seeds were subsequently scarified mechanically with sand paper and wings of

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