



Long-term impact of *Heracleum mantegazzianum* invasion on soil chemical and biological characteristics



Kateřina Jandová^{a,b,*}, Tereza Klinerová^b, Jana Müllerová^b, Petr Pyšek^{b,c}, Jan Pergl^b, Tomáš Cajthaml^{a,d}, Petr Dostál^b

^a Faculty of Science, Institute for Environmental Studies, Charles University in Prague, Albertov 6, CZ-128 43 Prague 2, Czech Republic

^b Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic

^c Faculty of Science, Department of Ecology, Charles University in Prague, Viničná 7, CZ-128 44 Prague 2, Czech Republic

^d Institute of Microbiology, Academy of Sciences of the Czech Republic, Vídeňská 1083, CZ-142 20 Prague 4, Czech Republic

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ABSTRACT

Exotic plant invasions often change ecosystem properties with subsequent impacts on the structure of invaded communities. Despite an increasing knowledge of post-invasion ecosystem changes, these modifications are only rarely studied within the temporal context of ongoing invasions. In this study we investigated 19 soil chemical and biological characteristics, as well as light conditions, in uninvaded grassland sites and compared them with those from sites invaded by giant hogweed (*Heracleum mantegazzianum*) for different times (from 11 to 48 years). We further related variation in these soil and light characteristics to richness and productivity of native plant species and hogweed cover measured in the field, and to common-garden performance of hogweed grown in soil inocula from the same sites.

Hogweed presence significantly reduced red/far-red light ratios but increased soil pH. Longer invasion history was associated with increasing soil conductivity and content of extractable phosphorus. There were also parameters that displayed opposite trends in different periods of invasion such as fungal/bacterial ratios or relative amount of photosynthetically active radiation (Δ PAR). These parameters initially increased (fungal/bacterial ratio) or decreased (Δ PAR), but after reaching a certain breakpoint they tended to return to pre-invasion conditions.

Differences in native species richness were best correlated with light availability and soil pH, and productivity with composition of soil microbial communities. Differences in hogweed cover were associated with soil pH and conductivity. The variation in hogweed performance in a common garden was related to the composition of soil microbial communities, soil conductivity and light availability of sites from which soil inocula were collected.

This study documents that ecosystem properties can be altered not only by an invasion event but are further modified as the invasion proceeds. These ecosystem changes likely underlie long-term impacts of invasive plants on native communities.

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1. Introduction

Impacts of invasive plants on ecosystem processes and properties are often coupled with those on the structure and composition of resident plant communities (Levine et al., 2003; Wolfe and Klironomos, 2005; Hejda et al., 2009; Ehrenfeld, 2010; Pyšek

et al., 2012). Multiple mechanisms, including post-invasion changes in resource availability, composition of soil microbial communities or fire regimes, have been documented to reduce native species richness and modify the composition of plant communities (Levine et al., 2003). For example, species richness and abundance of native forest seedlings decreased in dense cover of *Tradescantia fluminensis*, an invasive weed in New Zealand podocarp forests, due to marked reduction of light availability (Standish et al., 2001). Two other exotic plants, *Alliaria petiolata* and *Chromolaena odorata*, were shown to suppress native plant growth by disrupting their mutualistic associations with arbuscular mycorrhizal fungi or by promoting the accumulation of soil fungal

* Corresponding author. Faculty of Science, Institute for Environmental Studies, Charles University in Prague, Albertov 6, CZ-128 43 Prague 2, Czech Republic. Tel.: +420 775670135.

E-mail address: katerina.jandova@gmail.com (K. Jandová).

pathogens, respectively (Stinson et al., 2006; Mangla et al. 2007). Native shrubs in the western USA declined in communities invaded by exotic annual grasses due to an unprecedented increase of fire frequency (Mack, 1989; D'Antonio and Vitousek, 1992).

The above examples document that plant invasions can initiate ecosystem changes with significant effects on invaded communities. Invasion-altered communities may feed back (Ehrenfeld et al., 2005; Seastedt and Pyšek, 2011; Yelenik and Levine, 2011) to further modify ecosystem characteristics and thus the performance of native but also of exotic populations. These feedbacks then determine long-term dynamics within invaded communities (Bever et al., 1997; Cuddington and Hastings, 2004). For example, positive feedbacks play a role in the success of the above-mentioned example of annual grass *Bromus tectorum* (D'Antonio and Vitousek, 1992). Although it originally invaded interstices of shrubs (approximately a century ago), increased fire frequency promoted its dominance that in turn led to more fires, at the expense of native shrubland (reviewed by D'Antonio and Vitousek, 1992). In contrast, invasion-triggered ecosystem changes can promote the dominance of invaders over a short-term period, but further modification of biotic or abiotic conditions can be less favorable for the invaders than for the resident species, making co-existence of the exotics and natives possible over the long-term course (Yelenik and Levine, 2011; Tang et al., 2012).

Surprisingly, although there is a large body of evidence revealing ecosystem and community impacts of invasive plants (e.g. Simberloff, 2011; Vilà et al., 2011), for most of these systems information on the temporal scale of the changes is missing (discussed by Wolfe and Klironomos, 2005; Ehrenfeld, 2010). There are few studies that document an invader's and native population dynamics, together with changes in ecosystem properties during different time points of invasion. For example, in the Great Lakes region, Mitchell et al. (2011) surveyed wetlands invaded by exotic cattails (*Typha* sp.) for different lengths of time. They found that cattail dominance (stem density) increased linearly from the beginning of the invasion, but there was a delay of 10 years before native diversity started to decline, likely due to litter accumulation.

It also remains underexplored whether the mechanisms promoting the dominance of invaders are identical with the mechanisms causing the native species to decline. Allison and Vitousek (2004) found faster decomposition and nutrient release from invasive than native litter in Hawaii. The authors hypothesize that novel soil nutrient conditions should favor exotics at the expense of natives that are less nutrient-limited. Levine et al. (2003) pointed out, however, that the decline of native species in Hawaiian ecosystem is not necessarily due to new dynamics of nitrogen cycling, but rather due to increased levels of shading in the presence of invaders. Usually many environmental factors change simultaneously during invasion and their relative contributions to community change should be distinguished; yet they are rarely examined in concert (Hulme et al., 2013).

In this study, we examined soil biological and chemical characteristics together with light availability at five uninvaded grassland sites that served as controls for 19 sites invaded by giant hogweed (*Heracleum mantegazzianum*) for different time periods ranging from 11 to 48 years in the Slavkovský les, the Czech Republic. In these same communities, native plant richness and native productivity was reduced by hogweed invasion and this negative impact peaked in grasslands invaded for ca. 30 years. At sites with a longer invasion history both parameters tended to recover whereas hogweed cover declined linearly over the whole period assessed. Interestingly, hogweed performance in a complementary common garden experiment declined in non-sterile inocula collected at sites with a longer invasion history (Dostál et al., 2013).

Here we analyzed the effect of hogweed invasion (i.e., presence/absence) and its invasion history (i.e., time since invasion) on 19 soil and light parameters: pH (water), pH (KCl), conductivity, extractable phosphorus, carbon, nitrogen, carbon/nitrogen ratio, relative amount of photosynthetically active radiation, red/far-red light ratio, arbuscular mycorrhizal neutral lipid fatty acids (NLFA), fungal phospholipid fatty acids (PLFA), bacterial PLFAs, actinobacterial PLFAs, G+ bacteria, G− bacteria, total microbial biomass, fungal/bacterial ratio, G−/G+ ratio and ergosterol concentration. We also analyzed the effect of the invasion and of its history on the composition of soil microbial communities based on 19 PLFAs and NLFA detected at each site. We expected a post-invasion increase in available nutrients coupled with changes in soil microbial communities, but decrease in light availability.

In the second part of the study we used a subset of eight parameters, uncorrelated to each other, selected from the above characteristics, to investigate how they predict variation in native species richness and productivity, and hogweed performance that were studied by Dostál et al. (2013). We hypothesized that variation in native species richness and productivity would be related to changes in nutrient and light availabilities, whereas variation in hogweed performance would be related to differences in composition of soil microbial communities, indicating the presence of possible soil pathogen(s) of hogweed.

2. Methods

2.1. Study species

The giant hogweed (*Heracleum mantegazzianum*) is a monocarpic perennial umbellifer native to the Western Greater Caucasus (Russia, Georgia). It has spread in a number of European countries (Tiley et al., 1996; Pyšek et al., 2007b, 2008), Canada (Page et al., 2006) and the USA (Kartesz and Meacham, 1999). It may form extensive, almost monospecific stands with negative effects on biodiversity (Pyšek and Pyšek, 1995; Pergl et al., 2006; Thiele and Otte, 2007; Hejda et al., 2009). The species is rich in secondary metabolites and especially known for linear fouranocoumarins that defend the plant against herbivory (Berenbaum, 1981; Hattendorf et al., 2007) and for angular fouranocoumarins that serve as a defence mechanism against microbial infection (Ivrie, 1978; Fischer et al., 1978). Hogweed invasiveness is also attributed to allelopathic effects (Myras and Junttila, 1981) but allelopathy is probably of minor importance for its dominance (Wille et al., 2013).

2.2. Study region

We performed our research in the Slavkovský les Protected Landscape Area, located in the western part of the Czech Republic, where the giant hogweed was introduced as a garden ornamental plant in the 19th century. The species started to spread after World War II, probably due to a lack of appropriate landscape management caused by displacement of German inhabitants and establishment of a military zone (Müllerová et al., 2005; Pyšek et al., 2007c).

Müllerová et al. (2005, 2013) reconstructed the hogweed invasion dynamics in this region using a series of aerial photographs and identified sites invaded (i) in 1962 or earlier, (ii) between 1963 and 1973, (iii) between 1974 and 1991, (iv) between 1992 and 2006, together with (v) uninvaded sites. Using this information we carried out field surveys in 2010 and included 24 sites from 5 areas differing in invasion history in this study (each community type was thus represented by 5(4) replicates; see Appendix 1). We estimated mean age of the hogweed stands at each site, yielding a chronosequence of invasive populations of a differing age, i.e. (i) a

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