



Tree seedling responses to multiple environmental stresses: Interactive effects of soil warming, nitrogen fertilization, and plant invasion



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ARTICLE INFO

Keywords:

Acer rubrum
Alliaria petiolata
 Arbuscular mycorrhizal fungi
 N enrichment
 Soil warming
 Phenology
 Vegetative growth

ABSTRACT

Temperate deciduous forest ecosystems in northeastern North America are under increasing biotic and abiotic stresses that can have interactive effects on understory vegetation, and thus impact the next generation of forest canopy trees. We examined seedling responses of the common and increasingly dominant species *Acer rubrum* (red maple) to the combined effects of soil warming (+5 °C), chronic nitrogen fertilization (+50 kg N ha⁻¹ yr⁻¹), and invasion by the phytotoxic plant *Alliaria petiolata* (garlic mustard), and their interactions. We planted 296 first-year *A. rubrum* seedlings in a multifactorial field experiment to examine the effects of all combinations of the experimental treatments. Second-year *Acer rubrum* seedlings demonstrated higher aboveground growth under soil warming conditions. Further, soil warming positively influenced plant-soil feedbacks through higher arbuscular mycorrhizal colonization in fine roots. However, the positive growth responses and mycorrhizal colonization observed under soil warming were moderated by both N fertilization and *A. petiolata* invasion. Our results highlight the importance of developing management plans that consider how multiple environmental change factors affect tree seedling performance, particularly via the plant-soil interface.

1. Introduction

Temperate forest ecosystems in northeastern North America are undergoing modification via multiple anthropogenically-driven environmental change factors, thus presenting challenges for adaptive forest management (Chmura et al., 2011). Ongoing abiotic changes include both warming temperatures and atmospheric nitrogen (N) deposition, with long-term models for the Northeast predicting air temperature increases up to 5.3 °C and patterns of regionally high reactive N deposition (Galloway et al., 2014; Hayhoe et al., 2007; IPCC, 2013). Atmospheric and concomitant soil warming can increase growth in some forest species, alter mycorrhizal community composition, and stimulate carbon (C) loss from soil (e.g. Butler et al., 2012; Fernandez et al., 2017; Melillo et al., 2011). Chronic soil N enrichment via atmospheric N deposition can enhance tree growth and suppress microbial activity and soil organic matter decomposition, leading to soil C accumulation and fundamental shifts in the fungal community (e.g. Butler et al., 2012; Frey et al., 2014; Morrison et al., 2016). Further, soil warming can lead to N enrichment through increases in net N mineralization and nitrification (Butler et al., 2012; Melillo et al., 2011). Biotic changes include invasions by non-native organisms that can alter

the structure, diversity, and function of native forest communities. Invasive species often exploit abiotic disturbances (MacDougall and Turkington, 2005), but abiotic conditions can also mediate the impacts and dynamics of biological invasions (Eisenhauer et al., 2014). Thus, temperate forests are in a state of flux due to ongoing perturbations to climate, biophysical factors, and the biotic environment: these biotic and abiotic stressors can then interact to have complex effects on individual plant species and communities (Tylianakis et al., 2008). Understanding these interacting stressors is thus critical for predicting how key forest species will perform under future, changing climates and how land managers can best respond with appropriate management practices.

The impacts of plant invasions on recipient ecosystems have been widely documented (e.g. reviewed by Levine et al., 2003; Vitousek et al., 1997) and include changes to native plant performance via competition, allelopathy, and alteration of plant-microbial interactions (e.g. Schmidt et al., 2008; Stinson et al., 2006; Yuan et al., 2013). A growing body of literature also suggests that these impacts may intensify as changes in the abiotic environment facilitate both the performance and spread of invasive organisms (e.g. Dukes et al., 2009; MacDougall and Turkington, 2005; Valliere and Allen, 2016). However,

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we still know very little about the interactive effects of invasion and ongoing abiotic stresses on the growth, survival, and plant-soil interactions of native plants.

Acer rubrum L. (red maple) is one of the most widely distributed eastern temperate tree species (Chapman and Bolen, 2015). Across much of its range, this species is increasingly dominating forests, mainly in response to anthropogenic changes such as fire suppression and land use changes, and by selective inhibition of competitors by deer browsing, defoliating insects and pathogens (Abrams, 1998). Seedlings are strongly responsive to temperature, with leaf phenology, photosynthetic rates, respiration and growth all acclimating rapidly to atmospheric as well as direct soil warming (Kaye and Wagner, 2014; Lee et al., 2005; Sendall et al., 2015; Wheeler et al., 2016). However, recent research has highlighted the need to consider the aggregate effects of multiple environmental drivers on tree seedlings and forest understory species (e.g. Fisichelli et al., 2014; Petrie et al., 2016), including *A. rubrum*. For example, *A. rubrum* and *A. saccharum* saplings demonstrate increased growth under climate warming, but deer browsing inhibits this positive growth response (Fisichelli et al., 2012), and disturbance to understory vegetation communities by invasive earthworms is mediated by environmental factors like soil pH and precipitation (Fisichelli et al., 2013). This highlights the need to consider both abiotic conditions and biological stressors acting in conjunction to influence species and community responses.

Alliaria petiolata (M. Bieb.) Caversa and Grande, family Brassicaceae, is a Eurasian, non-mycorrhizal herb that invades both disturbed and pristine hardwood forest understories in the United States and Canada (Nuzzo, 1999). Though widely studied for its ecology and impacts on native organisms (reviewed in Rogers et al. 2008), how this invasive plant interacts with abiotic stressors to affect native forest species remains largely unexplored. *Alliaria petiolata* inhibits mycorrhizal colonization in tree seedling roots of *A. rubrum* and other forest species via the release of antifungal glucosinolate phytochemicals through root exudates and decaying litter (Barto et al., 2011; Stinson et al., 2006). Despite the short half-life of these compounds in soils, the legacy of mycorrhizal community disruptions from *A. petiolata* invasions have been shown to persist in forest soils for years, even after eradication (Lankau et al., 2014). These critical soil fungi are also affected by abiotic changes such as soil warming (e.g. Mohan et al., 2014) and N deposition (e.g. Egerton-Warburton and Allen, 2000; Lilleskov et al., 2001; Morrison et al., 2016; van Diepen et al., 2011). However, despite extensive research on the impact of this common invasive on plant and soil communities, it remains poorly understood how *A. petiolata* may interact with abiotic environmental changes to impact plant-fungal interactions and subsequent tree seedling growth.

Our objectives in this study were to determine how soil warming, chronic N fertilization, and invasion by *A. petiolata* interact to affect the survival, phenology, growth, and AMF colonization of *A. rubrum* seedlings. As part of an ongoing long term global change experiment (Contosta et al., 2011), we use soil warming as a treatment, as opposed to elevated air temperature. Soil temperature may be more important at the tree seedling stage, since seedlings have low growth forms that may be more closely ecologically linked to ground-level microclimatic conditions (Körner, 2003). Further, previous work has shown *A. rubrum* first-year seedling growth responds strongly to soil warming (Wheeler et al., 2016). Although other studies have examined the effects of concurrent environmental changes on temperate forest species (e.g. Maes et al., 2014), to our knowledge this is the first study to examine the interaction between invasion and concurrent global abiotic stresses, and as such, provides new data for categorizing and planning for forest responses to ongoing environmental change.

2. Methods

2.1. Field site description

We established our experiment within a long-running global change manipulation: the Soil Warming and Nitrogen Addition (SWaN) Study at the Harvard Forest Long-Term Ecological Research (LTER) site in Petersham, Massachusetts, USA. The experimental site is situated in a mixed, even-aged hardwood forest stand characterized by red and striped maple (*Acer rubrum*, *A. pensylvanicum*), red and black oak (*Quercus rubra*, *Q. velutina*), American beech (*Fagus grandifolia*), white birch (*Betula papyrifera*), and American chestnut (*Castanea dentata*). Air temperatures at the experimental site range from -25 to 30 °C through the year, with an annual mean of 7 °C; total annual precipitation is approximately 1100 mm, including the water equivalent of winter snowfall (Contosta et al., 2015). *Alliaria petiolata* is present in nearby tracts of contiguous forest of the same composition, but has no history of invasion at this experimental site prior to our study.

2.2. Field experiment

The SWaN Study, established in 2006, is a fully factorial field experiment, with $24 \times 3 \times 3$ m plots randomly assigned one of four treatments with six replicates per treatment: control, N addition, warming, or warming \times N addition. Soils in all heated plots are continuously warmed to 5 °C above ambient using buried electrical cables. Nitrogen fertilization is applied to all N treated plots in equal monthly doses between May–October as an aqueous solution of NH_4NO_3 at a rate of $50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. Due to mechanical failure in one set of buried heating cables, we used a subset of 20 plots (5 replicates per treatment) for our study. Further details on the SWAN experimental setup can be found in Contosta et al. (2011). The N fertilization rate simulates the rate of atmospheric N deposition currently found in parts of Europe and Asia (Vet et al., 2014) and predicted for many parts of the world by 2050 (Galloway et al., 2008). The soil warming level reflects the upper end of predicted changes in temperature in the Northeast in the next century (IPCC, 2013).

In order to simulate forest invasion by *A. petiolata* and to test the effect of secondary phytochemicals, we established pairs of invaded and uninvaded 1×1 m subplots within each of the abiotic treatment plots at the SWAN experiment. At each experimental plot, we transplanted 32 overwintered *A. petiolata* rosettes from a nearby forest (< 5 km) into one randomly selected subplot (invaded subplot) in April 2015. Since *A. petiolata* is a biennial, we added first year *A. petiolata* seedlings periodically throughout the growing season and into autumn, to simulate typical invasion demography and maintain similar experimental densities. With a final planting of first-year rosettes in December, we maintained the *A. petiolata* invasion overwinter until May 2016. To avoid accidental invasion to non-experimental areas, plants were removed prior to reproduction in May 2016. In addition to live plants, we added *A. petiolata* leaf litter periodically to all invaded plots through the summer to ensure consistent inputs of glucosinolates. Thus, the total experimental invasion treatment occurred over a period of twelve months, simulating the effects of a recent invasion followed by eradication. Uninvaded plots were disturbed with trowels to simulate the disturbance that occurred in the invaded plots, but these plots were not experimentally invaded with *A. petiolata* plants nor was litter added.

In October 2015, we transplanted 7–8 first-year *A. rubrum* seedlings into each uninvaded and invaded subplot within each abiotic (warmed or N amended) treatment for a total of $N = 296$ seedlings. Seeds were sourced from local Massachusetts genotypes and grown for one growing season by a local nursery (New England Wetland Plants, Amherst, MA). Prior to transplanting in October, we tagged plants by treatment and measured initial stem height (from root collar to tallest terminal bud) to ensure that initial seedling height was similar across all treatments. We also trimmed roots for each seedling down to a 7-cm diameter root ball

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