Forest Ecology and Management 411 (2018) 158–165

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Experimental drought and plant invasion additively suppress primary pine species of southeastern US forests

Julienne E. NeSmith[a,*], Christina Alba[b], S. Luke Flory[b]

[a] School of Natural Resources and Environment, University of Florida, Gainesville, FL 32611, United States
[b] Agronomy Department, University of Florida, Gainesville, FL 32611, United States

ARTICLE INFO

Keywords:
Climate change
Cogongrass
Invasive species
Multiple stressors
Slash pine
Loblolly pine

ABSTRACT

Climate change and non-native invasive species are two predominant drivers of global environmental change, yet little is known about how they might interact to affect native communities and ecosystems. Drought and plant invasions are intensifying in ecosystems worldwide, including ecologically and economically important pine forests of the southeastern United States. These stressors can alter resource availability and plant competition outcomes, and may together exert additive, synergistic, or offsetting effects on native species, but such outcomes are difficult to predict. We used a factorial common garden experiment to determine how simulated drought, invasion by *Imperata cylindrica* (cogongrass), and their interaction affected seedling survival and performance (relative growth rates of height and diameter, and biomass) of two native pine species, *Pinus elliottii* var. *densa* (South Florida slash pine) and *Pinus taeda* (loblolly pine). In general, loblolly pine outperformed slash pine over the course of the experiment, but the directions and magnitudes of each species' responses to the treatments were similar, with the two stressors often exhibiting additive negative effects on pine seedling performance. For both species, invasion significantly suppressed seedling survival, drought reduced relative growth rates in height, and drought and invasion had an additive negative effect on diameter compared to ambient conditions with resident plant communities. The suppressive effects of drought on these primary pine species suggests that increasing drought in the region could scale up to affect forest stand dynamics. Furthermore, the experimental demonstration of cogongrass impacts on pine seedling survival and performance should further motivate land owners and property managers to remove this noxious invasive species. To predict the long-term outcome of drought and invasion on forest stands, and more broadly on vegetation dynamics in ecosystems affected by these global change agents, additional evaluations of their separate and interactive effects are needed. Nonetheless, these results experimentally demonstrate that stress from experimental drought combined with competition from an aggressive grass invader can significantly suppress seedlings of primary pine species of southeastern US forests.

1. Introduction

Climatic change, including shifts in temperature and precipitation regimes, is creating novel abiotic conditions that can alter the structure and function of ecological communities. In particular, the extent and severity of drought is intensifying in many ecosystems worldwide due to climate change (Easterling et al., 2000; Hoerling and Kumar, 2004; IPCC, 2001), resulting in native species mortality (Breshears et al., 2005; Thomas et al., 2004; Vose et al., 2012) and displacement (Lenoir et al., 2008). Non-native invasive plant species also are threatening native ecosystem integrity (Vitousek et al., 1996) by competing with native plant species for limiting resources such as nutrients, light, and water (Wilcove et al., 1998), which can have cascading effects, for example, by modifying wildlife habitat conditions (e.g., food sources and availability; Vose et al., 2012). Native and invasive species likely will interact in new ways as novel abiotic conditions caused by climate change, and drought specifically, shift species ranges (Hoffman and Parsons, 1997; Pounds et al., 1999; Woodward, 1987) and transform plant community dynamics by opening niches (Walther et al., 2002) and altering habitat suitability. Although drought and invasive species are primary abiotic and biotic stressors, respectively, little is known about how they might interact to affect native ecosystems.

There are three scenarios for how multiple global change stressors may interact to affect native ecosystems. Drought and invasion may exert negative effects that manifest additively such that the combination of stressors is equal to the sum of each acting independently

* Corresponding author.
E-mail address: julesn@ufl.edu (J.E. NeSmith).

https://doi.org/10.1016/j.foreco.2017.12.045
Received 31 July 2017; Received in revised form 23 December 2017; Accepted 23 December 2017

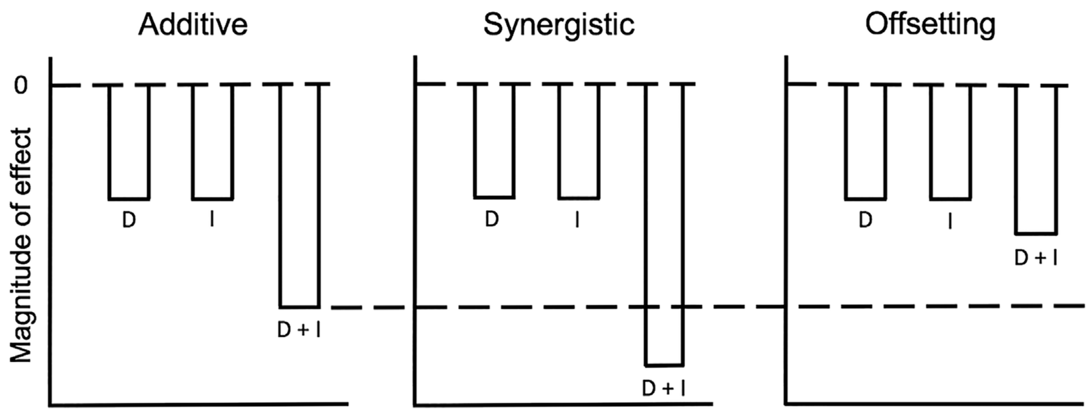

Fig. 1. Conceptual diagram illustrating three potential scenarios for the magnitude of independent (additive) or interactive (synergistic and offsetting) negative effects as a result of multiple stressors acting on ecological communities. Here, "D" represents drought and "I" represents invasion by a non-native species. The lower dashed line provides a reference point for the additive effects scenario.

(Breitburg and Riedel, 2005; Folt et al., 1999). Alternatively, two stressors may have synergistic interactive effects, whereby together they yield stronger negative effects than would be predicted based on each stressor acting in isolation. Finally, one stressor may act antagonistically with another and offset the effects of the other stressor, resulting in less negative impacts than would be expected compared to the additive scenario (Fig. 1). For example, a plant invader with a dense canopy may, under drought conditions, compete strongly against native species for both light and limited soil water, leading to synergistic negative effects. Alternatively, the dense invasion might offset drought stress by lowering ground-surface temperatures and air flow, thereby reducing evapotranspiration. Given the increasing severity and extent of both drought and plant invasions, the lack of quantitative studies investigating interactions between abiotic and biotic stressors (Todgham and Stillman, 2013) and the unpredictable nature of such interactions represent a critical knowledge gap.

Drought and plant invasions are intensifying in forests worldwide, including ecologically and economically important pine forests of the southeastern United States (Simberloff et al., 1997; Wang et al., 2010). Drought stress can degrade forest health and resistance to stressors such as fire, pathogens, insects, and plant invasions (Dale and Joyce, 2001; Vose et al., 2012), particularly in regions marked by high temperatures and long growing seasons (Aber et al., 2001). Both natural and planted coastal plain forests in the southeastern US are largely dominated by natural or improved varieties of *Pinus elliottii* (slash pine) and *Pinus taeda* (loblolly pine) forests. Because slash and loblolly pine forests have largely replaced *Pinus palustris* (longleaf pine) across its historic range, they represent important ecological refuges (Bremer and Farley, 2010; Gilman and Watson, 2006) and act as a major carbon sink in the US (Alavalapati et al., 2007; Turner et al., 1995). Furthermore, the economic importance of managed forests in the southeastern US is unrivaled as they supply 62% of the timber harvested in the U.S. (Smith et al., 2009) and 16% of global industrial wood, and the region produces more timber than any one country (Prestemon and Abt, 2002; Wear and Gries, 2002). Southeastern US forests are increasingly invaded by non-native plant species, including *Imperata cylindrica* (cogongrass), a perennial C4 grass native to Asia that can inhibit pine establishment (Daneshgar et al., 2008) and now covers hundreds of thousands of hectares across the region (Estrada and Flory, 2015; Schmitz and Brown, 1994). Cogongrass thrives in a wide range of soil conditions (MacDonald, 2004), is reportedly drought and fire tolerant (Bryson et al., 2010; Patterson, 1980), and strongly competes with native species for water and nutrients (Estrada and Flory, 2015; Kuusipalo et al., 1995; MacDonald, 2004). Thus, we hypothesized that drought, in combination with cogongrass invasion would have additive or synergistic negative effects on the survival and performance of pine seedlings.

We evaluated the independent and interactive effects of drought (simulated with rainout shelters) and invasion (by cogongrass) on slash and loblolly pine seedling survival and performance using a factorial common garden experiment. Across the drought and invasion treatments, we measured pine seedling survival, biomass, and relative growth rate, as well as abiotic conditions that might shape plant competitive outcomes, including soil moisture and light availability. Our results demonstrate that both drought and invasion significantly suppress the survival and performance of these ecologically and economically important pine species, and together these two stressors have the potential to dramatically alter southeastern US forests.

2. Materials and methods

2.1. Study species

Slash and loblolly pine occur naturally or are planted across tens of millions of hectares in the southeastern US and comprise more than half of the region's standing pine volume (Baker and Langdon, 1990). They provide critical habitat for wildlife and generate billions of dollars in revenue for regional economies each year (Nowak, 2015). Slash pine is moderately to highly drought tolerant relative to other pine species (Burns and Honkala, 1990; Gilman and Watson, 2006) and can grow across a range of soil conditions from seasonally dry to wet soils near streams and swamps, and in hammocks and mesic flatwoods (Ewel and Myers, 1990). Loblolly pine has low to moderate drought tolerance (Burns and Honkala 1990; Gilman and Watson, 2006) and predominantly occurs in poorly drained soils in mesic forests, floodplains, and hydric hammocks (Ewel and Myers, 1990). Both species have low to moderate shade tolerance and exhibit poor establishment under competition (Burns and Honkala, 1990; Gilman and Watson, 2006). *Pinus elliottii* var. *elliottii* is the most common and widely distributed *P. elliottii* variety, occurring across the southeastern coastal plain from Louisiana to South Carolina, and south to Central Florida (USDA NRCS, 2016). South Florida slash pine (*Pinus elliottii* var. *densa*) is endemic to Central and South Florida, and unlike *P. elliottii* var. *elliottii*, has a distinct grass seedling stage (Fowells, 1965). The two varieties hybridize naturally where their ranges overlap and produce offspring that are indistinguishable from either variety (Lohrey and Kossuth, 1990).

Cogongrass is one of the most prolific and aggressive plant invaders in the southeastern United States. It spreads vegetatively throughout the region via rhizomes but purportedly produces viable seed primarily outside of Florida (MacDonald, 2004; MacDonald, Personal communication). Cogongrass establishment and spread are facilitated by natural and anthropogenic disturbances including fire, timber harvests, mowing, and tilling (Holzmueller and Jose, 2012; Lippincott, 2000). Cogongrass is threatening in part, because it is highly flammable and