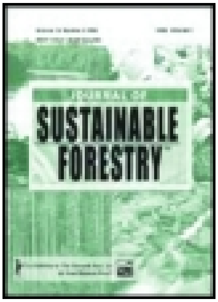

Journal of Sustainable Forestry
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/wjsf20

Growth and Infestation by Hemlock Woolly Adelgid of Two Exotic Hemlock Species in a New England Forest

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Version of record first published: 08 Sep 2008.

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Alexander M. Evans

ABSTRACT. The hemlock woolly adelgid (HWA, *Adelges tsugae* Annand) an invasive exotic insect, may extirpate eastern hemlock (*Tsuga canadensis* (L.) Carrière) trees from native forests, but other hemlock species could be planted to occupy their ecological niche. This study tests two of the most likely replacement species candidates: western hemlock (*T. heterophylla* (Raf.) Sargent) and Chinese hemlock (*T. chinensis* (Franchet) Pritzel). Low survival rates, slow growth, and infestation by HWA of western hemlock in eastern hemlock forests shows that the western hemlock is not a likely candidate for planting in the northern portion of eastern hemlock's range. In contrast, Chinese hemlock grew at rates similar to eastern hemlock and did not show any signs of HWA infestation. In this study, damage from deer was a much bigger problem than growth reductions from HWA.

KEYWORDS. *Tsuga chinensis*, Chinese hemlock, *Tsuga heterophylla*, western hemlock, enrichment planting, restoration

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The author is grateful to Drs. Ashton, Finkral, Gregoire, and Berlyn for many useful comments and to the Yale School Forests for research support.

Journal of Sustainable Forestry, Vol. 26(3) 2008
Available online at http://jsf.haworthpress.com

doi:10.1080/10549810701879735

INTRODUCTION

Forests of eastern northern America are under increasing stress from invasive species, climate change, and fragmentation. Introduced alien invasive insects have removed dominant species, reduced diversity, altered disturbance regimes, and affected ecosystem function (Liebhold et al., 1995; Mack et al., 2000). The danger exotic insects pose to native ecosystems is increasing with forest fragmentation (Murphy, 2005), the growth of foreign trade (Work et al., 2005), global climate change (Simberloff, 2000), and the presence of other alien species (Simberloff and Von Holle, 1999).

As exogenous factors threaten to impoverish forested ecosystems, forest managers need tools to maintain forest values including timber production, wildlife habitat, and aesthetics. One of those tools is enrichment planting (Waring and O'Hara, 2005). Enrichment planting is a common approach for restoring complex forest mixtures after logging, particularly in the tropics (Ramos and del Amo, 1992; Schulze et al., 1994; Maas-Hebner et al., 2005). Enrichment planting can also reintroduce tree species that have been removed from the ecosystem, such as American chestnut (*Castanea dentata* Mash.) (Tindall et al.,2004; McCament and McCarthy, 2005).

The hemlock woolly adelgid (*Adelges tsugae* Annand) is an excellent example of alien invasive species' threat to ecosystem integrity. The hemlock woolly adelgid (HWA) threatens to kill all eastern hemlock trees (*Tsuga canadensis* (L.) Carrière), a species that provides wildlife habitat, supplies timber, moderates climate, and is a component of many old growth forests in eastern North America. This paper explores the potential for planting other hemlock species to recapture some of the forest values that may be lost if the eastern hemlock is removed from northeastern forests. Experimental plantings of western (*T. heterophylla* (Raf.) Sargent) and Chinese hemlock (*T. chinensis* (Franchet) Pritzel) in an eastern hemlock forest provide a comparison of the probability of infestation among species. In addition, data on the survival and growth of exotic hemlock species in eastern hemlock forests will assist with restoration strategies, should they become necessary.

Eastern Hemlock

The eastern hemlock's native range runs from the southern Appalachian Mountains in Georgia to New Brunswick, Canada and as far west as northern Minnesota. Within its range, hemlock is a common species (e.g., Alerich, 2002a,b, Smith et al., 2004). Hemlock is an extremely shade tolerant and long lived species that can persist in the understory of closed canopy forest for decades, although in more open conditions hemlock can grow quite rapidly (Marshall, 1927; Godman and Lancaster, 1990). Hemlock is one of the few conifers in many northeastern forests and its presence can provide an addition to structural diversity (Beatty, 1984). HWA induced hemlock mortality affects wildlife (Ross et al. 2002, Tingley et al., 2002), nutrient cycling (Jenkins et al., 1999; Yorks et al., 2003; Stadler et al., 2005; Cobb et al., 2006), and allows other alien species to invade the released growing space (Orwig and Foster, 1998, Small et al., 2005). Hardwoods, particularly black birch (*Betula lenta* L.), naturally regenerates under thinning or dying hemlock stands (Orwig and Foster, 1998). However hardwoods create very different forest environments than the hemlock they replace. HWA challenges managers to preserve forest values in the face of the potential loss of eastern hemlock from the ecosystem.

Hemlock is either present as advanced regeneration at stand initiation or enters the stand as seed below an established canopy (Godman and Lancaster, 1990; Smith and Ashton, 1993; Liptzin and Ashton, 1999). Hemlock seedlings require some shade for initial establishment and survive well for a long time even under a dense canopy. Seedlings require only 5% full sun and trees can survive in suppressed conditions for up to 400 years (Godman and Lancaster, 1990). The slow growth of hemlock subjects them to suppression below young, fast growing hardwoods unless they are 3 meters (m) tall or more at stand initiation (Kelty, 1986). Hemlock and hardwood overstory trees compete very little. The presence of a hemlock understory does not reduce canopy tree growth and hemlock biomass is an addition to overall productivity (Kelty, 1989). Even in small gaps with lower light hemlock must be free of competition from hardwoods to reach the canopy (Hibbs, 1982). Since it grows so slowly, hemlock uses a patient strategy to reach the canopy in the mixed forests in which it is often found.

Enrichment Planting to Replace Eastern Hemlock After HWA Mortality

If HWA is not controlled, enrichment planting or restoration may be necessary to preserve some of the values eastern hemlock provides. In northern areas, balsam fir (*Abies balsamea* (L.) Mill.) and red spruce

(*Picea rubens* Sarg.) are planting possibilities. They are similar to hemlock in that both species are shade tolerant and maintain dense canopies (Ward et al., 2004). The ranges of balsam fir and red spruce do not extend far enough south to cover the full range of eastern hemlock, especially as the climate warms. Two potential replacement species in the southern portion of hemlock range are white pine (*Pinus strobus* L.) or Atlantic white cedar (*Chamaecyparis thyoides* (L.) B.S.P.) (Ward et al., 2004). White pine is structurally and functionally very different from hemlock. For example, it is a shade intolerant species that would require very different planting conditions than hemlock. Atlantic white cedar is restricted to wet sites and could not cover the ecological breadth that eastern hemlock does.

The grim predictions for the survival of eastern hemlock in natural stands have motivated investigation of exotic hemlock species to replace dead eastern hemlock (McClure, 1995; Bentz et al., 2002; Orwig and Kittredge, 2005). There are eight species of hemlock worldwide, six of which are not native to eastern North America and may be more resistant to HWA. *T. caroliniana* Engelmann shares the southern portion of the range of *T. canadensis*, but is at least as susceptible to HWA as eastern hemlock. The western species, *T. heterophylla* and *T. mertensiana* (Bong.) Carr., are divided along elevation gradients. Although *T. mertensiana* is more cold hardy than many provenances of *T. heterophylla*, it grows more slowly during the early part of its life (Means, 1990; Packee, 1990). The HWA exists at low levels in western forests of western north American and does not appear to cause mortality in *T. heterophylla* and *T. mertensiana* growing there (Havill et al., 2006). Japan has two species of *Tsuga*: *T. diversifolia* (Maximowicz) Masters and *T. sieboldii* Carrière. *T. diversifolia* is found in the north of the central island of Japan, Honshu, while *T. sieboldii* is found in southern Japan (Jisaburo, 1965). China has at least two species of *Tsuga*: Chinese hemlock, *T. chinensis*, and Himalayan hemlock, *T. dumosa* (D. Don) Eichler (Swartley, 1984; Farjon, 1990; Zhengyi and Raven, 1999). Observations suggest that when grown in North America some *T. sieboldii* and *T. diversifolia*, but not *T. chinensis*, have maintained HWA populations (Bentz et al., 2002).

One of the limitations of enrichment planting of exotic species over a large area is the availability of planting stock. Currently, the two exotic hemlock species most readily available are *T. heterophylla* and *T. chinensis*. Much of *T. chinensis*'s range falls in United States Department of Agriculture (USDA) plant hardiness zone 7 and 8, equivalent to the southern half of eastern hemlock's range (Farjon, 1990; Widrlechner, 1997; Zhengyi and Raven, 1999). Chinese hemlocks planted in an arboretum setting in southern New England have grown well (Del Tredici and Kitajima, 2004). Much of the range of *T. heterophylla* has milder growing conditions than found in eastern forests, but some interior provenances are more cold hardy (National Arboretum, 1990; Packee, 1990).

OBJECTIVES

The main objective of this study was to test the suitability of the two best-matched and readily available exotic *Tsuga* species in eastern northern American forests. Experiments were designed to test for differences in HWA infestation between species when they are planted in the same forest stand. A related goal was to compare the relative growth rate of species with lower populations of HWA because of greater resistance to that of eastern hemlock. In addition, four years of survival and growth data for native and exotic hemlock species in eastern hemlock forests will assist restoration planting, should it become necessary.

STUDY AREA

Experiments for this study were conducted at Yale Myers Forest (www.yale.edu/schoolforest). Yale Myers covers 3,172 ha in northeastern Connecticut at (N42°, W72.1°). The forest is set on rocky terrain cut by a number of parallel, small ridges that run from southwest to northeast. The elevation varies from 190 m to 330 m and slopes rarely exceed 40%. The last glaciation covered the metamorphic bedrock with glacial till soils, which are moderate to well drained sandy loams. The local climate is cool and humid with precipitation distributed throughout the year. The mean July high is 26.4°C, the mean January low is –8.2°C, and median annual precipitation is 130 cm (National Climatic Data Center, 2004). The forest is a mix of hardwood, pine, and hemlock that grew up after the area had been cleared for agriculture in the late 19th century. Experimental planting sites were hemlock stands or had a major hemlock component (Table 1). Many of these hemlock stands were woodlots during the agricultural period of the late 19th century. Woodlots were areas unfit for pasture or grazing because of wetness, steepness, or large rocks.

TABLE 1. Planting site characteristics

Experiment	Stand type	Basal Area (m^2ha^{-1})	Hemlock basal area (%)	Soil type	Aspect	Slope (%)
Experiments 2 and 3	Hemlock	34	60	Charlton-Chatfield complex	N	5
Experiments 2 and 3	Hardwood hemlock	28	40	Charlton-Chatfield complex	W	10
Experiments 2 and 3	Hardwood hemlock	28	40	Charlton-Chatfield complex	W	15
Experiments 2 and 3	Hemlock	32	60	Paxton and Montauk soils	W	15
Experiment 4	Hemlock	30	50	Charlton-Chatfield complex	SW	15
Experiment 4	Hardwood hemlock pine	34	60	Hinckley gravelly sandy loam	SW	5
Experiment 4	Hemlock	28	60	Charlton-Chatfield complex	N	5

METHODS

This study used planted seedlings in order to control for the age, health, and length of infestation. Planting healthy, uninfested seedlings in a forest with HWA permitted study of the probability of infestation and growth differences between species of *Tsuga*. I established four separate experiments. Experiment 1 was a comparison of growth between infested and uninfested seedlings of two species, eastern and western hemlock. The experiment started in 2002 when I randomly assigned 72 eastern hemlock seedlings and 72 western hemlock seedlings to 24 different 1 m^3 exclosures. I randomly selected 12 of the 24 exclosures to be infested with HWA after the first year. The seedlings were ~13 cm high, two-year-old plugs from Western Maine Nurseries (Fryeburg, ME, www. wmnurseries.com). The western hemlock seedlings were an interior British Columbian provenance and the eastern were a southern Maine provenance. The exclosures were raised cages with a fine mesh netting to protect from HWA. Previous studies of HWA have used fine mesh bags as HWA exclosures (Cheah and McClure, 2002; Montgomery et al., 2002). Each seedling was planted in an 18 cm pot. During the winter, I insulated the pots with household fiberglass insulation to reduce the impact of cold winter temperatures. This experiment was terminated after one year.

Experiment 2 began in 2002 and compared seedling infestation rates and growth of eastern and western hemlock for four growing seasons. Experiment 2 used the same seedlings from Western Maine Nurseries as in Experiment 1. They were planted in natural forest stands and monitored for four growing seasons. I planted 11 seedlings of each species on four sites with overstories composed of either thinned hemlock or a mix of hardwood and hemlock (Table 1). In both cases, the presence of naturally established hemlock seedlings demonstrated that sufficient light was available in the understory for hemlock growth. The planting sites and seedling ages are similar to those used in a study of enrichment planting of western hemlock in the Oregon coast range (Maas-Hebner et al., 2005). Four seedlings of each species were planted in white tailed deer (*Odocoileus virginianus* Boddaert) exclosures (1.2 m high metal fences ~1.5 m in diameter) because of the high rate of deer browse on hemlock (Kittredge and Ashton, 1995). The deer exclosures were approximately 33 m apart. There were four sites, with four exclosures at each site. For each species at each site, there was one seedling in each exclosure, for a total of four protected seedlings and seven unprotected seedlings. Thus, for Experiment 2, there were 16 protected and 28 unprotected seedlings of each species.

Experiment 3 compared Chinese and western hemlock growth. The experiment also began in 2002 with Chinese and western hemlock saplings grown by the Morris Arboretum (Philadelphia, PA). At time of planting, the seedlings were nine years old and ~1 m in height. The Chinese saplings were from the same set used in the Arnold Arboretum experimental planting described by Del Tredici and Kitajima (2004). I planted one randomly selected sapling of each species in the same 16 deer exclosures used in Experiment 2. Experiment 3 included four protect saplings at four sites for a total of 16 seedlings of each species. I monitored growth as well as HWA and scale infestations for four growing seasons.

Experiment 4 was comparison of seedling infestation rates across stands as well as growth of eastern and western hemlock begun in 2003. For Experiment 4, I used 60 seedlings of each species from Lawyer Nursery (Plains, MT, www.lawyernursery.com). The western hemlock came from seed collected in western Montana and northern Idaho while the source for the eastern hemlock was in Pennsylvania. The seedlings were ~50 cm high, 3–0 bare root stock. I planted 20 randomly chosen seedlings from each species, in each of three stands at Yale Myers Forest for a total of 60 seedlings of each species. The seedlings were protected from deer by 2.4 m high, wide mesh fencing surrounding the plantings. I monitored growth and counted HWA on infested seedlings for three growing seasons.

Analysis

In order to test for differences in growth rates between species, I calculated relative growth rate (RGR) (Fisher 1921) for height as:

$$\frac{\log_{(\text{height October 2006})} - \log_{(\text{height time 0})}}{\text{number of growing seasons}}$$

and RGR for root collar area as:

$$\frac{\log_{(\text{root collar area October 2006})} - \log_{(\text{root collar area time 0})}}{\text{the number of growing seasons}}$$

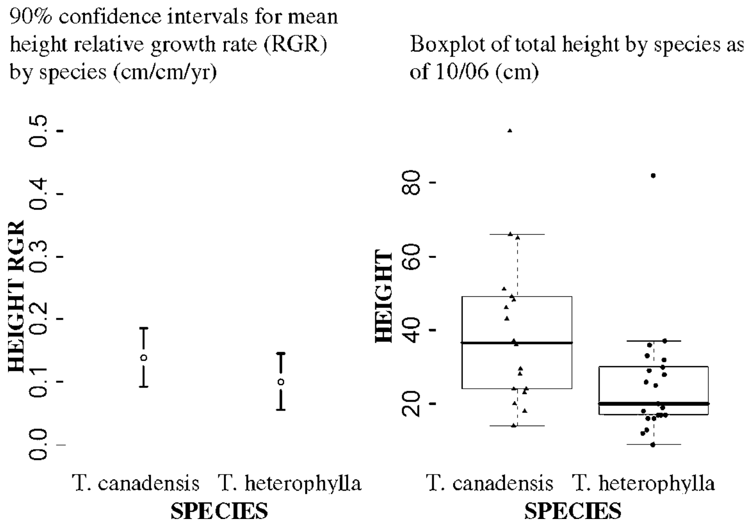
I calculated root collar based on the average of two perpendicular root collar diameter measurements. I used a general linear model to estimate RGR as a function of initial height or root collar area, species, HWA infestation, and site (Evans, 2006). Species and HWA infestation were binary classification variables. Site was a random blocking factor. I created a linear model for RGR of height and RGR of root collar area for each experiment. I retained the infestation variable and interaction effects only when they were significant at the 90% confidence level.

RESULTS

Experiments 1 and 2

Experiment 1 terminated early, after only one year, because all the western hemlock died, while the eastern hemlock seedlings continued to grow normally. In Experiment 2, 49% of the western hemlocks died while only 11% of the eastern hemlock perished. Deer damaged 22 of the remaining 40 eastern hemlock seedlings (55%) and two of the remaining 23 remaining western hemlock seedlings (9%). Deer damaged seedlings were excluded from all further results, leaving a sample size of 18 eastern hemlock seedlings and 22 western hemlock seedlings for the remaining analyses. Eastern and western hemlock did not have a statistically different height RGR (Figure 1), but the root collar RGR was 0.164 $cm^2 \cdot cm^{-2} yr^{-1}$

FIGURE 1. Experiment 2: Height growth of eastern and western hemlock.



Note: These and following boxplots follow convention: the box represents the interquartile range (IQR) and the whiskers represent the smallest and largest values within 1.5 times the IQR. Dots are actual data values.

greater for eastern hemlocks than for western hemlocks (90% confidence interval from 0.079 to 0.248 cm·cm^{-1}yr^{-1} Figure 2). Infestation of HWA occurred on 83% of eastern and 71% of western hemlock seedlings; infestation was not a significant predictor of RGR at the 90% confidence level.

Experiment 3

Chinese hemlock saplings in Experiment 3 had significantly greater RGR than the western hemlock saplings for both height (Figure 3) and root collar area (Figure. 4). Chinese hemlock's height RGR was 0.076 m·m^{-1}yr^{-1} greater than western hemlock (90% confidence interval 0.047 to 0.105 m·m^{-1}yr^{-1}). The root collar area RGR for Chinese hemlock was 0.077 cm^{2}·cm^{-2}yr^{-1} greater than western hemlock (90% confidence interval 0.030 to 0.124 cm^{2}·cm^{-2}yr^{-1}). I found no HWA on any of the Chinese hemlock saplings, but there was elongated hemlock scale (EHS, *Fiorinia externa* Ferris) on many of the saplings. In contrast, 75% of the western hemlock saplings had at least one HWA during the experiment.

FIGURE 2. Experiment 2: Root collar area growth of eastern and western hemlock.

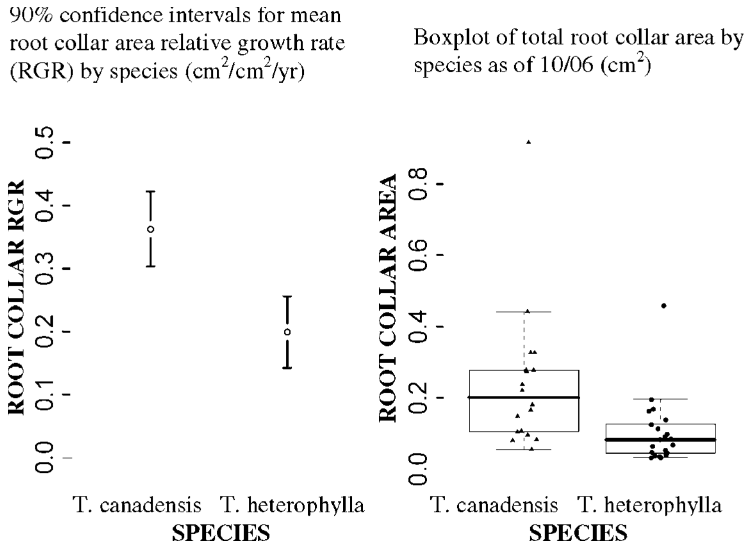


FIGURE 3. Experiment 3: Height growth of Chinese and western hemlock.

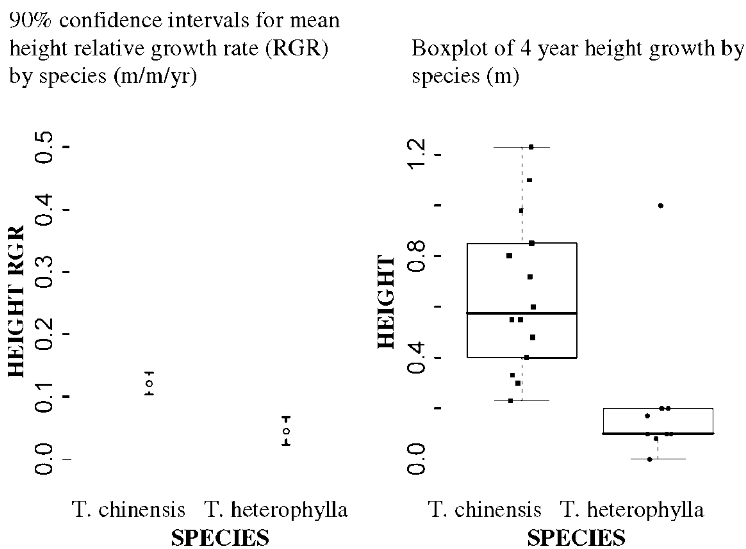
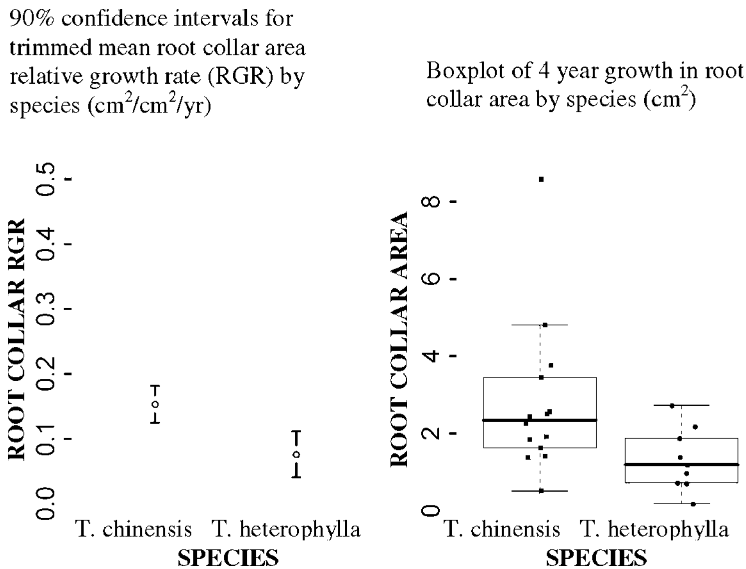


FIGURE 4. Experiment 3: Root collar area growth of Chinese and western hemlock.



Experiment 4

In Experiment 4, the infestation rate by species was not significantly different. Eastern hemlocks had a significantly higher RGR than western hemlock for height and root collar (Figure 5 and 6). Eastern hemlock had a relative height growth rate of an estimated 0.065 $cm \cdot cm^{-1}yr^{-1}$ greater than western hemlock (90% confidence interval 0.028 to 0.102 $cm \cdot cm^{-1}yr^{-1}$) and a RGR for root collar area 0.039 greater then western hemlock (90% confidence interval 0.023 to 0.056 $cm^2 \cdot cm^{-2}yr^{-1}$). By October 2006, 3% of the eastern hemlock and 13% of the western hemlock had died. Although HWA infestation was not a significant predictor of RGR at the 90% confidence level 58% of the living eastern hemlock and 50% living of the western hemlock were infested.

DISCUSSION

The two provenances of western hemlock tested in this study grew poorly and were infested by HWA at a rate similar to eastern hemlock. Chinese hemlock grew well in this short-term study and showed no signs

FIGURE 5. Experiment 4: Height growth of eastern and western hemlock.

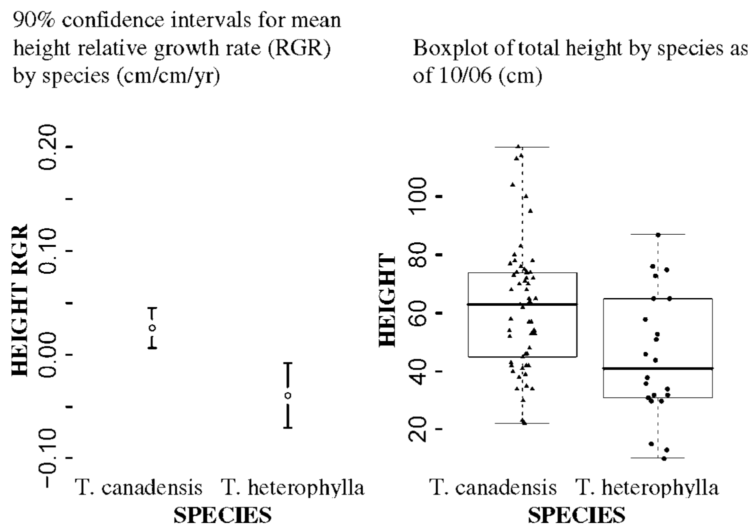
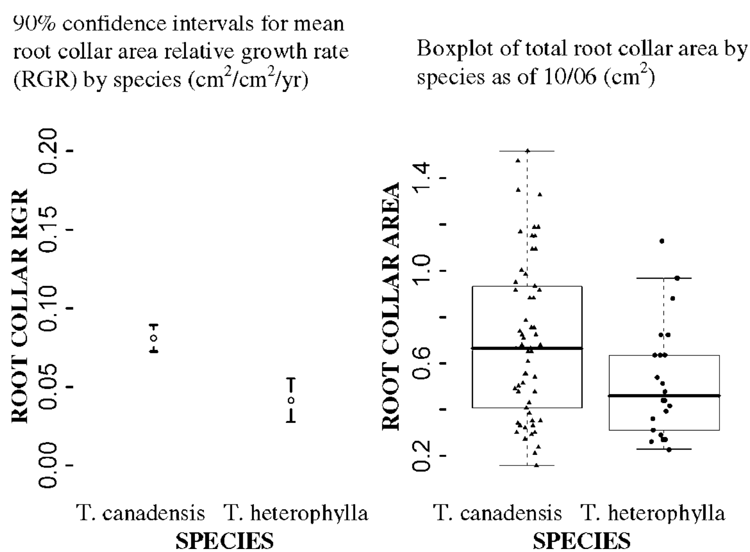


FIGURE 6. Experiment 4: Root collar area growth of eastern and western hemlock.



of infestation. Based on these early results, Chinese hemlock has potential as a substitute for eastern hemlock in areas of high HWA densities.

The experiments show that the western hemlock provenances used in this study are not appropriate for planting in the northern portion of eastern hemlock's range. Western hemlock survival in northeastern Connecticut was poor. It is likely that the increased exposure to cold of the raised cages used in Experiment 1 resulted in complete mortality of western hemlock while all the eastern hemlocks survived. In the field plantings, western hemlocks grew more slowly than eastern or Chinese hemlock and had a higher mortality rate. The probability of infestation for western and eastern hemlock was not significantly different in either Experiment 2 or 4. On the other hand, Chinese hemlock grew well in northeastern Connecticut and did not show any signs of HWA infestation.

Chinese hemlock is a good candidate for further studies on enrichment planting in southern New England and further south in eastern hemlock's range. In addition to the lack of HWA, Chinese hemlock grew in height and root collar area at relative growth rates similar to those of the eastern hemlock seedlings. The results of this study should encourage nurseries to grow Chinese hemlock as an alternative to eastern hemlock in areas with high density HWA. Although Chinese hemlock grew relatively fast in this forest, it was infested with EHS. Both the Chinese and western hemlocks had much higher populations of EHS then eastern hemlocks in the same stands. Further research into Chinese hemlock as a replacement for eastern hemlock damaged by HWA should include studies of the impact of EHS. It is even conceivable that planted Chinese hemlocks could permit EHS population to build to levels which would damage surrounding eastern hemlocks. EHS can be a serious pest on hemlock especially when paired with HWA (McClure, 1980; Danoff-Burg and Bird, 2002).

Hemlock and Deer

Deer browse is a particular problem for hemlock since deer prefer hemlock to other tree species and their browsing can cause failure of regeneration (Kittredge and Ashton, 1995; Mladenoff and Stearns, 1993; Long et al., 1998; Ziegler, 2000). For example, large deer populations on the Allegheny plateau, in combination with a drought, kept hemlock from regenerating after a windstorm (Peterson and Pickett, 1995). Another study of enrichment planting of western hemlock also documented the impact of ungulate browse (Maas-Hebner et al., 2005). In this study, damage and mortality caused by deer was a greater problem than growth reductions from HWA. In many areas with an ecologically important hemlock component, deer may be a more significant impediment to hemlock regeneration than HWA.

CONCLUSION

The introduction of any exotic species should be done with extreme caution. However, if HWA continues to eliminate eastern hemlock from its native environment, land stewards must weigh the risk of planting Chinese hemlock with the risk of completely losing the forest attributes that eastern hemlocks provide. Chinese hemlock lacks the classic characteristics of an invasion species (Williamson and Fitter, 1996).

Another exotic, Norway spruce (*Picea abies* (L.) Karst.), was not considered in this study, but should be examined in future research on enrichment planting to replace eastern hemlock. Norway spruce is shade tolerant with a dense canopy, can regenerate naturally, and has a long history of planting in eastern North American forests. Harvests or rapid mortality in hemlock stands provides an entrance for exotic plants because dense hemlock crowns prohibit advanced regeneration (Orwig and Foster, 1998; Small et al., 2005). Enrichment planting, particularly of shade tolerant species, before complete eastern hemlock mortality may fill available growing space and exclude invasives.

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RECEIVED: 02/11/07
REVISED: 05/18/07
ACCEPTED: 06/05/07