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Xylem Transport Models Optimize Effectiveness of Systemic Insecticide Applications for Controlling Hemlock Woolly Adelgid *(Adelges tsugae)*

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Cover photos: Sap flow probes in hemlock trees (left) and tree selected for stem injection of imidacloprid (right).

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Abstract

The hemlock woolly adelgid (HWA, *Adelges tsugae* Annand) is causing widespread decline and mortality of eastern hemlock trees (*Tsuga canadensis* (L.) Carr.). Stem injection of insecticide is widely used as a control measure, but its effectiveness depends on individual tree hydraulic characteristics. Recent work has shown that eastern hemlock daily water use is exponentially related to tree diameter, with smaller-diameter trees using significantly less water than larger-diameter trees. In this study we modeled daily water use for 20 eastern hemlock trees across a range of diameters. Based on expected daily water use and, thus, potential xylem transport of insecticide, we applied a dosage estimated to achieve a lethal and uniform xylem sap concentration of imidacloprid to half the trees (xylem transport treatment), and treated the remaining half based on the manufacturer-recommended dosage (MFR treatment), which is a linear function of tree diameter. At 4 and 56 weeks after treatment, we assessed all trees for the presence or absence of new shoot growth and live HWA population density. We found that both treatment dosages significantly reduced live HWA populations; however, 4 weeks after treatment, live HWA population density was 32 percent lower (LSMEANS) on xylem transport treatment trees compared with MFR treatment trees (treatment by time interaction, $P = 0.006$). Both treatment dosages also significantly increased the proportion of new shoot growth; however, over time xylem transport treatment trees had a significantly greater increase in new shoot production compared with MFR treatment trees. We conclude that dosages based on a xylem transport model not only significantly improved tree health more than the trees receiving the current recommended dosage, but also caused greater reductions in the live HWA population. Improving treatment dosages would reduce treatment cost, nontargeted effects, and would allow land managers to treat a greater number of trees.

Keywords: Eastern hemlock, hemlock woolly adelgid, imidacloprid, insecticide efficacy, sap flow, systemic insecticide, transpiration.

Introduction

Eastern hemlock (*Tsuga canadensis* (L.) Carr.) trees of all ages and sizes in the eastern and southernmost portion of their range are declining and dying as a result of attack by a nonnative invasive insect, the hemlock woolly adelgid (HWA, *Adelges tsugae* Annand) (Orwig and others 2002, U.S. Department of Agriculture 2006). Eastern hemlock decline and mortality has been rapid especially in the Southern Appalachians of Virginia and North Carolina (Nuckolls and others 2009, Skinner and others 2003). Because eastern hemlock has no known resistance to HWA, mortality can occur after 3 or more years of infestation (Nuckolls and others 2009, Orwig and others 2002). Eastern hemlock trees infested with HWA display progressive canopy thinning from decreased needle, bud, and new shoot production (Cobb and others 2006, Eschtruth and others 2006, Jenkins and others 1999, McClure 1991, McClure and Cheah 1999, Orwig and Foster 1998, Stadler and others 2005).

Chemical treatments have been effective in controlling HWA on individual trees, and application methods include foliar sprays and soil and stem application of systemic insecticides (e.g., imidacloprid, a chloronicotinyl (1-[(6-chloro-3-pyridinyl) methyl]-N-nitro-2-imidazolidinimine) insecticide) (Cowles 2009, Cowles and others 2006, Fidgen and others 2002, McAvoy and others 2005, Steward and Horner 1994, Webb and others 2003). The effectiveness of soil and stem applications, however, has varied based on injection method, timing of application, and other tree-specific characteristics (Cowles and others 2006, Doccola and others 2003, McAvoy and others 2005, Tattar and others 1998). Because uptake and transport of systemic insecticides occur via mass flow in the transpiration stream (Byrne and Toscano 2006, Castle and others 2006, Tattar and others 1998), treatment efficacy may be linked to the volume and velocity of xylem water movement, and thus the concentration of the insecticide in the xylem sap.

Differences in tree size and climate affect the amount and timing of water use among trees. For example, recent work (Ford and Vose 2007, Ford and others 2007) has shown that eastern hemlock daily water use is exponentially related to tree diameter, with smaller-diameter trees using significantly less water than larger-diameter trees. In addition, models have been developed that predict daily tree water use (and thus potential imidacloprid uptake and transport) from climatic variables (average daytime air temperature and vapor pressure deficit), day of the year, and tree diameter at breast height (d.b.h.) (Ford and others

2007). The exponential relationship between mass flow of water and tree size in eastern hemlock means that an exponential volume or mass of insecticide should also be applied to trees per unit diameter to achieve a consistent and known concentration in the tree xylem sap across tree sizes. Most previous studies of imidacloprid effectiveness used a constant dosage per unit diameter, consistent with the manufacturer-recommended dosage (MFR) (Doccola and others 2003, 2005; Fidgen and others 2002, McAvoy and others 2005, Webb and others 2003). Based on our earlier research on hemlock water use (Ford and others 2007), we predict that the dosages used in those studies would have resulted in imidacloprid concentrations higher than required for a lethal dose for smaller-diameter trees and lower than required for lethal concentrations in larger trees (Cowles 2009, Cowles and others 2006). For example, if the recommended dosage is 0.55 g active ingredient (AI) cm^{-1} d.b.h., an 80-cm tree would receive 44 g of AI, while a 20-cm tree would receive 11 g of AI. Under the same climatic conditions, estimated daily water use by those trees would predict mean imidacloprid concentration of 0.22 g l^{-1} for the 80-cm tree and 2.2 g l^{-1} for the 20-cm tree. This tenfold difference in imidacloprid concentration could affect the effectiveness of HWA treatments and result in variable efficacy among trees of different sizes (Byrne and Toscano 2006, Doccola and others 2003).

Imidacloprid is a highly effective insecticide (Elbert and others 1991, Nauen and Elbert 1994), and several studies have shown that HWA populations are significantly reduced

Table 1—Characteristics of experimental trees

Treatment[a]	Replicate	d.b.h.[b]	Expected daily water use[c]	Treatment dosage
		cm	*kg*	*mg AI tree^{-1}*
Xylem transport	1	10.9	2.64	221
	2	17.4	3.93	443
	3	20.9	4.86	443
	4	24.6	6.09	664
	5	30.8	8.89	996
	6	38.5	14.22	1328
	7	41.2	16.77	1661
	8	52.2	32.80	3321
	9	59.5	51.20	4982
	10	61.4	57.49	5646
MFR	1	11.6	2.76	664
	2	13.3	3.06	886
	3	20.9	4.86	1328
	4	26.2	6.72	1661
	5	31.0	9.00	1993
	6	35.5	11.84	1993
	7	40.1	15.68	2325
	8	50.1	28.86	2989
	9	54.2	37.06	3321
	10	65.0	71.61	3985

[a] Treatments consisted of imidacloprid dosages scaled as a linear function of stem diameter (recommended by the manufacturer, MFR) or as an exponential function of stem diameter (based on a xylem transport model). The mass of active ingredient (AI) in the latter dosage was estimated to achieve xylem sap concentrations required for 100 percent HWA mortality based on controlled laboratory experiments (Cowles and others 2006).

[b] Diameter at breast height, 1.3 m above ground height.

[c] Expected daily water use was modeled using tree diameter and long-term climate data (Model 1 in Ford and others 2007) for October 2007.

on trees receiving imidacloprid compared to those not receiving imidacloprid (Doccola and others 2003, 2005). Less is known about optimal dosages, especially in the Southern Appalachians where the mild climate promotes year-round water use in eastern hemlock. Hence, our approach was to compare efficacy results on trees receiving different dosages as opposed to results from comparisons with untreated controls. Specifically, our objectives were to compare HWA infestation and new shoot production on trees experiencing the same climate but receiving different imidacloprid dosages: those based on a linear scalar of tree diameter (e.g., consistent with the MFR dosage), or an exponential scalar of tree diameter (e.g., based on xylem sap transport models). We hypothesized that (1) live HWA population will be lower on trees receiving dosages that account for variation in xylem sap transport compared with trees receiving the linearly scaled dosage treatments, and (2) new shoot production (a proxy for tree health) will be greater on trees receiving the exponentially scaled dosage treatment compared with trees receiving the linearly scaled dosage treatment.

Methods

Study Site

The study site was located in a cove habitat in a third-order treatment catchment (WS28) in the Coweeta basin in the Nantahala Mountain Range of western North Carolina, USA. WS28 is a 144-ha watershed ranging from 900 to 1500 m in elevation with a moist valley or cove at its center (39 ha) wherein slopes average 27 percent. This watershed was a multiple-use demonstration treatment watershed, with the cove area thinned in 1963–64 (then a 40-year-old stand) to promote growth of yellow-poplar (*Liriodendron tulipifera* L.), eastern hemlock, and flowering dogwood (*Cornus florida* L.) (Douglass and Swank 1976, Swank 1998). Climate in the Coweeta basin is classified as marine, humid temperate (Swift and others 1988). Long-term average annual precipitation and temperature near WS28 are 1948 mm and 11.6 °C, respectively (Swift and others 1988).

Within the cove, we selected 20 eastern hemlock trees spanning a d.b.h. range of 10 to 65 cm (table 1). No visible differences in health among selected trees existed. Based on visual inspection, all trees were infested with HWA; however, tree crowns were still in good condition (i.e., < 30 percent needle loss) and appeared healthy at the beginning of the study. None of the trees had been previously treated by chemicals or biological control organisms.

Field Treatments

We ordered the 20 trees by diameter and divided the diameter range into 10 diameter categories. Two trees in each diameter category were assigned to receive one of two treatment dosages of imidacloprid. Thus, for each treatment, 10 trees spanning a range of diameters were used as replicates (n = 10 per treatment). Although the 10 replicates were not the same size diameter, the same amount of diameter variation existed in the 10 replicates of both treatment categories. We used a range of tree diameters for two reasons. First, we wanted to encapsulate the natural variation in tree replicates that is evident in a second-growth Southern Appalachian forest. Second, we expected to find an effect of diameter with the two treatments (described below), and using a range of tree diameter replicates would allow the effect of diameter to be explored though correlation and regression techniques.

The secondary peak of water use of eastern hemlock trees in the Southern Appalachians occurs in October (Ford and Vose 2007), which is also the timing of peak HWA feeding activity after breaking diapause (Ward and others 2004). We applied a water use model (Model 1 in Ford and others 2007) to the 20 eastern hemlock trees to estimate average daily water use for October 2007 (table 1) based on tree diameter and long-term climate data. We combined the model-based predictions of daily water use (and thus potential xylem sap dilution and transport of the insecticide) with the HWA mortality versus imidacloprid xylem sap concentration relationship of Cowles and others (2006) extrapolated to 100 percent HWA mortality (e.g., 100 ppm imidacloprid concentration). We applied this dosage to half the trees (xylem transport treatment, n = 10, table 1 shows actual treatment dosages). The remaining half of the trees were treated with the MFR dosage (n = 10): 56–67 mg AI cm^{-1} d.b.h., following the manufacturer-recommended dosages, except for the three trees < 25 cm, which we dosed at the same rate recommended for trees > 25 cm, so that this group of trees would receive about the same dosage (table 1 shows actual treatment dosages). All trees were treated during the first week in October 2007. Dosages were applied using the appropriate number of 2 or 3 ml Mauget® Imicide® capsules (10 percent imidacloprid, 110.7 mg ml^{-1}, J. J. Mauget Co., Arcadia CA). The contents of each capsule were introduced into the xylem stream by drilling holes 2 to 3 cm deep, equally spaced around the circumference of the tree at about 1 m above ground height. Each hole was angled slightly downward, the capsule nozzle was inserted into the hole, air bubbles were eliminated, and the contents of the capsule effused into the xylem stream. The contents of most capsules emptied within 24 hours after installation. If the contents of a capsule did not empty within 24 hours, the capsules were primed again by squeezing repeatedly to remove any air bubbles. All capsules had emptied after 72 hours and were thus removed from each tree.

Sampling

At 4 and 56 weeks after the treatment application, we sampled branches from all trees by dividing the canopy into 12 sections: vertically the canopy was divided into 3 sections based on height of the live crown; radially the canopy was divided into quarters based on cardinal direction. From each tree section, we excised a main branch and clipped four to five subsample branches and placed them into a bag with a towel saturated with deionized water. All samples were refrigerated until HWA population assessment. Counts of live HWA population were assessed on all 12 subsampled branches by randomly choosing 3 of the possible 4 to 5 subsampled branches, and then choosing 5 sub-subsamples per branch. From each sub-subsample, we removed the terminal 4 cm of growth and counted all live HWA nymphs and adults on this length using a stereo microscope and a dissecting probe to assess HWA viability. No eggs or ovisacs were included in these counts. The presence or absence of new tree growth was also noted on each sample. Therefore, for each tree, 7.2 m of terminal branch growth was analyzed for HWA populations and the presence of new growth (4 cm x 12 tree sections x 3 subsample branches x 5 sub-subsamples = 7.2 m). All HWA population assessments were completed within 6 weeks of sampling.

Statistical Analyses

To determine if significant differences in live HWA populations existed among trees with differing treatments, we used a generalized linear model (McCullagh and Nelder 1989) to analyze the counts of live individuals with a Poisson probability density function and a log link. We modeled HWA counts per unit length as a function of treatment, sampling time, and their interaction using analysis of deviance (a generalization of analysis of variance, McCullagh and Nelder 1989) (PROC GENMOD, SAS Institute, Inc. Cary, NC, USA).

To determine if significant differences in the presence or absence of new shoot growth existed among trees with differing treatments, we again used a generalized linear model with a binomial probability density function and a logit link. We modeled the proportion of samples with the presence of new growth as a function of treatment, sampling time, and their interaction using analysis of deviance (PROC GENMOD). We used the Type III approach to both analyses of deviance and reported the estimated least-squares means where appropriate. All statistical tests were performed at $\alpha = 0.05$ level.

We computed simple correlation coefficients (Pearson's R) between the difference in proportion of new shoot growth in 2008 from 2007 and d.b.h. for each tree. Because we expected this relationship to be negative for the trees with linearly scaled dosage treatments, we utilized a one-tailed test of the transformed Fisher's z statistic. Finally, we computed a simple nonparametric correlation coefficient (Spearman's R_S) between the presence of new shoot growth and live HWA population density across both sampling times and treatments.

Results and Discussion

Live HWA population density differed significantly between treatments ($\chi^2_{0.05,1} = 23.75$, P < 0.001) and sampling times ($\chi^2_{0.05,1} = 6.18$, P = 0.01); however, the relationship between treatments was not consistent between sampling times (interaction $\chi^2_{0.05,1} = 7.62$, P = 0.006; fig. 1). At 4 weeks after

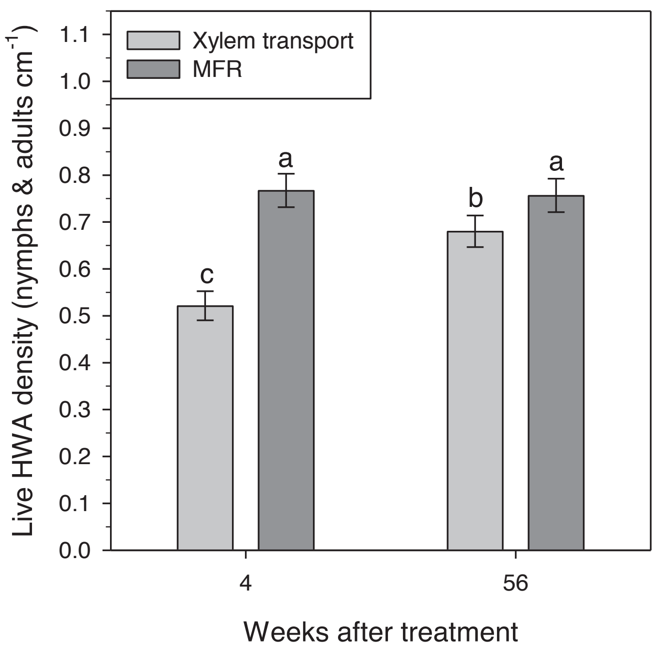

Figure 1—Live hemlock woolly adelgid (HWA) population density on trees assessed 4 and 56 weeks after treatment. Treatments are imidacloprid dosages based on linear (MFR, manufacturer-recommended) or exponential (xylem transport model) function of stem diameter. Vertical bars are the least-squares means (LSMEAN) and error bars are one standard error of the LSMEAN. Vertical bars with different lowercase letters are statistically different between times and treatments at $\alpha = 0.05$.

Table 2—Proportion of sample branches on each tree with new shoot growth at 4 and 56 weeks after treatment, and the factor of increase between sampling times

	Proportion of sample branches with new growth[b]		Factor of increase in LSMEANS estimates of proportion of new growth from pre- to post-treatment
Treatment[a]	4 weeks	56 weeks	
Xylem transport			
LSMEAN	0.01	0.61	66.2
(Upper–Lower)	(0.003–0.03) c	(0.51–0.74) a	
MFR			
LSMEAN	0.12	0.59	4.8
(Upper–Lower)	(0.09–0.16) b	(0.48–0.69) a	

[a] Treatments consisted of imidacloprid dosages scaled as a linear function of stem diameter (recommended by the manufacturer, MFR) or as an exponential function of stem diameter (based on a xylem transport model).

[b] Least-squares means (LSMEAN) and upper and lower standard error plus LSMEAN given. Different lowercase letters beside treatment LSMEANS are statistically different between times and treatments at α=0.05.

treatment application, live HWA population density was 32 percent lower (LSMEANS) on trees receiving the xylem transport dosage treatment compared with trees that received the MFR dosage treatment. Hence, HWA control was more effective when dosage was adjusted for differences in xylem sap transport to provide a lethal concentration across all tree sizes, thus supporting our first hypothesis. At 56 weeks after treatment, live HWA population density remained lower on trees that received the xylem transport dosage treatment compared with trees that received the MFR dosage treatment; however, it was only 10 percent lower (LSMEANS). The live HWA population density did not change over time on trees that received the MFR dosage treatment.

The proportion of new shoot growth also differed significantly between treatments ($\chi^2_{0.05,1}$ = 9.30, P = 0.002) and sampling times ($\chi^2_{0.05,1}$ = 82.26, P < 0.001). The increase in new shoot growth between sampling times was significantly greater in trees that received the xylem transport dosage treatment compared with trees that received the MFR dosage treatment (interaction $\chi^2_{0.05,1}$ = 10.37, P = 0.001; table 2), confirming our second hypothesis. Differences in new shoot growth assessed at 4 weeks after treatment reflected conditions before treatments, as this shoot growth occurred several months before our experimental treatments began. New shoot growth assessed at 56 weeks reflected the growth that was put on the spring after imidacloprid exposure, and this increased for both treatment groups. On average, trees from both treatments had 95 percent of samples showing new shoot production;

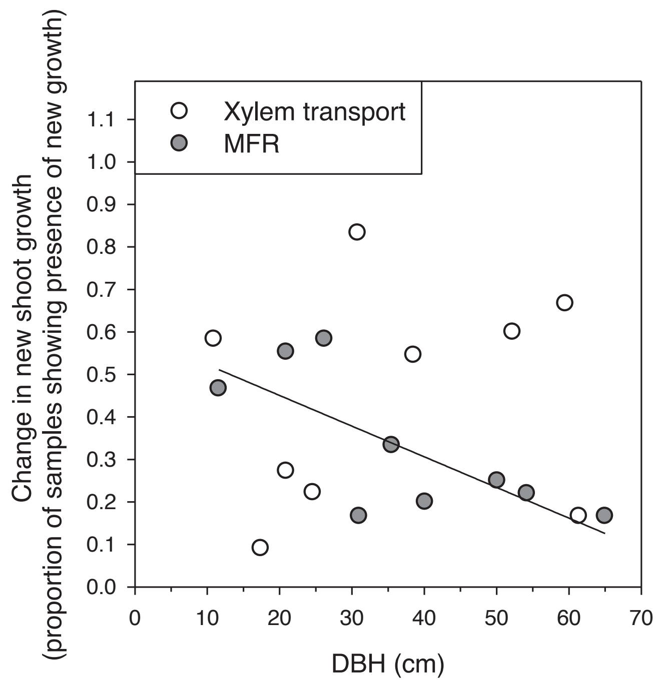

Figure 2—Change in new shoot growth among trees spanning a range of stem diameters (d.b.h.), i.e., the difference in proportion of sample branches showing presence of new growth from pretreatment to 56 weeks post-treatment. Treatments are imidacloprid dosages based on linear (MFR, manufacturer-recommended) or exponential (xylem transport model) function of stem diameter. Line shows an ordinary least–squares regression fit to MFR data (R^2 = 0.54, P = 0.02; y = 0.59 – 0.007x). One tree from each treatment group showed no new shoot production after treatment, thus n = 9 for both treatments.

however, from one growing season to the next, trees receiving the xylem transport dosage treatment had a greater increase in new shoot growth (i.e., a 66-fold increase from 4 to 56 weeks for xylem transport versus a 5-fold increase for MFR) compared with trees receiving the MFR dosage treatments (table 2). The difference in proportion of new shoot growth from 2007 to 2008 was negatively correlated with d.b.h. in the trees receiving the MFR treatment (R = 0.74, z = 0.95, P = 0.01; fig. 2), indicating that the larger-sized trees did not respond as well as smaller-sized trees in this treatment. In contrast, there was no correlation between tree size and new shoot growth in xylem transport dosage treatments (R = 0.28, z = 0.29, P = 0.74; fig. 2).

Using dosages based on xylem transport models compared to manufacturer-recommended dosages resulted in a lower amount of imidacloprid applied to small diameter trees, but a greater amount applied to large diameter trees. The tree diameter where the amount of imidacloprid applied using a dosage based on the xylem transport model equaled the amount applied using the MFR dosage was ~48 cm. Live HWA population densities showed that for small diameter trees, the xylem transport and MFR dosages were equally effective. In contrast, in the larger-diameter trees, xylem transport dosages were more effective than the MFR dosages. These results confirm those of Cowles (2009), who found that low dosages of soil-applied imidacloprid were effective at reducing HWA populations on small diameter trees (0.125 g AI 2.5 cm^{-1} d.b.h.), but that the effective dosage required to reduce HWA populations by the same amount on large diameter trees was fourfold greater (0.5 g AI 2.5 cm^{-1} d.b.h.). Results from current and previous studies (Ford and Vose 2007, Ford and others 2007) suggest that the primary mechanism of systemic imidacloprid effectiveness against HWA is linked to the volume and velocity of xylem water movement, and thus concentration of the active ingredient in the xylem sap. By extension, we would expect efficacy of other systemic insecticides (e.g., dinotefuran) to require an exponentially scaled dosage of d.b.h., including those that are soil applied and absorbed through the root system (e.g., soil drench or soil injection). Previous studies show some indication that soil-applied imidacloprid is more effective at reducing HWA population density than stem-injected imidacloprid treatment because it increases in concentration in the foliar tissue over time (Tattar and others 1998) and remains effective at reducing HWA populations for many years (Cowles 2009). A direction for future work would be to use a similar approach as presented here to optimize soil imidacloprid applications across tree sizes and climates with information on tree water use.

Numerous studies have shown that imidacloprid is an effective chemical treatment against HWA. Although we did not sample HWA populations on our trees before treatment, live HWA population density in non-treated eastern hemlock trees sampled in the Coweeta basin during

Table 3—Example of tree size and density in *Tsuga canadensis*-dominated (comprising at least 50 percent of the basal area) riparian areas in the Coweeta basin

	Treatment[a]				
Replicate plot	MFR	Xylem transport	Hemlock diameter range		Hemlock density
	g AI ha^{-1}		*cm*		*trees ha^{-1}*
1	537.78	320.62	2.6	44.4	375
2	789.25	603.09	7.2	60.5	475
3	674.68	531.43	6.5	63.3	450
4	527.70	243.13	4.0	34.3	575
5	1027.70	662.46	2.8	61.0	875
6	748.16	391.99	1.9	50.3	1,150
7	592.20	302.98	1.8	46.1	950
8	485.63	788.75	2.8	70.5	375
Average	672.89	480.56			
(SE)	(63.53)	(69.05)			

[a] Potential amount of imidacloprid (active ingredient, AI) applied per hectare if all hemlock trees were treated with dosages calculated according to the manufacturer's recommendations (MFR) or the xylem transport model.

the study period (fall 2008) averaged 2.1 (±0.5 SE) nymphs and adults cm^{-1}.[1] Compared with our experimentally treated trees, these untreated trees had live HWA populations that were about threefold higher, confirming the effectiveness of imidacloprid for controlling HWA. While our exponentially scaled treatment dosage was intended to achieve a concentration in the tree that would result in 100 percent HWA mortality, live HWA nymphs and adults were still evident on our treated trees at 4 and 56 weeks following treatment. Previous studies have shown that a single application of soil-applied imidacloprid can remain effective against HWA for at least 3 years (Cowles 2009); however, less is known about the long-term effectiveness of stem-injected imidacloprid.

Management Implications

Trees receiving dosages based on a xylem transport model were significantly healthier compared with dosages based on a linear increase in AI with tree diameter—they had significantly lower densities of live HWA populations and a greater proportion of new shoot growth. Hence, our results clearly indicate that improved control is possible when dosages are adjusted for climate and tree size-based variation in xylem sap flow. Because of the effectiveness of imidacloprid as an insecticide, land managers are limited to a maximum application of 0.45 kg AI ha^{-1} in the Southern Appalachians to prevent nontarget and offsite impacts. Our xylem transport-based dosage application resulted in less AI applied (19 705 mg for xylem transport versus 21 145 mg for MFR) to the same number of similar-sized trees (table 1) and resulted in greater HWA control and tree recovery. To examine this outcome further, we used tree diameter and density data from eight randomly located plots in riparian areas within the Coweeta basin that contained at least 50 percent *T. canadensis* (Nuckolls and others 2009) to calculate dosage. Using those data, dosage determined with the xylem transport model would require 29 percent less AI applied per ha compared with the MFR dosage (table 3). The combination of increased effectiveness and lower application rates suggests that our xylem transport dosages have the potential to significantly improve the control of HWA in the Southern Appalachians. Chemical treatment of eastern hemlock for HWA infestation is a short-term solution, and treatments are often reapplied after a few years. In riparian trees that may warrant systemic injection of imidacloprid to protect against contamination of surface water sources, dosages based on xylem transport would likely result in increased tree health and fewer live HWA infesting large-diameter trees compared with MFR dosages. In nonriparian areas, improving treatment dosages would not only reduce cost and nontargeted effects (Dilling and others 2009, Kreutzweiser and others 2009, Raupp and others 2004), but would potentially allow land managers to treat a greater number of trees in most Southern Appalachian stands. Finally, a spreadsheet application that may be used to estimate tree water use for a given tree diameter and treatment window, as well as the dosage (g AI) based on the xylem transport of the systemic insecticide, can be found at http://www.srs.fs.usda.gov/pubs/ja/31601-Model_application.xls.

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The hemlock woolly adelgid (HWA, *Adelges tsugae* Annand) is causing widespread decline and mortality of eastern hemlock trees (*Tsuga canadensis* (L.) Carr.). Stem injection of insecticide is widely used as a control measure, but its effectiveness depends on individual tree hydraulic characteristics. Recent work has shown that eastern hemlock daily water use is exponentially related to tree diameter, with smaller-diameter trees using significantly less water than larger-diameter trees. In this study we modeled daily water use for 20 eastern hemlock trees across a range of diameters. Based on expected daily water use and, thus, potential xylem transport of insecticide, we applied a dosage estimated to achieve a lethal and uniform xylem sap concentration of imidacloprid to half the trees (xylem transport treatment), and treated the remaining half based on the manufacturer-recommended dosage (MFR treatment), which is a linear function of tree diameter. At 4 and 56 weeks after treatment, we assessed all trees for the presence or absence of new shoot growth and live HWA population density. We found that both treatment dosages significantly reduced live HWA populations; however, 4 weeks after treatment, live HWA population density was 32 percent lower (LSMEANS) on xylem transport treatment trees compared with MFR treatment trees (treatment by time interaction, $P = 0.006$). Both treatment dosages also significantly increased the proportion of new shoot growth; however, over time xylem transport treatment trees had a significantly greater increase in new shoot production compared with MFR treatment trees. We conclude that dosages based on a xylem transport model not only significantly improved tree health more than the trees receiving the current recommended dosage, but also caused greater reductions in the live HWA population. Improving treatment dosages would reduce treatment cost, nontargeted effects, and would allow land managers to treat a greater number of trees.

Keywords: Eastern hemlock, hemlock woolly adelgid, imidacloprid, insecticide efficacy, sap flow, systemic insecticide, transpiration.