

forest management

Systemic Control of Nantucket Pine Tip Moth (*Rhyacionia frustrana* Scudder in Comstock, 1880) Enhances Seedling Vigor, Plantation Establishment, and Early Stand-Level Productivity in *Pinus taeda* L.

John S. King, Alexia M. Kelley, and Richard Rees

Establishment is a vulnerable and expensive stage of stand development in intensively managed pine plantations. We evaluated the capacity of establishing loblolly pine (*Pinus taeda* L.) plantations to increase productivity by systemic control of Nantucket pine tip moth (*Rhyacionia frustrana* Scudder in Comstock, 1880). In January 2009, four genotypes of improved genetics loblolly pine were planted in whole-plot treatments of herbaceous competition control at an upper coastal plain (UCP) site and phosphorus fertilization at a lower coastal plain (LCP) site, and split-plot treatments of tip moth control. Trees were monitored for tip moth infestation levels, vigor, survival, and stand-level biomass production for 2 years. During this time, tip moth infestation levels were very high at both sites, averaging 69% at UCP and 70% at LCP. However, levels averaged only 8% at UCP and 39% at LCP in treatments that included applications of systemic insecticides at planting. At LCP, biomass production averaged 2,159 kg ha⁻¹ after 2 years. Protection from tip moth increased LCP biomass by 11% averaged across genotypes and 20–30% for the most responsive genotypes. At UCP, 2-year pine biomass production was much lower at 114.5 kg ha⁻¹ and was increased 150% by protection from tip moth. At UCP, there was a strong effect of genetics whereby one genotype experienced very high mortality (mean of 30%) attributed to meteorological conditions of the establishment year; however, this was greatly decreased (17%) by protection from the interacting stress of tip moth damage. We conclude that systemic control of tip moth using imidacloprid soil tablets has the potential to greatly enhance pine plantation establishment success and early productivity in areas of heavy pest pressure, which may compound through stand development.

Keywords: carbon gain, forest pest, imidacloprid, interacting stresses, herbaceous competition, physiographic regions

European history demonstrates that advanced social development is inevitably linked to increased demand for natural resources, resulting in increased land use intensity (Diamond 2005). As the rest of the world achieves advanced social development, increased land use intensity is becoming common around the world. The inverse relationship between land use intensity and carbon (C) storage in terrestrial agro-ecosystems is well established (Lal 2005). However, the capacity of advanced forest management to affect C capture and storage, although often discussed, has not been fully explored (Jackson and Schlesinger 2004, Markewitz 2006).

Forest C cycling is strongly influenced by not only climate, soils, and decomposition processes but also productivity as the driver of organic inputs (Olson 1963, Schlesinger 1997, Callesen et al. 2003). Management has a large influence on productivity, and in the United States, the Southeast increased its share of national wood production from 41 to 58% between 1953 and 1997 (Prestemon and Abt 2002, Wear and Greis 2002, Wear et al. 2007). However, the southeastern economy is shifting. It has been estimated that urbanization of the Southeast will result in a decrease in forestland of more than 30,000 km² by the year 2050 (Nowak and Walton

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Affiliations: John S. King (john_king@ncsu.edu), North Carolina State University, Department of Forestry and Environmental Research, Raleigh, NC. Alexia M. Kelley (alexia.kelley@gmail.com), North Carolina State University, Department of Forestry and Environmental Research. Richard Rees (richard.rees@bayer.com), Bayer CropScience LP.

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2005). Associated changes in land use and energy consumption will have a large impact on regional C balance. Therefore, in the US Southeast, a rapidly rising population will demand greater provisioning of ecosystem services (wood, C storage, energy, and others) on a declining land base, requiring further increases in the efficiency of intensive forest management (Southern Forest Futures Project 2011).

The success of US Southeast forestry arises from its high productivity due to favorable growing conditions and advances in silviculture, mainly of loblolly pine (*Pinus taeda* L.). Improvements in nutrition, genetics, competition control, and other silvicultural treatments have increased mean annual increment of loblolly pine plantations from 2–6 m³ ha⁻¹ year⁻¹ in the 1960s to 9–12 m³ ha⁻¹ year⁻¹ today; with the very best genetics and nutrition, productivity can approach 21–28 m³ ha⁻¹ year⁻¹ (Coile and Schumacher 1964, McKeand et al. 2003, Stanturf et al. 2003, Allen et al. 2005, Carter and Foster 2006, Fox et al. 2007). Advanced pine silviculture increases profitability for land owners (McKeand et al. 2006), and it also represents a regional opportunity to mitigate harmful CO₂ buildup in the atmosphere through enhanced C storage in tree biomass (Aspinwall et al. 2012) and possibly forest soils. A large fraction of the total cost of advanced pine silviculture is in plantation establishment (Allen et al. 2005), and it is the stage of stand development that is most vulnerable to biotic and abiotic stresses (Niinemets 2010). Therefore, making plantation establishment more robust has great potential to yield both economic and environmental benefits.

The function and ecosystem services provisioning of forests across North America are increasingly threatened by outbreaks of native and introduced forest pests (Hain 1988, Logan and Powell 2001, Peterson et al. 2001, Williams and Liebhold 2002, Gan 2004, Poland and McCullough 2006, Ford and Vose 2007, Kurz et al. 2008, Gandhi and Herms 2010). In the US Southeast, one of the most common pests of loblolly pine is Nantucket pine tip moth (*Rhyacionia frustrana* Scudder in Comstock, 1880), which targets young trees and is probably benefiting from the widespread deployment of uniform pine plantations. Severity of infestation is generally positively correlated with management intensity or site index (Hertel and Benjamin 1977, White et al. 1984, but see Hood et al. 1988, Nowak and Berisford 2000). Top whorl shoot damage is well correlated to the level of whole-tree infestation and provides a suitable metric for estimating pest pressure in plantations (Stephen and Wallis 1978, Fettig and Berisford 1999), but there is significant geographic variation in pest pressure that is not well understood (Beal 1967, Ross et al. 1990, Asaro et al. 2003). Although tip moth infestations are thought to rarely result in tree mortality, they can severely decrease rates of height growth and plantation development, especially under conditions of low site quality or environmental stress (Asaro et al. 2003). Repeated damage to apical meristems is associated with development of poor stem form, creating sinuous, forked, or “bushy” trees. It has been suggested that damage from tip moth may be associated with infection by fusiform rust and pine pitch canker (Hedden et al. 1991, Runion et al. 1993), but further study is needed. Similarly, data are few and equivocal regarding the lasting impact of tip moth infestation on plantation yield at the end of a rotation (Asaro et al. 2003), and there are virtually no data on regionwide economic losses due to this pest.

Because Nantucket pine tip moth has the potential to greatly decrease gains due to advanced pine silviculture, we sought to determine how the systemic control of this arthropod affects individ-

ual tree growth and stand-level productivity (C gain). Commercially available genotypes of improved-genetics loblolly pine were planted under operational conditions at two physiographically distinct sites representative of major timber-producing regions of the US Southeast. A tip moth control treatment was crossed with operationally appropriate treatments of herbaceous competition control or phosphorus (P) fertilization, and biomass production was quantified after 2 years. Our first hypothesis was that stand-level forest productivity would be enhanced by protection from the tip moth and that the relative stimulation would be greatest at low site quality (poorer soils or low fertilization) because this would represent multiple, interacting stresses to the trees. Second, previous research (Ross and Berisford 1990, Ross et al. 1990, Asaro et al. 2003) suggests that tip moth damage may be more severe with decreased herbaceous competition because the improved nutritional status of the trees provides a better food source for pests (but the literature data are equivocal, e.g., see Nowak et al. 2003), so our second hypothesis was that the relative stimulation of forest productivity due to tip moth control would be greater under conditions of decreased herbaceous competition.

Materials and Methods

Field Sites

The study was conducted at two sites representative of upper coastal plain (UCP) and lower coastal plain (LCP) physiographic regions commonly used for intensive pine production across the US Southeast. Both sites are part of the land holdings of North Carolina State University (NCSU) and are managed operationally for revenue by the North Carolina State Natural Resources Foundation and the College of Natural Resources. The UCP site, named Taylor Tract (36°07'44" N, 77°44'42" W, elevation 40 m), is part of a 56-ha farm recently donated to the College that was in corn-soybean-winter wheat rotation for many decades before establishment of the study. The mean annual temperature (1971–2000) of the closest National Oceanic and Atmospheric Administration (NOAA) weather station (Rocky Mount #123, 33 km away) is 15.7° C, with a mean low in January of 2° C and a mean high in July of 28° C (National Climatic Data Center, Asheville, NC; Figure 1A). Mean annual precipitation for the UCP site is 1,181 mm, with a variable distribution throughout the year but with at least some precipitation in every month (Figure 1C). Soils are of the Goldsboro and Norfolk series with sand-loam texture and are moderately well-drained (USDA Natural Resources Conservation Service 2011). Site preparation was not used at this site because the previous soybean crop had just been harvested, and the soil was mostly bare, with some soybean residues. Although this site may have benefited from subsoiling, volumetric soil water content was too high at the time of study initiation to permit it. In terms of C cycling, this site represents land use conversion from long-term agriculture back to a forested condition. The LCP site is located at NCSU's 32,374-ha Hofmann Forest (34°49'37"N, 77°17'03" W, elevation 14 m), of which approximately 20,234 ha are operationally managed for timber production using silvicultural methods specific to the LCP physiographic regions (Allen and Campbell 1988). Mean annual temperature of the nearest NOAA weather station (Hofmann Forest #69, 3.3 km away) is 17.2° C, with a mean low in January of 3° C and a mean high in July of 28° C (Figure 1B). Mean annual precipitation for the LCP site is 1,434 mm, with a variable distribution throughout the year but with at least some precipitation in every month (Figure 1D). Soils are of the Rains series with fine sand-loam

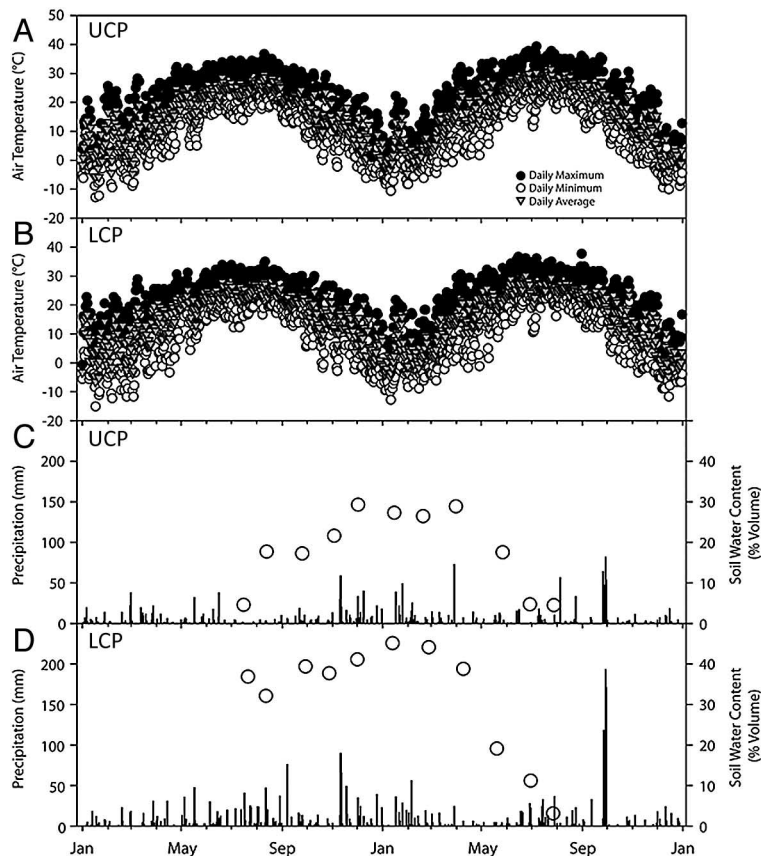


Figure 1. Maximum, minimum, and mean daily temperature (A and B) and precipitation (C and D) from NOAA weather stations near the UCP and LCP experimental sites, respectively, in eastern North Carolina for 2 years (2009 and 2010). Volumetric soil water content (C and D) was measured on site using a portable time domain reflectometry system. (NOAA data source: National Climatic Data Center, Asheville, NC.)

texture, high in organic matter and poorly drained (USDA Natural Resources Conservation Service 2011). Silvicultural prescriptions call for ditching and drainage and planting trees in elevated beds (approximately 40 cm high). Although the water table is high during winter, it drops during the growing season as a result of increased evapotranspiration, allowing the trees adequate aerated soil volume. Because of the mild climate and high water and nutrient availability, such sites are considered the most productive for pine silviculture across the Southeast (H. Lee Allen, North Carolina State University, pers. comm., Oct. 17, 2008). One year before establishment of the current study, a 38-year-old stand of loblolly pine had been harvested, followed by operational site preparation consisting of V-shearing and bedding on a 6-m spacing leaving the coarse woody residues in place, fertilization with P (see below), and preplanting competition control.

Experimental Design

In December 2008, the study sites were set up as two independent randomized complete block design experiments of whole- and split-plot treatments, replicated four times. Whole-plot factors were low and high herbicide at UCP and low and high P fertilization at LCP. Herbicide treatment was selected for UCP because initial soil analyses showed high levels of nitrogen (N), calcium, and magnesium (data not shown), and we reasoned that this site would experience intense herbaceous competition as a legacy of the previous agriculture (a correct assumption). The herbicide treatment was an application of Arsenal (BASF, Research Triangle Park, NC) at the

labeled rate (0.58 L ha^{-1}) and half the labeled rate (0.29 L ha^{-1}) for the high and low treatments, respectively, in late spring/early summer of both years of the study. There was no untreated control to this treatment (e.g., no plots with zero herbicide applied) because it is well known that pine plantation establishment and early productivity are seriously hindered if herbaceous competition is not controlled (Fox et al. 2007) and herbicide treatment represents standard practice. An untreated control (zero herbicide application) would therefore not have been operationally relevant. The intent of the herbicide treatment was to look at the effect of a more or less dense weed canopy on tip moth infestation and damage (Berisford 1988, Asaro et al. 2003). Replicated clip-plots revealed mean (SE) above-ground weed biomass of 658.4 (85.2) and 514.0 (118.0) g m^{-2} in the low and high weed control treatments, respectively, which, along with visual observations, indicates that the treatment had the intended effect on the size and structure of the weed community relative to the tree seedlings. At LCP, P fertilization at planting is a necessary silvicultural practice because exchangeable P is below the threshold for sufficient uptake by pine in the organic soils (Allen and Campbell 1988). Standard operational practice for this site is $13.6 \text{ kg P ha}^{-1}$ applied as diammonium phosphate once at the beginning of the rotation (Jerry Nobles, North Carolina State University Hoffmann Forest, pers. comm., Oct. 20, 2008). For the current study, we chose P application rates of 9.1 and 18.2 kg ha^{-1} to provide conditions of insufficient or more than sufficient P availability in the low and high treatments, respectively. Foliage analysis after 2 years of growth revealed little difference in tissue P concentrations (data

Table 1. Improved-genetics loblolly pine (*Pinus taeda* L.) and provenance of seedlings (ArborGen Corporation, Summerville, SC) in a tip moth control study conducted at UCP and LCP sites in eastern North Carolina.

Stock code/reference	Genetics	Provenance*	Stock type	Mean (SE) seedling biomass at planting (g)
AGM-12 "C2"	Full-sib	Atlantic coastal plain—South	Bareroot	5.34 (0.58)
AGM-24 "C1"	Full-sib	Atlantic coastal plain—North	Bareroot	5.94 (0.40)
PM-212 "V1"	Clone	Atlantic coastal plain—South	Containerized	7.88 (0.34)
NQ-26 "V2"	Clone	Atlantic coastal plain—South	Containerized	10.63 (0.38)

$n = 20$, except for V2 for which $n = 5$.

*Provenance refers to the general location from which the parents of the study trees were collected during tree improvement programs. "North" refers to North Carolina provenances; "South" refers to South Carolina or Georgia provenances.

not shown) between the low and high P treatments, indicating that the treatment was not sufficient to alter pine nutrition at this time (probably because of the small size of the trees). This result does not preclude a fertilization effect becoming apparent later in stand development, because the operational fertilization provides sufficient P for the entire rotation.

The split-plot factor at both sites was tip moth control. Tip moth control was achieved by applying SilvaShield (Bayer CropScience LP, Research Triangle Park, NC) to seedlings in one-half of the area of each level of the whole plots at both sites. SilvaShield (now marketed as CoreTect) is applied as a soil tablet placed next to the tree root system at the time of planting. The tablet contains 1 g of the active ingredient imidacloprid, a neonicotinoid insecticide that has been shown to be active against pine tip moth (Asaro and Creighton 2011) and to induce salicylate-associated plant defense responses (Ford et al. 2010). SilvaShield tablets also contain a small amount of fertilizer (12–9–4 NPK). SilvaShield was applied in accordance with the label, which restricts application to less than 0.99 kg of imidacloprid $\text{ha}^{-1} \text{year}^{-1}$. The imidacloprid is taken up systemically as roots become established and confers protection from tip moth for approximately 2 years (Asaro and Creighton 2011).

Finally, the split-split-plot factor was tree genetics. This was accomplished by planting four distinct genotypes of improved loblolly pine in blocks within each split-plot at both sites (Table 1). Tree seedlings were purchased from available stock at ArborGen Corporation (Summerville, SC) and consisted of two bareroot full-sib families produced by controlled mass pollination and two containerized varieties (clones) produced by somatic embryogenesis. The containerized trees were larger than the bareroot trees (Table 1) and had root systems with intact soil-root ball, so early comparisons between full-sibs and clones require caution. Effects on productivity of such differences in stock type have been reported to disappear within 4 years of planting at Hofmann Forest (Aspinwall et al. 2011). The rationale for selecting these highly improved tree genotypes, as opposed to less expensive half-sib trees from open-pollinated (OP) sources, was to assess the value of tip moth control in protecting the investment in the more expensive seedlings. Trees were planted at 3.04×3.04 -m spacing at UCP and 1.52×6.08 -m spacing at LCP (due to the bedding), resulting in 985 trees ha^{-1} , consistent with standard forestry practice in the US Southeast and in compliance with the SilvaShield label. Split-plots were surrounded by two rows of bareroot OP seedlings to act as a buffer for edge effects and to separate treatments, and five rows of OP seedlings separated whole-plot treatments (e.g., fertilized from unfertilized treatments). For each block (replicate), the experimental design resulted in 50 trees for each level of the split-split-plot treatment (genetics), 200 trees for each level of the split-plot factor (tip moth control), and 400 trees for each level of the whole-plot factor (her-

bicide level [UCP] or P fertilization level [LCP]). This resulted in a total of 5,088 trees planted at each experimental site, with 3,200 subjected to the experimental treatments and 1,888 serving as buffers. Nondestructive measurements were confined to the centermost trees (3×6 -tree blocks) within each split-split-plot, and destructive measurement trees were located one row out from this.

Measurements and Data Analysis

Tip moth infestation was quantified by counting the number of shoots on all branches in the top whorl of the center nondestructively measured 18 trees in the split-split-plots. Tip moth damage was quantified as destroyed apical meristems, shoot dieback, the presence of resin-covered larval silk tents, or other effects, twice in 2009 and three times in 2010. Top whorl shoot damage is well correlated to the level of whole-tree infestation and provides a suitable metric for estimating tip moth pressure in plantations (Stephen and Wallis 1978, Fettig and Berisford 1999). During this study we also monitored tip moth populations using pheromone traps (data not shown). For both years of the study, the trap data showed good correlation of high tip moth numbers to the first growth flush of the pines in April/May and then less distinct peaks in moth numbers poorly correlated to the second and third growth flushes. These later "peaks" in moth numbers were difficult to distinguish from the continuous background moth numbers. The trap data and pine shoot infestation data (both measurements and anecdotal observations) showed a continuous tip moth presence for the duration of the growing season until late fall. Even so, the focus of the current study is on the (cumulative) plant response and not a detailed analysis of tip moth biology. Our measurements of infestation (Figure 3) were temporally separated enough to be on subsequent shoot growth flushes and, therefore, by definition, we sampled subsequent "generations." Further, our end of year (December/January) tree growth metrics sampling on which biomass production responses were based, integrated the damage from all tip moth activity that occurred during the year, which is the main emphasis of the current study. The objectives of collecting the infestation data were to show the overall level of infestation for our area (very high) and the effects of the systemic treatment with imidacloprid.

To estimate beginning and end biomass, stem diameter was measured with calipers at the groundline, and total tree height was measured with a height pole at the time of planting (January 2009) and in December 2010. In January 2009, a subsample of seedlings from each stock type (containerized, bareroot) and genotype ($n = \text{C1: } 20; \text{C2: } 20; \text{V1: } 20; \text{and V2: } 5$) were separated into above- and belowground portions and dried at 70°C to constant mass and weighed for development of site-specific and genotype-specific allometric biomass regressions (King et al. 2005, Aspinwall et al. 2011). Additional trees were harvested in January and December of 2010

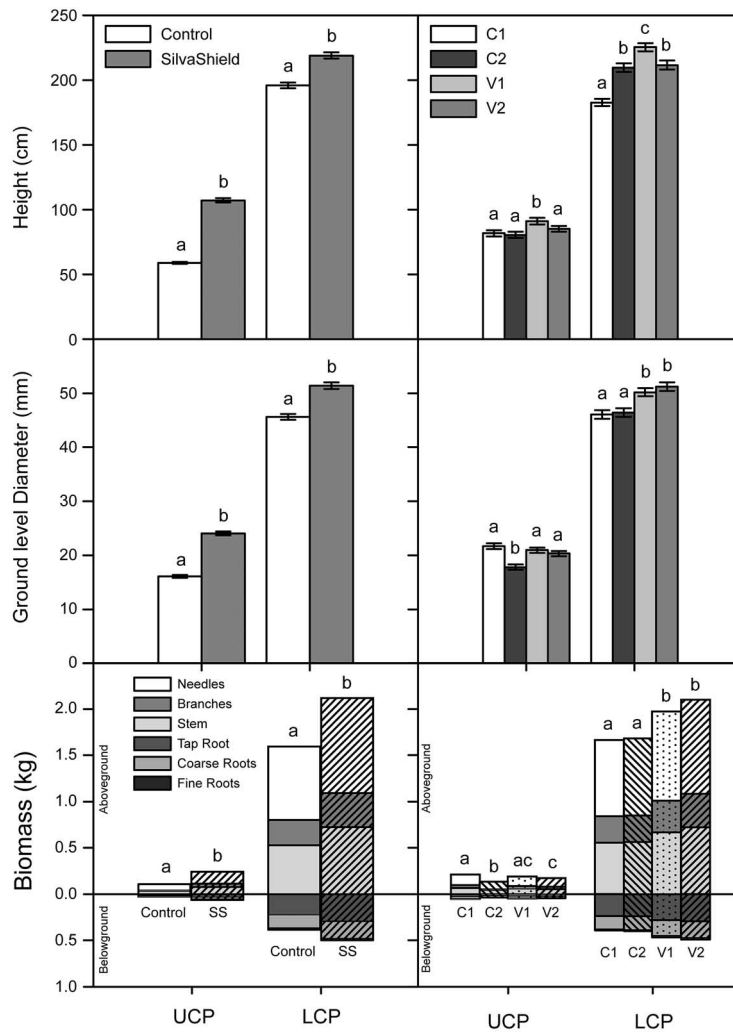


Figure 2. Mean (SE) individual tree height, diameter and biomass of improved-genetics loblolly pine after 2 years of growth along the UCP and LCP of North Carolina as affected by protection from tip moth and genetics. The lower case letters indicate significant differences within each site at a 0.05 level.

(32 trees at UCP and 16 at LCP) to update the allometric models for the expanded range of tree sizes in the experiment. Allometric biomass regressions from Aspinwall et al. (2011) were used to estimate tree biomass at LCP in 2010 because they were of similar age and size, and those relationships were developed at an adjacent study (same site) that showed little effect of genetics on the allometry of the young trees. Allometric analysis (King et al. 1996, 1999) showed that tree allometry had not been significantly affected by genotype, treatment, or tree size, allowing use of common regression models for each site. Allometric models (not shown) were applied to the height and diameter data collected on the nondestructively measured trees to estimate individual tree biomass at the time of planting and at the end of 2010. Tree biomass estimates were summed to the plot level, corrected for tree mortality, and expressed on an area basis (kg ha^{-1}). Tree mortality was assessed by visual inspection of all treated trees in the experiment during the winters of 2009 and 2010.

Data were analyzed for each experiment (UCP and LCP) independently by analysis of variance using Proc GLM for a randomized complete-block design (SAS version 9.2; SAS Institute, Inc., Cary, NC). Initial tree size was used as a covariate to account for differences between the containerized and noncontainerized planting stock. Experimental block was considered a random factor to ac-

count for variation in environmental conditions across the field sites. Inspection of residuals and normal probability plots allowed identification of outliers and appropriate transformations (natural log) to normalize variances, satisfying the assumptions of analysis of variance (Steel and Torrie 1980). Data are presented as means (SE), corrected for back-transformation bias (Baskerville 1972), and treatment effects are considered significant at $P \leq 0.05$.

Results

Comparison Between Sites

Although the UCP and LCP sites hosted independent experiments, precluding a statistical comparison, they were planted at exactly the same time with the same genetics, and therefore it is instructive to contrast growth between the two regions (UCP versus LCP). Averaged across all treatments, mean individual tree height, diameter, and biomass at UCP were 75 cm, 18 mm, and 0.27 kg, respectively, compared with 200 cm, 48 mm, and 1.85 kg at LCP after 2 years of growth (Figure 2), representing an almost 7-fold difference in mean tree biomass at LCP compared with that at UCP. The seasonal progression of high and low temperatures was similar at both sites (Figure 1); however, LCP was on average 1.5°C warmer than UCP. Long-term average precipitation from the nearest

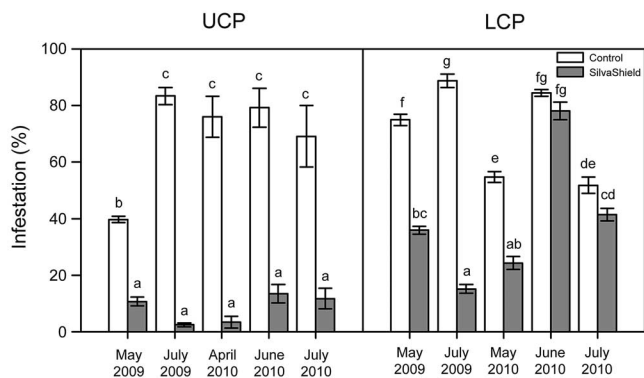


Figure 3. Mean (SE) tip moth infestation rates (%) in loblolly pine as affected by imidacloprid protection for two growing seasons (2009 and 2010) in the UCP and LCP of North Carolina. The lower case letters indicate significant differences within each site at a 0.05 level.

weather stations was 253 mm year⁻¹ greater at LCP than at UCP, and in both years of this study UCP received less precipitation than LCP and experienced severe growing season droughts (Figure 1). As part of soil respiration monitoring (to be reported elsewhere), we began measuring soil temperature and volumetric water content (VWC) to a 12-cm depth on site in July 2009. By that time, VWC at UCP had already dropped to 4.5% compared with 36.9% at LCP and remained much lower for most of the following year (Figure 1). Soil VWC was restored to field capacity at both sites during the following fall and winter but declined precipitously during summer 2010. Even so, water availability was probably higher at LCP because of the relatively high water table common to the LCP physiographic region (but lower than our 12-cm probes).

Infestation

Tip moth infestation rates were very high at both sites with a mean of 69% at UCP and 70% at LCP for unprotected controls, averaged over the two growing season monitoring period (Figure 3). There was a highly significant tip moth control × time interaction at both sites ($P < 0.0001$), caused primarily by variation in tip moth control efficacy through time and especially by decreasing efficacy in the second year of the study at LCP (Figure 3). Averaged through time, the tip moth control treatment decreased infestation rates to 8 and 39% at UCP and LCP, respectively. There was also a genetics × time interaction ($P = 0.003$) at LCP, caused by genotype C1 having a significantly lower rate of infestation than the other three genotypes early in the study, which was absent in late 2009/early 2010 (data not shown).

Treatment Effects on Individual Tree Size

At both sites, tip moth control and genetics were the most significant factors affecting individual tree height, diameter, and biomass after 2 years, and there were few statistically significant interactions among treatments (Table 2; Figure 2). At UCP, trees protected from tip moth increased height from 59 to 107 cm (+106%), increased diameter from 16 to 24 mm (+50%), and increased total biomass from 0.14 to 0.30 kg (+114%) on average, compared with trees with no protection from tip moth. At LCP, trees protected from tip moth increased height from 196 to 219 cm (+12%), increased diameter from 46 to 51 mm (+11%), and increased biomass from 1.90 to 2.51 kg (+32%) on average, com-

pared with trees without protection from tip moth. Genetics significantly affected individual tree height, diameter, and biomass, even though we used initial tree size as a covariate in the statistical analysis to control for differences in size of bareroot and containerized planting stock. At UCP, bareroot genotypes (C1 and C2) were slightly shorter than containerized genotypes after 2 years of growth, and C2 had significantly smaller diameter and biomass than the other genotypes. At LCP, the bareroot genotypes had smaller height, diameter, and biomass compared with containerized genotypes, with genotype V2 being the best performer at that site. Finally, there was a significant effect of the herbicide treatment on individual tree height at UCP (Table 2). After 2 years of growth at UCP, tree height increased with competition control, from 60 to 110 cm (+83%) in the low- and high-herbicide treatments, respectively.

Tree Mortality

At UCP, tip moth control and genetics significantly affected tree mortality, and there were no statistically significant interactions among experimental treatments (Table 2). Without tip moth control, mortality ranged from 6% in V2 to 30% in C2, and the statistical significance of genotype as a factor was mainly due to the relatively high mortality of the latter family (Figure 4). Protection from tip moth at UCP decreased mortality to 8.5% averaged across genotypes, but C2 still had relatively high mortality at 17%. At LCP, mortality averaged less than 5% and was not significantly affected by tip moth control or genetics (Table 2). Although not statistically significant, genotype C2 also had the highest mortality rate at this site, averaging 4% across tip moth control treatments (Figure 4).

Stand-Level Biomass Production

Treatment-specific individual tree size and mortality rates were used to scale results to stand biomass production using the annually measured height and diameter data. At both UCP and LCP, the split-plot factor, tip moth control, and the split-split-plot factor, genetics, almost always had highly significant effects on end 2010 stand-level biomass of foliage, branches, stems, tap roots, coarse roots, and fine roots, and there were no statistically significant interactions between factors (Table 3). The level of significance of genetics was much higher at UCP than at LCP. The whole-plot herbicide treatment was marginally significant ($P = 0.06$) for all biomass components at UCP. Similarly, at LCP there were many marginally significant ($0.06 > P < 0.10$) two-way interactions between fertilization, tip moth control, and genetics for all biomass components except fine roots (Table 3).

At UCP, there were significant differences in growth and response to tip moth control between genotypes. End 2010 total biomass for the smallest genotype, C2, averaged 64.5 kg ha⁻¹ compared with an average 135.2 kg ha⁻¹ for the other three genotypes (Table 4), representing a 109% increase due to genotype. Protection from tip moth increased end 2010 total biomass of the C2 genotype to 209.6 kg ha⁻¹ and an average 327.2 kg ha⁻¹ for the other genotypes, increases of 225 and 142%, respectively. Genotype C1 had the greatest end 2010 biomass at the UCP site, at 141.6 and 360.1 kg ha⁻¹ without and with tip moth protection, respectively, an increase of 154%. Averaged across treatments, stand-level biomass was partitioned after 2 years of growth at UCP as foliage, (42.7%), branches (11.2%), stem (25.3%), taproots (12.5%), coarse roots (8.3%), and fine roots (2.7%), and there was very little variation in this partitioning between treatments (Table 4).

Table 2. Statistical results (*P* values) of the effects of the whole-plot (fertilization or herbicide), split-plot (tip moth control), and split-split plot (genetics) factors on individual loblolly pine tree height, diameter, biomass, and mortality in improved genetics loblolly pine after 2 years of growth along the UCP and LCP of North Carolina.

UCP (Taylor Tract)					LCP (Hofmann Forest)				
Source*	Height	Diameter	Biomass	Mortality	Source*	Height	Diameter	Biomass	Mortality
H	0.009	0.104	0.105	0.140	F	0.145	0.454	0.399	0.969
S	0.000	0.000	0.000	0.000	S	0.002	0.002	0.002	0.929
H × S	0.042	0.494	0.184	0.523	F × S	0.892	0.319	0.530	0.120
G	0.015	0.000	0.000	0.000	G	0.000	0.021	0.007	0.230
S × G	0.328	0.512	0.182	0.592	S × G	0.054	0.187	0.066	0.567
H × G	0.723	0.950	0.769	0.840	F × G	0.252	0.086	0.062	0.912
H × S × G	0.843	0.662	0.505	0.783	F × S × G	0.166	0.428	0.455	0.902

*Sources of variation at UCP are herbicide (H), tip moth control (imidacloprid) (S), and genetics (G). Sources of variation at LCP are fertilization (F), tip moth control (imidacloprid) (S), and genetics (G).

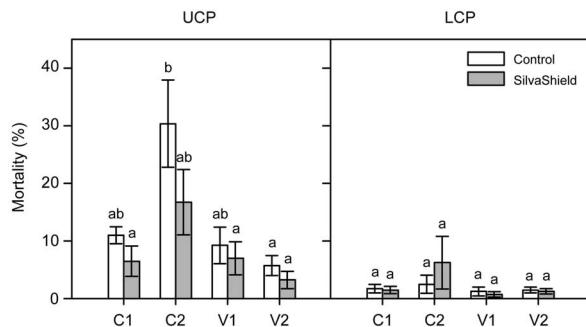


Figure 4. Mean mortality rate (SE) of improved loblolly pine after 2 years of growth (December 2010) along the UCP and LCP of North Carolina as affected by protection from tip moth and genetics. The lower case letters indicate significant differences within each site at a 0.05 level.

Biomass production was much greater at LCP than at UCP, and although similar in direction, responses to the treatments were of smaller magnitude (Table 4). End 2010 total stand-level biomass at LCP averaged 2,088.1 kg ha⁻¹ for the bareroot genotypes and 2,228.9 kg ha⁻¹ for the containerized genotypes, a 6.7% greater biomass production due to genetics (stock type). Averaged across all genotypes, end 2010 total biomass increased from an average of 2,158.6 kg ha⁻¹ to 2,406.3 kg ha⁻¹ with protection from tip moth, an 11.5% increase in total biomass production. However, bareroot genotypes had no significant change in end 2010 biomass, whereas the containerized genotypes did, consistent with the marginally significant tip moth control × genetics interaction (Table 3). Genotype V1 increased end 2010 biomass from 2,219.9 to 2,666.9 kg ha⁻¹ with tip moth control, a 20% increase. Similarly, genotype V2 had the greatest biomass production at this site and the greatest response to tip moth control. End 2010 stand-level total biomass of this genotype averaged 2,237.9 and 2,931.5 kg ha⁻¹ without and with protection from the tip moth, respectively, equating to a 31% increase in biomass production (Table 4). Finally, averaged across treatments, biomass was partitioned after 2 years of growth at LCP as foliage (39.7%), branches (13.9%), stem (27.2%), taproots (11.3%), coarse roots (7.0%), and fine roots (0.6%), and there was very little variation in partitioning between treatments.

Discussion

We sought to quantify effects on seedling vigor, tree mortality, and early stand-level production in intensively managed loblolly pine plantations of systemic control of a common forest pest, Nan-

tucket pine tip moth. We hypothesized that protection from tip moth would increase stand-level growth and that the relative stimulation would be greatest under conditions of low resource availability (or low site index) or decreased herbaceous competition. Results show that systemic control of Nantucket pine tip moth infestations can greatly increase tree vigor (growth), stand establishment (decreased mortality), and productivity (and therefore stand-level C gain), but that interactions with site resource availability and competition were not always consistent with expectations.

Relevance of Experimental Design to Assessment of Early Stand-Level Productivity and Carbon Gain

Effects of Nantucket pine tip moth infestations on growth and yield in loblolly pine have been active areas of research for decades (Berisford and Kulman 1967, Lashomb et al. 1978, Cade and Hedden 1987, Berisford 1988, Fettig et al. 1998, Asaro et al. 2003, McCravy et al. 2004). In general, most studies have been of short duration and small scale, single-tree or small-row plots, although a few longer-term assessments have been conducted (Williston and Barras 1977, Lashomb et al. 1978, Hedden et al. 1981, Thomas and Oprean 1984, Berisford et al. 1989, Nowak and Berisford 2000). These studies were useful for understanding the life history of the insect and testing the efficacy of new control measures using insecticide sprays and some biological control agents. Because the number and timing of tip moth generations is synchronized with the semideterminate shoot elongation of loblolly pine across its range, some of the earlier work was focused on developing spray-timing models based on cumulative heat sum and pheromone trap counts in an attempt to maximize efficacy (Fettig et al. 1998, 2000a, 2000b). The success of such spray-timing models was mixed, and the recent advent of systemic insecticides that persist for several growing seasons appears to have obviated the need for such complicated control programs (Asaro and Creighton 2011). Our results are consistent with this body of past research, which has generally shown significant enhancement of early pine performance with tip moth control. The long-term effects of tip moth control on loblolly pine productivity and economic return at the end of the rotation (e.g., 25 years), however, still remain poorly understood. Asaro et al. (2003) provide a comprehensive review of the earlier literature.

Our study of tree vigor, stand-level productivity, and carbon gain of systemic tip moth control in loblolly pine is unique in several important ways, most notably for its large size and fully replicated (4×) crossed treatments of main plot (fertilization level and herbicide level), split-plot (tip moth control), and split-split-plot (genetics) factors. Including buffer trees, each level of the main plots

Table 3. Statistical results (*P* values) of the effects of the whole-plot (fertilization), split-plot (tip moth control), and split-split-plot (genetics) factors on stand-level biomass of improved genetics loblolly pine after 2 years of growth (2010) along the UCP and LCP of North Carolina.

Source	Foliage	Branch	Stem	Tap roots	Coarse roots	Fine roots
UCP (Taylor Tract)						
H	0.067	0.067	0.065	0.065	0.06	0.066
S	0.000	0.000	0.000	0.0000	0.000	0.000
H × S	0.226	0.186	0.251	0.276	0.342	0.832
G	0.000	0.000	0.000	0.000	0.000	0.000
S × G	0.251	0.179	0.296	0.341	0.448	0.731
H × G	0.702	0.626	0.739	0.771	0.834	0.960
H × S × G	0.420	0.385	0.437	0.451	0.477	0.480
LCP (Hofmann Forest)						
F	0.450	0.436	0.431	0.448	0.447	0.484
S	0.002	0.002	0.002	0.002	0.002	0.002
F × S	0.422	0.480	0.505	0.429	0.434	0.326
G	0.060	0.043	0.038	0.058	0.056	0.110
S × G	0.094	0.073	0.066	0.091	0.089	0.148
F × G	0.094	0.093	0.093	0.094	0.094	0.107
F × S × G	0.405	0.397	0.394	0.404	0.403	0.429

*Sources of variation at UCP are herbicide (H), tip moth control (imidacloprid) (S), and genetics (G). Sources of variation at LCP are fertilization (F), tip moth control (imidacloprid) (S), and genetics (G).

Table 4. Beginning and end mean (SE) stand-level biomass of loblolly pine as affected by tip moth control (split-plot factor) and genetics (split-split-plot factor) during 2 years of growth at two sites in the UCP and LCP of North Carolina.

Parameter	Control				Tip moth control			
	C1	C2	V1	V2	C1	C2	V1	V2
UCP (Taylor Tract)								
Beginning 2009 biomass (kg ha ⁻¹)								
Foliage	1.54 (0.20)	1.30 (0.13)	2.97 (0.25)	1.12 (0.09)	1.34 (0.08)	1.30 (0.07)	2.85 (0.03)	1.23 (0.21)
Branches	0.36 (0.05)	0.30 (0.03)	1.00 (0.35)	0.26 (0.02)	0.32 (0.02)	0.30 (0.02)	0.67 (0.01)	0.29 (0.05)
Stem	0.84 (0.11)	0.74 (0.07)	1.71 (0.13)	0.68 (0.05)	0.73 (0.05)	0.74 (0.04)	1.66 (0.02)	0.75 (0.13)
Tap root	0.32 (0.06)	0.29 (0.03)	1.42 (0.15)	1.60 (0.04)	0.26 (0.02)	0.29 (0.02)	1.35 (0.02)	1.64 (0.08)
Coarse root	0.21 (0.04)	0.18 (0.02)	0.83 (0.06)	0.93 (0.04)	0.17 (0.01)	0.18 (0.01)	0.81 (0.01)	0.95 (0.05)
Fine root	0.11 (0.02)	0.10 (0.01)	0.36 (0.02)	0.43 (0.01)	0.09 (0.01)	0.10 (0.01)	0.37 (0.00)	0.44 (0.02)
Total	3.38 (0.47)	2.91 (0.20)	8.30 (0.98)	5.02 (0.24)	2.90 (0.20)	2.91 (0.16)	7.72 (0.08)	5.29 (0.84)
End 2010 biomass (kg ha ⁻¹)								
Foliage	58.38 (7.01)	26.01 (4.93)	54.76 (8.80)	53.65 (10.00)	153.37 (18.31)	87.68 (7.98)	136.35 (13.62)	126.88 (14.56)
Branches	14.85 (1.87)	6.24 (1.24)	13.75 (2.37)	13.45 (2.76)	42.90 (5.71)	23.21 (2.33)	37.61 (4.12)	34.55 (4.33)
Stem	35.03 (4.10)	16.01 (2.97)	33.04 (5.14)	32.38 (5.76)	88.14 (9.98)	51.67 (4.49)	78.84 (7.53)	73.78 (8.11)
Tap root	17.41 (1.99)	8.12 (1.49)	16.50 (2.49)	16.17 (2.76)	42.27 (4.57)	25.30 (2.12)	38.00 (3.50)	35.72 (3.79)
Coarse root	11.73 (1.28)	5.71 (1.01)	11.22 (1.60)	11.01 (1.73)	26.58 (2.61)	16.58 (1.28)	24.13 (2.05)	22.88 (2.25)
Fine root	4.18 (0.33)	2.44 (0.38)	4.15 (0.42)	4.08 (0.40)	6.81 (0.36)	5.15 (0.26)	6.45 (0.33)	6.35 (0.38)
Total	141.58 (16.58)	64.53 (12.02)	133.42 (20.82)	130.74 (23.41)	360.07 (4.92)	209.59 (18.46)	321.38 (3.91)	300.16 (4.3)
LCP (Hofmann Forest)								
Beginning 2009 biomass (kg ha ⁻¹)								
Foliage	1.50 (0.07)	1.39 (0.07)	2.96 (0.17)	1.29 (0.06)	1.54 (0.08)	1.49 (0.08)	2.86 (0.10)	1.34 (0.10)
Branches	0.35 (0.02)	0.32 (0.02)	1.00 (0.33)	0.30 (0.01)	0.36 (0.02)	0.35 (0.02)	0.68 (0.02)	0.82 (0.02)
Stem	0.82 (0.04)	0.79 (0.04)	1.71 (0.09)	0.79 (0.04)	0.84 (0.04)	0.85 (0.05)	1.66 (0.06)	0.82 (0.06)
Tap root	0.31 (0.02)	0.31 (0.02)	1.41 (0.11)	1.69 (0.02)	0.32 (0.02)	0.33 (0.02)	1.36 (0.06)	1.72 (0.04)
Coarse root	0.20 (0.01)	0.19 (0.01)	0.83 (0.05)	0.99 (0.01)	0.21 (0.02)	0.20 (0.02)	0.81 (0.04)	1.00 (0.02)
Fine root	0.10 (0.01)	0.10 (0.01)	0.36 (0.02)	0.46 (0.01)	0.11 (0.01)	0.11 (0.01)	0.37 (0.02)	0.47 (0.01)
Total	3.28 (0.17)	3.10 (0.17)	8.27 (0.77)	5.52 (0.15)	3.38 (0.19)	3.33 (0.19)	7.74 (0.30)	6.17 (0.25)
End 2010 biomass (kg ha ⁻¹)								
Foliage	832.99 (123.68)	836.66 (66.47)	883.67 (66.27)	889.08 (100.58)	815.77 (94.80)	789.29 (54.94)	1,048.41 (94.50)	1,142.12 (77.43)
Branches	287.21 (47.93)	288.52 (25.94)	307.15 (26.61)	310.16 (39.77)	282.67 (37.11)	273.81 (21.24)	372.92 (37.74)	412.82 (31.92)
Stem	560.10 (97.68)	562.65 (52.99)	600.98 (54.93)	607.82 (81.83)	552.50 (76.01)	535.44 (43.45)	736.64 (77.94)	821.21 (66.76)
Tap root	241.24 (36.37)	242.32 (19.56)	256.18 (19.58)	257.86 (29.64)	236.39 (27.91)	228.75 (16.14)	304.80 (27.89)	332.68 (22.94)
Coarse root	149.49 (22.74)	149.85 (12.24)	158.84 (12.29)	159.63 (18.57)	146.25 (17.47)	141.54 (10.08)	189.04 (17.49)	206.62 (14.43)
Fine root	12.78 (1.43)	12.82 (0.75)	13.34 (0.69)	13.33 (1.13)	12.42 (1.08)	11.99 (0.69)	15.12 (1.04)	16.03 (0.79)
Total	2,083.51 (329.80)	2,092.82 (177.96)	2,219.87 (180.33)	2,237.88 (271.44)	2,046.01 (254.33)	1,980.82 (146.26)	2,666.94 (256.59)	2,931.48 (214.26)

Stand-level estimates of biomass were calculated from site-specific allometric relationships derived from destructively harvested trees that spanned the range of tree size classes applied to annual measurements of height and diameter of 18 nondestructively monitored trees within each split-split-plot.

contains 648 trees distributed over 0.6 ha of land (e.g., 1 block = 1.2 ha). Each level of the split-plots (tip moth control) contains 200 trees distributed across 0.2 ha. Thus, the experiment provides reasonable simulation of treatment effects on stand-level infestation,

tree mortality, individual tree productivity, and the cumulative impacts on ecosystem accumulation and cycling of C with limited edge effects. Importantly, processes of above- and belowground litter inputs to soil, root distributions, soil fauna, and microbial

communities are realistically represented. The impacts of tree-tree and tree-weed competition are fully integrated over the course of stand development, including their influence on light interception and stand micrometeorological conditions.

Infestation, Tree Size, and Tree Mortality

We found that systemic protection from tip moth had very significant effects on infestation levels, which averaged ~70% on unprotected controls at both sites as estimated by the number of top-whorl branches with shoots showing evidence of tip moth damage. With tip moth control, infestation decreased to 8 and 39% at UCP and LCP sites, respectively. Why the efficacy was less at LCP is not known, but the pattern of response (e.g., effective at LCP during May 2009–2010, but efficacy declining rapidly thereafter) strongly suggests a dilution of imidacloprid in plant tissues to levels below those required to induce mortality of tip moth larvae at an appreciable scale in these very rapidly growing trees. Our methodology of estimating infestation pressure was consistent with that in other studies (Fettig and Berisford 1999, Asaro and Creighton 2011). Because of the recent advent of systemic forestry insecticides, the study of Asaro and Creighton (2011) is the only other published report of tip moth control in loblolly pine using imidacloprid. These authors reported that the tip moth infestation rate of 30% on unprotected trees (averaged from seven Virginia Piedmont sites over the first 2 years) was decreased by fipronil and imidacloprid treatments to 10 and 7%, respectively. Beal (1967) developed a tip moth pressure landscape classification scheme for several southern states with the following categories of whole-tree damage: very light (1–10%), light (11–40%), medium (41–70%), and heavy (71–100%). Although not commonly thought to cause widespread plantation stagnation and mortality (Asaro et al. 2003), our data (and personal observations) clearly show that the UCP and LCP regions of eastern North Carolina are under heavy tip moth pressure, with potentially large negative consequences for regional productivity and C assimilation. High levels of tip moth infestation have been recorded in other parts of the Southeast (Ross et al. 1990). Renewed quantification and monitoring of the spatial distribution of tip moth infestation rates in pine plantations across the Southeast would aid in management, allow estimation of impacts on regional economy and C cycling, and provide temporal resolution to changes in environmental conditions.

The infestation experienced by our experimental stands had serious negative impacts on individual tree size over the first 2 years of plantation establishment, and in support of our first hypothesis, this effect was much more pronounced at the less favorable UCP site. At UCP, we saw significant increases in tree height (+106%), diameter (+50%), and total tree biomass (+32%) with protection from tip moth. At LCP, individual tree size still benefited from tip moth control, but the relative stimulation was much less for height (+12%) and diameter (+11%). Still, increases in individual young pine biomass of 30–114% rival those due to fertilization and competition control (Ross et al. 2005, Fox et al. 2007) or elevated atmospheric CO₂ (Tchaplinski et al. 1993, King et al. 2005) and point to the value of tip moth control as a silvicultural prescription in landscape settings known to experience heavy pest pressure. This finding differs from Asaro and Creighton (2011), who found insignificant effects of tip moth control on individual tree performance, which could be related to the much lower tip moth population levels reported for that study. Although genetics affected individual tree size in the current study, we suspect this was mainly due to stock

type effects with the (more expensive) containerized varieties having initially larger size and potentially better establishment potential. In an analysis of the effects of genetic homogeneity on loblolly pine productivity conducted at LCP not far from the current study, Aspinwall et al. (2011) showed that the early effects of stock type on tree size disappeared by the fourth year of growth.

In addition to effects on individual tree performance, tip moth control had profound effects on stand-level mortality at UCP but not at LCP, again supporting our first hypothesis. Statistically, the effects of tip moth control and genetics at UCP were additive (Table 2); however, there were powerful differences in response between genotypes. Averaged across genotypes, mortality at UCP was approximately 15%, and this declined to 9% with protection from tip moth. This response was heavily influenced by the C2 genotype, which experienced 30% mortality when not protected from tip moth, with some individual plots having much higher mortality (data not shown). Application of tip moth control decreased mortality in this genotype to less than 17%, much closer to that of the other genotypes. We believe this finding is evidence of an interaction between biotic and abiotic stress factors. Shortly after planting of the study seedlings in January 2009, eastern North Carolina experienced several weeks of below-average low temperatures (<–10° C), followed by significant drought stress later that summer at the UCP site (Figure 1). The LCP site actually experienced lower winter temperatures for a longer period in winter 2009, suggesting that drought stress later that spring at UCP was the predominant stress factor influencing mortality, because genetics were identical at both sites. The C2 genotype was the least tolerant to these abiotic stresses, and the added stress of heavy forest pest pressure resulted in high mortality during both growing seasons. Relief of the biotic pressure through systemic tip moth control resulted in much higher tolerance to the other stresses. Although we lack the data to understand the exact physiological mechanisms of enhanced stress tolerance at our sites (e.g., plant water potential and rates of physiology), our results illustrate that ecosystem function is highly sensitive to genetic composition of dominant tree populations as has been shown, for example, for genetic variation in tolerance to the tropospheric ozone of *Populus* (Karnosky et al. 2003).

Systemic control of a major biotic stress, tip moth in our case, decreased the negative effects of other stresses on plantation establishment by enhancing individual tree vigor and decreasing stand-level mortality. These results are consistent with Asaro and Creighton (2011), who reported mortality rates of about 26% across seven sites in the Piedmont of Virginia, which decreased to approximately 14% by treatment with systemic imidacloprid. Increased tree survival in response to tip moth control was the driver of enhanced productivity in that study, because individual tree performance was not affected. Asaro and Creighton (2011) observed protective effects of systemic tip moth control against other nontargeted forest pests, such as pales weevils (*Hylobius pales* Herbst). In the current study, we noted a significant decrease in the percentage of trees infested by pine webworm (*Prococera robustella* Zeller) with imidacloprid (control of 12.4% [SE 1.8%] versus imidacloprid of 3.8% [0.6%], $P = 0.01$). This and other reports of efficacy against a variety of forest pests (Grossman et al. 2002, Grossman and Upton 2006, Meyer et al. 2006, Robison et al. 2006, Asaro and Creighton 2011) suggest that there may be generalized value of systemic tip moth control to enhance pine seedling survival and

vigor during plantation establishment. Mortality at LCP was extremely low (3%) and not affected by any of the experimental factors, probably reflecting the more favorable climatic conditions (Figure 1) and higher availability of soil resources at such operationally managed LCP sites (Allen and Campbell 1988). Higher soil resource availability may have played a role in the observed decrease in partitioning to fine root biomass (and the fraction of annual gross primary production allocated to fine root turnover) at LCP (0.6% of total biomass) than at UCP (2.7%), which has been advanced as a mechanism of greater aboveground productivity with advanced silviculture (Albaugh et al. 1998).

Stand-Level Biomass Production and C Gain

Scaling from individual trees to the stand, our results clearly show systemic protection from tip moth greatly enhanced early biomass production in loblolly pine plantations and the relative magnitude of the response was greatest at the lower site index (UCP) where higher levels of tip moth control were also observed. This provides strong support for our first hypothesis. However, interaction of the tip moth protection treatment with the whole-plot factors (herbicide at UCP and P fertilization at LCP) did not follow our expectations. The herbicide treatment at UCP was marginally significant ($P = \sim 0.07$) for biomass production, and there was a significant herbicide \times tip moth control interaction for height growth (Tables 2 and 3); however, there was no statistically significant herbicide effect (or interaction) on infestation rate. Therefore, results provided some, but perhaps not strong, support for our second hypothesis that decreased herbaceous competition would enhance productivity responses to tip moth control. Although many studies of the effects of weed control on tip moth infestation have been conducted (Ross et al. 1990, McCravy and Berisford 2001, Asaro et al. 2003, Ross et al. 2005), results have varied and a consensus remains elusive. Lack of growth response to P fertilization at LCP indicates that P availability in the low P treatment was sufficient to meet demand of the small trees over the first 2 years of establishment but does not preclude an effect later in stand development when the trees are larger and P demand is correspondingly greater (Allen and Campbell 1988). Any differences in tissue nutrient concentrations from the fertilization treatment were not sufficient to alter tip moth infestation. Similar to the herbicide literature, there have been mixed results on the effects of N and P fertilization on tip moth infestation (Asaro et al. 2003, Ross et al. 2005), and a better understanding of tip moth control responses to variation in resource availability is still needed.

In contrast to Asaro and Creighton (2011), enhanced stand-level productivity with tip moth control in the current study was driven by both improved individual tree performance and decreased population-level mortality. At the site of higher resource availability (LCP), enhanced productivity was driven solely by increases in individual tree performance. It is interesting that there was such a great difference in stand-level productivity between the UCP and LCP sites planted with exactly the same genetics at exactly the same time. Averaged over all genotypes, total stand-level biomass (above- and belowground) after 2 years of growth without tip moth control was 114.5 (17.0) kg ha⁻¹ at UCP compared with 2,158.7 (239.8) kg ha⁻¹ at LCP (Table 4), a remarkable 19 times more biomass produced at the LCP site. The level of productivity at LCP is comparable to that in Aspinwall et al. (2011), who reported an average 2-year total biomass of approximately 1,471.3 (30.1) and 2,824.1 (31.0) kg ha⁻¹ across 10 genotypes planted at 539 and 1,077 trees

ha⁻¹, respectively. The slightly higher productivity of Aspinwall et al. (2011) could have been due to different genetics, higher planting density, or, importantly, much milder (warmer on average, with few extreme low temperature events) meteorological conditions during the establishment of that study during spring 2005 (National Climatic Data Center, pers. observ., Asheville, NC). These rates of productivity are consistent with other reports of highly productive pine plantations undergoing intensive silviculture (Burke et al. 2003, Roth et al. 2007, Samuelsson et al. 2008).

Averaged across genotypes, systemic protection from tip moth increased total 2-year stand-level biomass by 150% at UCP and 11.5% at LCP. However, even at LCP the largest and most responsive genotypes showed an increase of 20–30%. In the extreme case of genotype C2 at UCP, where interacting stresses led to poor stand productivity (62.9 kg ha⁻¹) and very high mortality, use of systemic tip moth control enhanced total biomass production by 224% and avoided what could have been plantation failure. Although the extent to which these early enhancements in plantation productivity persist through time remains to be seen, our results show they are already accelerating the rate at which the trees outcompete herbaceous competition, resulting in more robust plantation establishment, early stand productivity, and consequently C gain. Greater leaf area production results in higher light interception fueling greater productivity above- and belowground, in turn delivering greater organic C inputs to the forest floor and soil microbial communities. These processes are increasing the C sink strength of the young pine stands and may result in significantly shorter rotation lengths, depending on silvicultural objectives (e.g., pulp, bioenergy, and saw timber). Ultimately, systemic tip moth control has the potential to enhance regional C storage capacity by increasing the establishment success and productivity of intensively managed pine plantations, including the production of coarse root systems and ephemeral litter inputs that fuel the formation of forest floor and mineral-associated soil organic C.

Conclusions

This study demonstrates that during high tip moth population levels, use of systemic insecticides at planting may result in greater individual pine seedling growth and decreased population-level mortality over the first 2 years of stand development. Both factors contribute to greater plantation establishment success and higher productivity. Our data also suggest that removal of the biotic stress of tip moth damage may increase tree seedling tolerance to other environmental stresses, such as extreme weather events. These findings have important implications for the economics of plantation establishment and possibly regional C cycling, because it is strongly affected by forest productivity.

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