



## Phenolic inputs by invasive species could impart seasonal variations in nitrogen pools in the introduced soils: A case study with *Polygonum cuspidatum*

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### ARTICLE INFO

#### Article history:

Received 17 May 2012

Received in revised form

8 September 2012

Accepted 13 September 2012

Available online 28 September 2012

#### Keywords:

Soil nitrogen

Organic nitrogen

Plant invasion

Polyphenols

*Polygonum cuspidatum*

Tannin

Peroxidase

Knotweed

### ABSTRACT

One cascading feature of the spread of introduced species of plants is their capacity to alter levels of resource availabilities for other species. However, the effects of introduced species on temporal patterns of soil nutrient availability remain unexplored, which could be critical for invasion where the growing seasons are short. To test the hypothesis that the invasive species could alter seasonal patterns of resource availability via suppression of soil processes through secondary compounds in autumnal litter-fall, we measured nutrient dynamics in soils inside and outside stands of invasive *Polygonum cuspidatum* at four sites in northeastern US over the growing season. In the uppermost soil (0–5 cm depth), both concentrations of inorganic N and rates of N mineralization were 60% lower inside than outside stands of knotweed in spring but became as high or higher inside than outside by fall. Carbon and nitrogen mineralizing soil microbial enzymes also followed a similar seasonal trend with lower activity inside the knotweed stands than outside during spring and these differences disappearing by summer. Concentrations of dissolved organic N (DON) and phenolic compounds showed the opposite seasonal pattern and a strong correlational trend; they were nearly 3 times higher inside than outside stands in spring and similar inside and outside in fall. The estimated flux of tannins from knotweed litter to soil was calculated as  $189.5 \pm 39.2 \text{ g m}^{-2} \text{ year}^{-1}$ . Further, exogenous application of knotweed tannin reduced the soil N-mineralization and paralleled the field observed inhibition of mineralization. At 5–15 cm depth, concentrations of phenolics were uniformly low and differences between soils inside and outside stands were mostly non-significant. Our results suggests that invasion by polyphenol rich, yet fast growing exotic species would make the soil N pools more dynamic, which could facilitate invasion by creating stints of apparent deficiency and sufficiency of resources, and due to the localization of the invader effect the amelioration practices could be focused on the surface 0–5 cm layer of the mineral soil.

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### 1. Introduction

Invasions by introduced plant species can result in substantial economic losses and reductions in biodiversity (e.g., Vila et al., 2010). Less than one percent of all exotic species become invasive in their introduced habitats (Williamson and Fitter, 1996), thus post-introduction processes driven by the exotic species could be of prime importance in deciding the success of any invasion (Dietz and Edwards, 2006; van Kleunen et al., 2010). One important mechanism underlying both economic and ecological costs is the alteration of ecosystem processes by introduced species (Dietz and

Edwards, 2006; van Kleunen et al., 2010), particularly those alterations that facilitate persistence of the species that cause the changes (Levine et al., 2003; Laland and Boogert, 2010; Seastedt and Pysek, 2011). Sometimes referred to as niche construction (Hobbs et al., 2006), this type of positive feedback can prevent the reversion of habitats to their pre-invasion status even after the removal of the invasive species (Vinton and Goergen, 2006; Marchante et al., 2009; Larson and Larson, 2010; Green et al., 2011). Understanding mechanisms that drive niche construction by introduced species is of basic interest in plant and soil ecology and of applied interest in habitat restoration.

Alteration of resource availability is generally agreed to be one of the factors that increase invasibility of habitats (Davis et al., 2000; Dawson et al., 2012), and alterations of ecological processes that result in a higher availability or greater sequestration of resources

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have been associated with a number of biological invasions (Hawkes et al., 2005). Since nitrogen is a limiting soil nutrient in many terrestrial ecosystems, a number of studies have concentrated on changes in N cycling attributable to invasion (Ehrenfeld, 2003; Suding et al., 2005; Liao et al., 2008). Observed changes include increases and decreases in N availability due to N fixation or increased or decreased rates of mineralization or leaching (Allison and Vitousek, 2004; Hughes and Denslow, 2005; Rout and Callaway, 2009). These alterations may interact with physiological traits of invasive species such as high capacity resource acquisition (Tharayil et al., 2009) or high resource use efficiencies (Funk and Vitousek, 2007) to partly explain the success of various introduced species (Laungani and Knops, 2009; Seastedt and Pysek, 2011).

Even though many studies have emphasized the ability of invasive species to alter the habitat N availability, to our knowledge, no field-level attempts have been made to elucidate the invader-induced variation in the temporal pattern of this resource availability. Such alterations are plausible because N cycling in soils is a complex biogeochemical process that is influenced by the seasonal effects of temperature and moisture on the growth and metabolism of autotrophs and soil heterotrophs (Deluca and Keeney, 1994; Grogan and Chapin, 1999). If introduced species have phenologies and N demands that differ from the natives in a habitat, the invader induced seasonality of N availability could shift the balance of competition between introduced and native species.

One possible biochemical route for alteration of the seasonality of N cycling is via the production of phenolic compounds comprising of simple phenolics, flavonoids, and tannins (Handley, 1961; Rice and Panchoy, 1973; Wardle and Lavelle, 1997; Schimel et al., 1998). Due to their biological activity, as in the inactivation of microbial enzymes by tannins; and relative chemical recalcitrance, as in the slower decomposition rates of lignins and tannins by microbes, polyphenols are thought to be a major factor in terrestrial carbon and N cycling (Northup et al., 1995; Hattenschwiler and Vitousek, 2000; Kraus et al., 2004). Recent studies show the potential for phenolics to facilitate plant invasion by altering soil biogeochemical processes. For example, catechin exuded from the roots of *Centaurea stoebe* can inhibit nitrification (Thorpe et al., 2011), and tannins in the litter of slow growing *Kalmia angustifolia* can reduce microbial enzymatic activities and reduce N mineralization (Joanisse et al., 2007, 2008).

Since most phenolic input to the soil comes through leaching, decomposition of litter, and exudation by young actively growing roots, the phenolic composition in the soils of habitats where litter-fall is seasonal might exhibit a seasonal trend (Muscolo and Sidari, 2006), which in turn could control temporal patterns of N cycling. Because of their inhibition of N mineralization (Joanisse et al., 2008), phenolic compounds could also alter the composition of soil nitrogen pools, resulting in higher amounts of organic nitrogen (Northup et al., 1995). Although some organic forms of N are an

important source of N for plants in certain habitats (Nasholm et al., 1998; Averill and Finzi, 2011; Inselsbacher and Näsholm, 2012), little is known about the influence of an introduced, invasive species on the seasonal dynamics of this N-pool, which in turn could alter the competitive advantage in their favor.

*Polygonum cuspidatum*, or Japanese knotweed, is a rhizomatous, herbaceous perennial which was introduced to the U.S. during the late eighteenth century as an ornamental and as a source of fodder (Barney et al., 2006). The species has since spread widely in at least 35 states, five of which list it as a noxious weed. *Polygonum cuspidatum* can form persistent monocultures that appear to prevent regrowth of native vegetation (Holzner, 1982; Siemsen and Blossey, 2007), and to provide poor habitat for native animals (Maerz et al., 2005; Lecerf et al., 2007).

One likely mechanism by which *P. cuspidatum* might alter these habitats and promote its own persistence is the alteration of N cycling due to litter chemistry. *P. cuspidatum* has high productivity (Aguilera et al., 2010) and high concentrations of secondary compounds in its leaves (Miyagi et al., 2010). Shoots can reach over 2 m in height and they die back to the ground in the fall, producing large amounts of litter. A thick layer of humus can accumulate under established stands of knotweed (Maurel et al., 2010). Although standing concentrations of inorganic N have been reported not to differ in soils (0–10 cm) under and adjacent-to stands (Aguilera et al., 2010), soils under stands do appear to have a lower rate of loss of N (Dassonville et al., 2011), suggesting that *P. cuspidatum* may suppress cycling of N from organic forms to inorganic forms that are more susceptible to loss from the soil.

Based on the high concentration of polyphenols in the litter of *P. cuspidatum*, the potential effects of polyphenols on N cycling, and the strong seasonality and large amount of knotweed litter-fall in its invaded ranges in eastern North America, we hypothesized that *P. cuspidatum* seasonally suppresses N cycling, as litter dropped in the fall decomposes with the onset of the growing season. We specifically predicted that 1) both the size of pools of inorganic N relative to those of organic N and rates of N mineralization will be lower under than adjacent-to stands of *P. cuspidatum*, 2) these effects will be most pronounced in the spring where the mineralization will be inhibited by polyphenols derived from the litter of the previous fall, 3) the size of pools of organic N will be positively related to concentrations of polyphenols in soils.

## 2. Materials and methods

### 2.1. Sampling design

We studied the effects of *P. cuspidatum* on the dynamics of N in the soil at four sites in the northeastern U.S. (Table 1). The main criteria for the selection of sites were presence of a well-established population of *P. cuspidatum* (>15 years old and >1000 m<sup>2</sup> in area) that was actively spreading (>0.5 m<sup>2</sup> y<sup>-1</sup>) into adjacent vegetation, apparent lack of recent disturbance, and well-developed and

**Table 1**  
Study sites.

Site	Soil	Db <sup>a</sup>	pH	Coordinates	Habitat and some dominant plants outside stands
Amherst, MA	Loam	1.33	6.0	42° 24'N, 72° 31'W	Old field; <i>Aesculus</i> sp., <i>Asclepias</i> sp., <i>Dactylis</i> sp., <i>Elytrigia repens</i> , <i>Galium</i> sp., <i>Lepidium</i> spp., <i>Oxalis stricta</i> , <i>Plantago</i> spp., <i>Rhus glabra</i> , <i>Schedonorus phoenix</i> , <i>Setaria pumila</i> , <i>Trifolium</i> sp., <i>Vicia</i> sp.
Holyoke, MA	Loam	1.42	6.4	42° 23'N, 72° 32'W	Waste area; <i>Lespedeza</i> sp., <i>Schedonorus phoenix</i> , <i>Solidago</i> sp., <i>Verbascum thapsus</i> , <i>Vicia</i> sp.
Northampton, MA	Sandy loam	1.51	5.6	42° 19'N, 72° 35'W	Riparian forest; <i>Acer negundo</i> , <i>A. saccharinum</i> , <i>Carya</i> sp., <i>Osmunda cinnamomea</i> , <i>Populus deltoides</i> , <i>Ulmus rubra</i> , <i>Vitis labrusca</i>
Cayuta, NY	Silty loam	1.35	6.6	42° 17'N, 76° 42'W	Old field; <i>Asclepias</i> sp., <i>Dactylis</i> sp., <i>Chrysanthemum</i> sp., <i>Lepidium</i> spp., <i>Plantago</i> spp., <i>Schedonorus phoenix</i> , <i>Solidago</i> sp., <i>Vicia</i> sp.

<sup>a</sup> Bulk density (g cm<sup>-3</sup>).

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