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Elevated light levels reduce hemlock woolly adelgid infestation and improve carbon balance of infested eastern hemlock seedlings

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ABSTRACT

The rapid loss of eastern hemlock (*Tsuga canadensis*) due to infestation with hemlock woolly adelgid (*Adelges tsugae*, HWA) has greatly altered structure and function of eastern forests. Numerous control strategies including local pesticide use and biocontrol with predator beetles have been implemented with considerable cost and varying success. Silviculture treatments that increase incident light on surviving hemlock trees to reduce infestation and ameliorate carbon starvation have been proposed as another possible conservation strategy, yet no controlled studies have evaluated the coupled plant-insect responses to increased light. We conducted a nursery experiment on artificially infested eastern hemlock seedlings under varying levels of ambient light, ranging from 0 to 90% shade. We measured HWA infestation (ovisac density), short- and long-term indicators of carbon balance (leaf chlorophyll fluorescence, net photosynthesis, total nonstructural carbohydrate content, and shoot growth), and nutrition (leaf N content). We hypothesized that higher light would result in reduced HWA densities, higher C assimilation rates, and improved tissue non-structural carbohydrate balance; and these effects would ameliorate the effects of infestation on C balance and lead to improved seedling growth. HWA density decreased with increasing light, and was highest in the 90% shade treatments. However, photosystem II efficiency and net assimilation were also lower under the higher light treatment. Despite tradeoffs between reduced infestation and reduced leaf function from higher light, and little variation in sugar content among treatments, both leaf and root starch content and seedling growth were higher under the higher light treatment. Increasing light levels improves long-term carbon balance for hemlock seedlings in the presence of HWA. Although hemlock typically occurs in deeply shaded forests, our results suggest that silvicultural treatments such as forest thinning that increase light exposure may reduce HWA abundance and lead to better tree C balance, and may be an effective component of large-scale conservation and restoration strategies.

1. Introduction

Invasive species can have substantial impacts on ecosystem structure and function, particularly when foundation species are affected (Ellison et al., 2005; Lovett et al., 2006, 2016). Several recent examples of invasive pests and pathogens in forests demonstrate the effects of defoliation and/or tree mortality on stand structure, community composition, productivity, evapotranspiration, and nitrogen cycling (Lovett et al., 2010; McManamay et al., 2011; Flower et al., 2013; Brantley et al., 2013). One of the most severe recent invasive pest outbreaks affects eastern hemlock (*Tsuga canadensis* (L.) Carr.), a foundation species in forests of eastern North America (Ellison et al., 2005; Orwig et al., 2012). The natural range of eastern hemlock extends from northern Georgia and Alabama to southern Canada and westward into the central Great Lakes states (McWilliams and Schmidt, 2000). At present, eastern hemlock trees of all ages and sizes in the eastern and southernmost portion of the range are declining and dying as a result of attack by, and their susceptibility to, the hemlock woolly adelgid (HWA, *Adelges tsugae* Annand) (Orwig et al., 2002; Ford et al., 2012). Decline is progressive and mortality can occur within four years of infestation (Orwig et al., 2002; Ford et al.,

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2012). Morbidity and mortality of hemlock has affected riparian forest and stream ecosystem function (Ellison et al., 2005; Ford and Vose, 2007; Ford et al., 2012; Orwig et al., 2012; Webster et al., 2012; Brantley et al., 2013, 2015), demonstrating a need for effective mitigation and restoration strategies that can be implemented quickly and at large scales.

A wide variety of management strategies are being developed and implemented to reduce the impacts of HWA on eastern hemlock, including chemical control (Cowles et al., 2006), biological control (Onken and Reardon, 2011), host gene conservation (Jetton et al., 2013), and enhancement of host resistance (Montgomery et al., 2009). Although chemical control has been used with great success to temporarily protect individual trees, financial costs, logistical constraints of manually treating large areas, and environmental constraints greatly limit its use as a sustainable strategy for protecting natural stands (Vose et al., 2013). Biological control shows some promise as several released predatory species are successfully establishing in eastern forests (Mausel et al., 2010; Hakeem et al., 2013; Vose et al., 2013; Mayfield et al., 2015; Zietlow, unpublished data); but the time required for widespread predator proliferation and dispersal, and timing predator release effectively for outbreak species such as HWA, may limit the effectiveness of biological control as a standalone strategy. Coupling these control strategies with forest management practices that improve tree host resistance and increase stand resilience (*sensu* Holling, 1973) may provide a long-term management solution, but direct evidence supporting the efficacy of such treatments is scant.

One possible strategy to reduce the effects of HWA in infested hemlock stands is to increase light availability for surviving eastern hemlock trees through silvicultural treatments such as thinning or selective harvests (Fajvan, 2008). Eastern hemlock is one of the most shade-tolerant tree species in eastern North America and can survive in environments where as much as 99% of incident sunlight is intercepted by the canopy (Bourdeau and Laverick, 1958; Hadley, 2000). However, growth in such environments is slow and individual trees may not reach full height unless openings in the canopy allow enough light into the understory for trees to grow more rapidly (Bourdeau and Laverick, 1958; Spurr and Barnes, 1980; Brissette and Kenefic, 2000). For example, in a long-term study in Maine, eastern hemlock recruitment, regeneration, and growth all responded positively to selective harvesting that created large canopy openings (Brissette and Kenefic, 2000). Increases in ambient light from silvicultural treatments may similarly improve survival and growth of infested hemlock trees by increasing ambient light availability for improved photosynthate production for physiological maintenance, growth, reproduction, and/or defense.

Although the exact mechanism of mortality in eastern hemlock from HWA is still unknown, HWA has been shown to both induce water stress and negatively affect tree C balance (Gomez et al., 2012; Domec et al., 2013; Gonda-King et al., 2014). The hypothesized mechanism with the most observational support is one involving C starvation (McClure, 1991; Young et al., 1995; Broeckling and Salom, 2003; Domec et al., 2013; Gonda-King et al., 2014). As eastern hemlock trees are infested, HWA crawlers (mobile, first instar nymphs) settle at the base of leaves (needles) and insert their stylets into xylem ray parenchyma cells (Young et al., 1995). After insertion, nymphs become sessile and feed on carbohydrates in the xylem ray parenchyma cells until maturity (McClure, 1989). In addition to direct carbohydrate extraction, hydraulic changes from infestation include result in reduced stomatal conductance. This reduction may be due to physical injury from stylet insertion or from chemical cues in response to the infestation (Radville et al., 2011; Gonda-King et al., 2014). Reduced photosynthesis resulting from these hydraulic changes leads to loss of leaves, further depletion of carbohydrates, and subsequent lack of new shoot growth. Thus, the C starvation hypothesis suggests that these feeding nymphs negatively affect whole-tree C balance both directly, through photosynthate extraction, and indirectly through a series of structural and physiological changes that alter hydraulic function of the tree (Domec et al., 2013; Gonda-King et al., 2014). Creating artificial canopy openings to increase light exposure might improve C balance in infested hemlock by both reducing infestation and reducing light limitation for photosynthesis, thus mitigating the effects of carbohydrate extraction and leaf loss, and reducing the risk of C starvation from HWA infestation.

Increased light may also benefit infested eastern hemlock trees indirectly by reducing HWA infestation severity. Several studies suggest that increased light and temperature can reduce HWA densities (Sussky and Elkinton, 2015; Mayfield and Jetton, 2013; Hickin and Preisser, 2015; Mech, 2015) which benefits eastern hemlock by reducing stored carbon extraction at the leaf base. In prior artificial infestation studies using potted seedlings, HWA adult densities increased with increasing shade (Mayfield and Jetton, 2013), and HWA settlement was higher on second year growth under high- compared to low- shade treatments (Hickin and Preisser, 2015); however, these studies did not address a full range of possible light conditions and did not assess concurrent physiological responses on seedlings. Temperature extremes related to increased exposure from more open canopies may also affect HWA survival. For example, extreme heat events, characterized by abnormally high maximum air temperatures over several days to several weeks negatively affect HWA survival (Sussky and Elkinton, 2015; Mech, 2015). Extreme cold (*e.g.* <−30 °C) has also been shown to reduce HWA populations (Parker et al., 1998, 1999; Skinner et al., 2003). Data across the eastern US in a cold event when temperatures ranged from −16 to −31 °C, showed HWA mortality ranging from 17 to 100% (McAvoy et al., 2014); however, the progrediens generation was recovered at all sites the following spring, indicating HWA populations can recover from extreme cold events (McAvoy et al., 2014).

To examine the effects of light environment on HWA infestation, and hemlock C balance in the presence of HWA, we measured HWA density and several key indicators of C balance following artificial infestation of hemlock seedlings under shade treatments from 0% (full sunlight) to 90% shade over one year. We assessed short-term, semi-integrated measures of leaf physiological function and stress, as well as long-term integrated measures of C balance. Specifically, we measured leaf-level gas exchange and chlorophyll fluorescence; total nonstructural carbohydrates (TNC) (soluble sugar and starch) in leaves, stems, and roots; and seedling growth parameters including diameter and height increment, and shoot growth of infested seedlings. These data will help answer three questions related to environmental effects on the plant-insect system and physiological mechanisms of plant mortality: (1) is HWA infestation affected by ambient light levels?, (2) how do short- and long-term indicators of plant C balance respond to light treatment in the presence of HWA? and (3) how does overall seedling growth respond to light in the presence of HWA? We predicted that increased light would improve plant C balance indirectly by reducing HWA infestation levels, and directly by promoting plant C fixation and storage thus reducing mortality risk from C starvation. Results from this study will contribute to our understanding of the mechanisms of hemlock mortality and may suggest strategies for implementation of large scale silvicultural practices that will contribute to hemlock conservation.