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# The tree crown distribution of hemlock woolly adelgid, *Adelges tsugae* (Hem., Adelgidae) from randomized branch sampling

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**Abstract:** An exotic insect, the hemlock woolly adelgid, *Adelges tsugae* Annand (Hem., Adelgidae), is spreading through eastern North America, killing hemlock trees [*Tsuga canadensis* (L.) Carrière], and thereby impoverishing ecosystems. *Adelges tsugae*, like many alien invasive insects, is difficult to monitor or sample in the forest. Monitoring of *A. tsugae* has been hampered by lack of information about its distribution within tree crowns. In order to assist future monitoring and biocontrol of *A. tsugae*, this study investigates the crown distribution of *A. tsugae* by sampling from the entire height of mature hemlock trees in a forest with an established infestation. In addition to *A. tsugae*, sampling includes scale insects, which are another group of important pests on hemlock trees. This study demonstrates the utility of a randomized branch sampling (RBS) plan for monitoring both invasive insects as well as native insects that are difficult to sample. Results from the RBS show that in trees with high populations of *A. tsugae*, branches from the lower crown have slightly higher densities of *A. tsugae* than upper crown branches. In trees with low *A. tsugae* populations, the upper crown may have higher *A. tsugae* densities than the lower crown. North pointing branches also have higher densities of *A. tsugae* than branches pointing in other cardinal directions. Future sampling efforts for *A. tsugae* can take advantage of higher densities in certain portions of the crown to increase accuracy.

**Key words:** *Fiorinia externa*, hemlock scale, invasive species, monitoring

## 1 Introduction

The sampling of arboreal insects can present a challenge for researchers and forest managers. Researchers are able to sample some species effectively using attractants such as light traps or pheromones (Pedigo and Buntin 1993). Species with limited or no independent movement can make sampling more difficult. Exotic insects present an additional difficulty because their habits and potential attractions are often unknown. At the same time, exotic species often pose a much greater threat to ecosystem stability than native insects. The exotic insects introduced to forests 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 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).

The hemlock woolly adelgid, *Adelges tsugae* Annand (Hemiptera: Adelgidae), is a prime example of both the destructive potential and the difficulty of sampling exotic insects. *A. tsugae* has caused widespread mortality of eastern hemlock trees [*Tsuga canadensis* (L.) Carrière] and threatens to remove the species from

North American forests. *Adelges tsugae*-induced mortality is a concern because hemlock provides important forest structure, habitat, economic benefits and aesthetic values in eastern North American forests. Another alien insect, the hemlock elongated scale (*Fiorinia externa* Ferris Hem., Diaspididae) is also spreading through the forests of eastern Northern America. *Fiorinia externa* can cause damage to hemlock trees and may accelerate hemlock mortality (McClure 1980; Danoff-Burg and Bird 2002). Therefore, although it is not the main focus of this study, we have included scale insects in our sampling.

Researchers have learned a great deal about the biology and control of *A. tsugae* (Onken and Reardon 2005), but there is still no established sampling or monitoring protocol for *A. tsugae*. Sampling *A. tsugae* is complicated by its small size, lack of pheromones, passive dispersal and tree crown habitat. *Adelges tsugae* does not react to any known attractants (Ward et al. 2004). In fact, *A. tsugae* is capable of directed movement for only a brief portion of its life. While able to crawl, *A. tsugae* only travels short distances along hemlock branches to new feeding sites. *Adelges tsugae* is passively dispersed within and between forest stands with the aid of wind, animals and humans (McClure 1990). *Adelges tsugae*'s preference for hemlock, which

can reach 50 m in height (Godman and Lancaster 1990), also makes sampling arduous.

In this study, we investigated whether *A. tsugae* populations varied significantly with branch height, branch aspect or crown stratum. Our goal was to test whether the current sampling paradigm for *A. tsugae*, in which only the lower crown is sampled, affects estimates of *A. tsugae* density. This paper also explains and demonstrates the utility of randomized branch sampling (RBS) for arboreal insects, particularly those that are difficult to monitor. Our analysis of scale insects in hemlock trees is of both ecological interest, because of the interactions between *A. tsugae* and scale insects, as well as methodological interest, because it shows that RBS can be used for multiple objective sampling.

## 2 Materials and Methods

### 2.1 Study site

We sampled hemlock trees at the Yale Myers Forest, the main land holding in the Yale School Forest system (<http://www.yale.edu/schoolforest>). Yale Myers covers 3172 ha in north-eastern Connecticut at (N42°, W72.1°). The forest is set on rocky terrain cut by a number of parallel, small ridges that run from south-west to north-east. The elevation varies from 190 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 a mean July high 26.4°C, mean January low -8.2°C and median annual precipitation 130 cm (National Climatic Data Center 2004). The forest is a mix of hardwood, pine and hemlock, which grew up after the area had been cleared for agriculture in the late 19th century. The sample sites within the forest were hemlock stands or had a major hemlock component. The forest has been infested with *A. tsugae* since approximately 1990.

### 2.2 Sampling *A. tsugae*

Initial attempts to characterize *A. tsugae* distributions within stands with a binomial sampling method were unsuccessful (Gray et al. 1998). Gray et al. (1998) pointed to the interaction of tree and pest over multiple years as the source of failure for binomial sampling. To avoid the difficulties Gray and colleagues faced with pest and tree interactions, Fidgen et al. (2006) recently developed a binomial sequential sampling plan for *A. tsugae* suitable the early stages of infestation before crown dieback (i.e. the first few years of infestation). Unfortunately, because Fidgen and colleagues' binomial sequential sampling plan is based on trees unaffected by *A. tsugae* it is not suitable for forests with older *A. tsugae* infestations, such as the forest in this study. McClure (1989,1990) sampled *A. tsugae* during wind-aided dispersal with sticky traps. Sticky traps are problematic for two reasons. First, *A. tsugae*'s small size (1.5 mm) makes it a proverbial needle in a haystack. Second, sampling *A. tsugae* during dispersal also has the disadvantage that resulting population estimates cannot be tied unambiguously to a particular tree or location.

Sampling of *A. tsugae* within hemlock tree crowns has, in large part, been limited to those branches within 5 m of the ground (McClure and Cheah 1999; Adams et al. 2002; Casagrande et al. 2002; Cheah and McClure 2002; Danoff-Burg and Bird 2002; Mayer et al. 2002; Fidgen et al. 2006).

Cheah and McClure (2002) used a bucket truck to sample for *A. tsugae* predators and Pontius et al. (2006) used shotgun sampling to measure foliar chemistry of upper crown branches of *A. tsugae*-infested trees. Because of the difficulties in sampling *A. tsugae*, many studies have used tree damage as a surrogate for *A. tsugae* populations (Royle and Lathrop 1997; Orwig and Foster 1998; Bonneau et al. 1999; Brooks 2001; Tingley et al. 2002).

### 2.3 Randomized branch sampling

We used a novel implementation of a well-established sampling methodology called RBS. Researchers have used RBS to estimate fruit production (Jessen 1955), insect densities (Furness 1976), tree weight (Valentine et al. 1984), total foliar area (Gregoire et al. 1995), stem length and surface area (Gregoire and Valentine 1996), needle mass (Gaffrey and Saborowski 1999), tree biomass (Good et al. 2001), coarse woody debris (Gove et al. 2002) and floral distribution (Chen et al. 2003). Although RBS has been used in forest entomology before, this study is a new implementation of RBS to estimate insect populations in entire tree crowns (Valentine and Hilton 1977).

In an RBS scheme, samples are chosen probabilistically, which removes potential for selection bias. Because samples have a known selection probability, design-based inference is possible. In other words, inference about the population sampled with RBS need only rely on the sampling design, and not on any models or assumptions about the population (Gregoire 1998). RBS treats a tree as a series of paths from the ground to each terminal shoot. A path follows randomly selected branches from a chosen start (usually the base of the trunk) to an arbitrary final node. The sample consists of the attribute of interest measured along the path to the final node and on all branches beyond the final node. The RBS path can be terminated at any branching node to allow sampling of entire branches. The closer a final node is to a terminal node, then the sample is smaller, and the easier task of measurement, but small samples may increase variance of the estimator. All branches are treated similarly, including the tree trunk, regardless of size or age. As RBS treats all branches in the same manner there is no need to define 'trunk', 'branch', 'twig' or any other unit of the tree, which makes it easy to implement consistently. The path is created by a series of random selections at each node. Put another way, at each fork in the branch the researcher randomly chooses which branch to follow. The researcher can adjust the probability of selecting a branch to increase the likelihood of sampling more of the quantity of interest, so long as the probabilities at any particular fork sum to one. No design bias is introduced if the selection remains probabilistic. The sample selection probabilities at each node provide an expansion factor to estimate the quantity of interest for the entire tree. More than one path can be selected within one tree, and may coincide with previous paths partially, or even completely. The basic framework of RBS permits further modification such as stratification. Stratification of the tree crown, as with any stratification, can help to reduce the variance of the estimator. Further details of RBS have been described elsewhere (Gregoire et al. 1995; Gregoire and Valentine 1996).

### 2.4 Adaptation of RBS to *A. tsugae*

In this study, we tailored the implementation of RBS to the problem of estimating the number of *A. tsugae* in hemlock crowns. The attribute of interest was the number of sistens per 100 needles of new growth. We counted the number of

sistens per 100 new growth needles in the sample (that is, on the RBS path). We differentiated old and new growth by colour of needles and twigs and then counted both. Under a dissecting microscope, we counted all the sistens on the section of branch selected at the final node of the RBS path. We counted sistens because this provided a measure of *A. tsugae* density that could be tied to a specific time. As sistens are the first *A. tsugae* generation to emerge after hemlocks produce new growth, they settle on this desirable tissue. Once progrediens hatch, counts of *A. tsugae* ovisacs include a combination of two generations and are no longer connected to a specific year. The absolute number of sistens in a tree or branch is hard to place in context and the impact of sistens is related to tree size and health. Focusing on the absolute number of *A. tsugae* would make stand comparisons difficult. Therefore, we used counts of sistens per 100 new growth needles to allow comparison between trees and branches of different sizes and health. We also took advantage of the same samples to record the number of scale insects per 100 needles. There were so few scale insects that we used the number of scale per 100 total needles rather than per 100 new needles.

When sampling *A. tsugae*, we first felled the sample tree to permit access to the full crown. Felling damaged the crowns, but comparisons of branches broken in the fall and all other branches showed no significant difference. Anecdotally, we noticed that branch tips, which were the majority of the samples, were flexible enough to avoid damage during felling. We selected trees randomly from a list we created of those trees in the stand that we could safely fell. No bias was added, unless the population of *A. tsugae* on easy to fell trees differs from more difficult to fell trees. The potential for bias was further reduced by working in recently harvested stands where canopy openings made more trees easy to fell.

After felling the sample tree, we measured tree height and the height of the live crown. We stratified the live crown into equal thirds based on length and took at least three samples from each third. As noted above, the selection probabilities at each node can be adjusted to increase the likelihood of selecting more sistens per 100 new growth needles. We measured the diameter and then calculated the branch cross sectional area of all branches at each node. The selection probability was proportional to the branch cross sectional area divided by the sum of all branch cross-sectional areas at that node. The higher selection probability of larger branches reflected their greater cross-sectional area and their tendency to have more needles and hence more *A. tsugae*.

In this study a field computer, a palm pilot with a custom application, recorded the selection probabilities, provided a pseudo-random number, and selected the branch to be included in the RBS path. When a suitably small branch was selected (< 30 cm in length), we clipped it, placed it in an envelope, and brought it back to the laboratory for counting. In the laboratory, we recorded the length of old and new growth, number of old and new needles, sistens and scale insects. Our counts of scale did not differentiate between elongated *F. externa*, circular hemlock scale (*Nuculaspis tsugae* Marlatt Hem., Diaspididae), native hemlock scale (*Abgrallaspis ithacae* Ferris Hem., Diaspididae) and cryptomeria scale (*Aspidiotus cryptomeriae* Kuwana Hem., Diaspididae) because all four damage hemlock and the combined population of scale insects was below damaging levels in our study site. The number of insects in the sample could be expanded to estimate the total number of insects in the tree using the methodology laid out by Gregoire et al. (1995). In this study, we analysed the number of insects on a per needle basis to make comparison between crown segments. We also catalogued tree and branch attributes such as tree height,

crown height, branch direction and branch height. We recorded the direction that first order branches left the trunk and did not assign a direction to branches near the very top of the crown because they pointed straight up.

In some trees, we found no *A. tsugae* in any of the samples. In these cases, we scoured the tree to determine if there were any *A. tsugae* on the tree. If we discovered *A. tsugae* during this exhaustive search of the entire tree crown, then we clipped the branch segment (< 30 cm) as a purposeful sample. Purposeful samples were important to document very low levels of *A. tsugae* and were also used in the analysis of trees with low overall *A. tsugae* density.

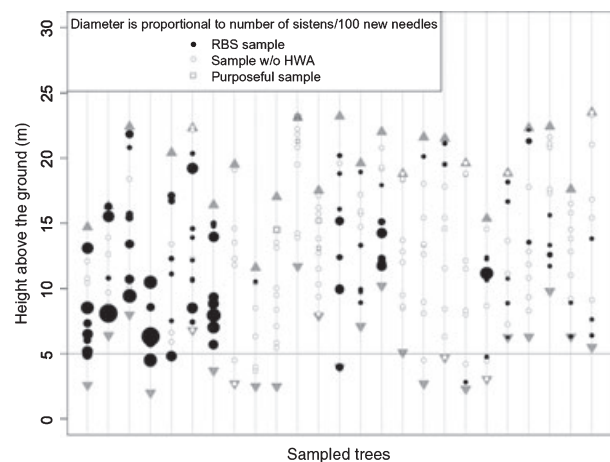
## 2.5 Data analysis

We used a mixed model to compare *A. tsugae* and scale populations between crown segments and directions. We treated crown segments as a fixed effect, trees as a random effect, and branches as repeated measures for comparison of canopy heights and branch direction (Evans 2006). Using GLIMMIX in SAS, we constructed confidence intervals for the least-squares means estimate of mean number of insects per 100 needles in a given crown segment (SAS Institute Inc. 2002). The branch level subsamples were skewed with a large number of zero values, so we used a Poisson distribution with overdispersion in the GLIMMIX model (Evans 2006). We also constructed 90% confidence intervals for the difference between crown segments. The estimators of the number of insects per 100 needles from the RBS sampling provided the data used in the mixed model.

## 3 Results

### 3.1 Branch height

We sampled *A. tsugae* sistens on 225 branches from 25 trees to better understand how *A. tsugae* is distributed through the crown (fig. 1). We divided the crown in sections and compared the number of sistens per 100 new growth needles in each section into order to test for

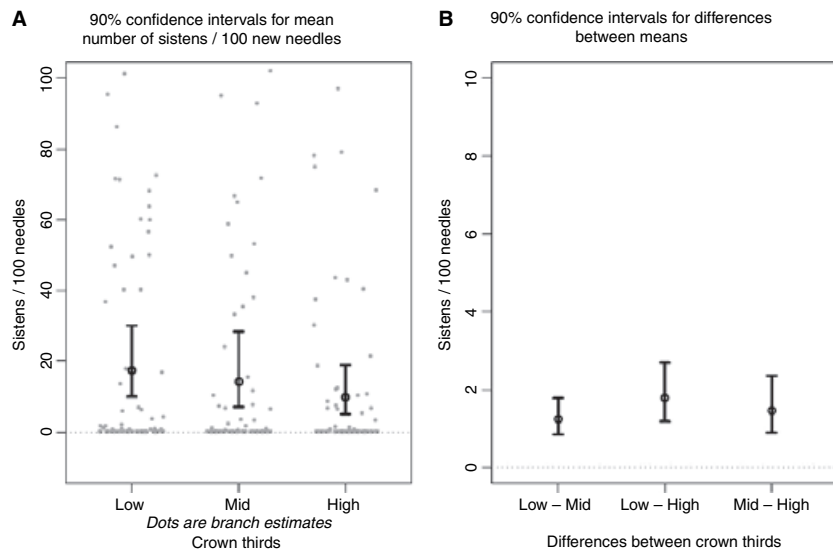


**Fig. 1.** Height above the ground and *Adelges tsugae* populations by tree. The diameter of the circles represents the number of sistens on new growth. The triangles denote the top and bottom of the live crown for each tree, while the small grey open circles indicate the height of samples with no *A. tsugae*

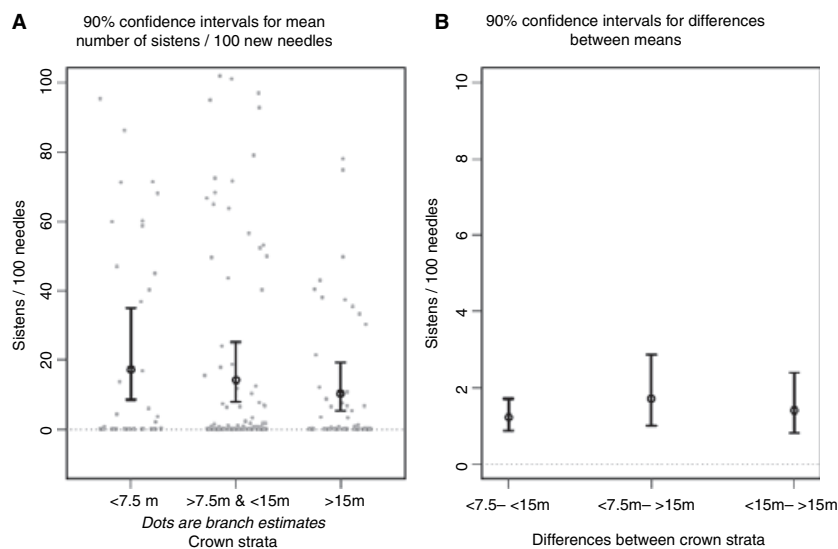
a pattern in branch height and *A. tsugae* density. We analysed the data with each crown split into thirds based on the individual tree's live crown height. We also examined the data based on absolute strata defined by heights above the ground. We used 7.5 m to define the top of the lowest stratum, 15 m to define the top of the middle stratum and 15 m to define the bottom of the top stratum. Some trees had no low or no top stratum under this definition. We estimated both the number of sistens per 100 new growth needles in crown thirds (fig. 2) as well as for absolute crown strata (fig. 3). The lowest crown third had an estimated 1.78

more sistens per 100 new growth needles than the top third (90% confidence interval 1.18–2.68). Both crown divisions suggest a trend of increasing population of sistens per 100 new growth needles lower in the crown. The average number of new growth needles per cm for this study was 13.5 (median 13.1). The average number of new growth needles per cm ranges from 10.6 to 19.1 by tree. The difference in number of new growth needles per cm does not vary significantly by crown strata or crown third at the 95% confidence level.

The overall pattern of decreasing *A. tsugae* density with branch height obscures a very different trend



**Fig. 2.** Confidence intervals (90%) for sistens per 100 new growth needles in crown strata and differences between strata. The confidence intervals in the first panel are for the low, middle and high crown strata. The confidence intervals in the second panel are for the difference between the low and middle crown strata, the low and high crown strata and the middle and high crown strata. The dots represent branch subsamples in both figures ( $n = 225$  branch subsamples, 25 tree samples)



**Fig. 3.** Confidence intervals (90%) for sistens per 100 new growth needles in crown thirds and differences between thirds. The confidence intervals in the first panel are for the crown segments below 7.5, between 7.5 and 15 m, and above 15 m. The confidence intervals in the second panel are for the difference between the crown segment below 7.5 and the segment between 7.5 and 15 m, the crown segment below 7.5 and the segment above 15 m, and the crown segment below between 7.5 and 15 m and the segment between 7.5 and 15 m. The dots represent branch subsamples in both figures ( $n = 225$  branch subsamples, 25 tree samples)

observed in trees with low *A. tsugae* populations. In order to quantify the difference in *A. tsugae* distribution in the crown between the dense and the light infestations, we analysed all trees with low *A. tsugae* populations as a group (fig. 4). In this analysis, we included purposeful samples from trees where the *A. tsugae* population was below the RBS detection threshold. We considered trees with fewer than 20 sistens per 100 new growth needles as low density. Although none of the crown thirds or strata were significantly different at the 90% level, the trend was that the number of sistens per 100 new growth needles increased higher in the crown. The distribution of sistens per 100 new needles in tree crowns can also be examined as a continuous distribution (fig. 5). A plot of the *A. tsugae* distributions suggests that in high population trees a large percentage of the total number of *A. tsugae* are in the lower crown, while in low population trees a large percentage of the total number of sistens is at the upper crown (fig. 5). For example at the 50th quantile, for high *A. tsugae* population trees 65% of the total number of *A. tsugae* per tree were detected. In contrast, only 42% of the total number of *A. tsugae* were detected for low population trees.

A third way to examine the effect of sample height on the estimate of *A. tsugae* density is to compare the crown strata of *A. tsugae* detections between high and low *A. tsugae* density trees (table 1). The percentage of *A. tsugae* detections in the lower crown was lower for trees where we estimated the overall population of *A. tsugae* was less than 20 sistens per 100 new growth needles. A final piece of evidence that suggests greater populations of *A. tsugae* higher up in the crown of trees with low populations is that exhaustive searches of the crowns of the trees in which RBS did not detect *A. tsugae* also uncovered small infestations in the top or middle crown (fig. 1).

### 3.2 Branch direction

An unexpected result of our crown sampling was that north side of trees had more sistens per hundred new growth needles. We compared the number of sistens per 100 new growth needles on branches pointing each of the cardinal directions across all tree samples using the mixed model (fig. 6). Branches pointing north had 2.22 more sistens per hundred needles than branches pointing other directions (90% confidence interval from 1.33 to 3.70). The pattern of higher *A. tsugae* density on the northern branches was consistent across high and low population trees, although the differences were not significant for low population trees at the 90% confidence level. As with crown strata, it is instructive to examine the presence and absence of *A. tsugae* in samples across all stands and years by cardinal direction (table 2). There was a higher percentage of *A. tsugae* detections from the north side of trees.

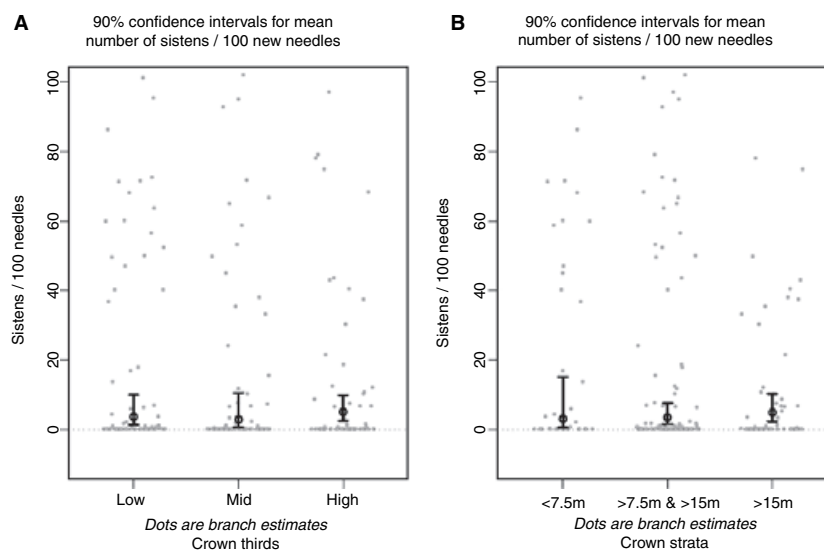
### 3.3 Scale insects

Our study site had very low populations of scale insects. The densest scale population on any tree was an estimated 2.44 per 100 needles. Scale populations did not show any significant differences with crown strata or crown thirds.

## 4 Discussion

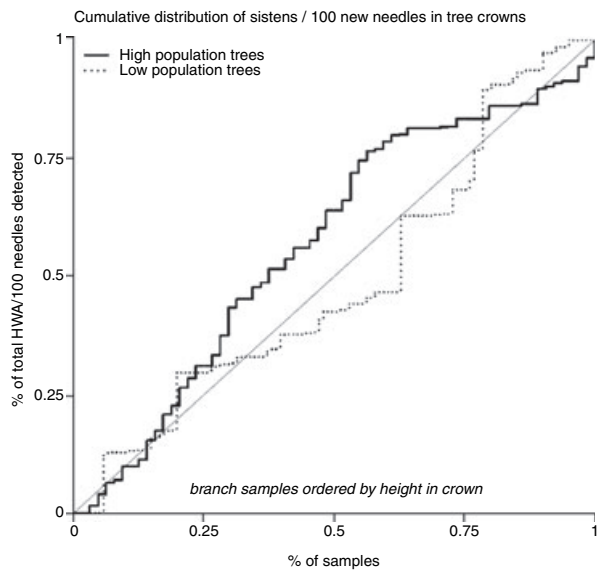
### 4.1 Ecology of crown distribution

In our study area, there are more sistens per 100 new growth needles in the lower crown than the upper crown on trees with high *A. tsugae* populations. At low densities of *A. tsugae*, this trend appears to reverse.



**Fig. 4.** Confidence intervals (90%) for sistens per 100 new growth needles in crown thirds and strata for trees with low densities. The confidence intervals in the first panel are for the crown segments below 7.5, between 7.5 and 15 m, and above 15 m. The confidence intervals in the second panel are for the low, middle and high crown strata. The dots represent branch subsamples in both figures. This graph includes purposeful samples from trees where RBS sample failed to detect HWA infestation ( $n = 161$  branch subsamples, 13 tree samples)



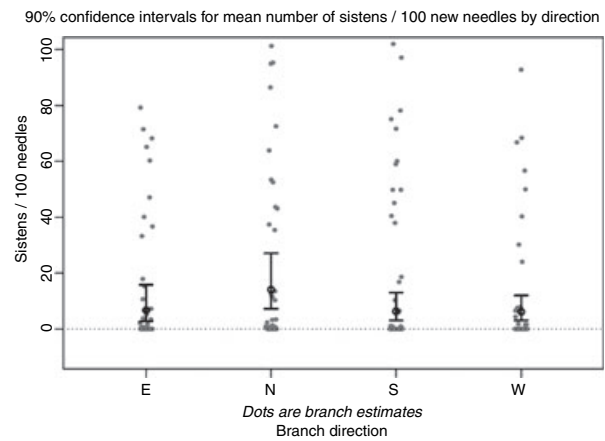


**Fig. 5.** Percentage of total sistens per 100 new needles ordered by height above the ground for high and low population trees ( $n = 225$  branch subsamples, 25 tree samples)

**Table 1.** Percentage of *Adelges tsugae* detections in branch samples from three crown strata. Low population trees were estimated to have fewer than 20 sistens per 100 new growth needles and high population trees were estimated to have more than 20. The number of *A. tsugae* detections in each crown segment is divided by the total number of branch detections in low or high *A. tsugae* population trees

	≤7.5 m	> 7.5 and ≤15 m	> 15 m
Low <i>A. tsugae</i> population trees (%)	16	52	32
High <i>A. tsugae</i> population trees (%)	27	48	25
	≤8.5 m	> 8.5 and ≤15 m	> 15 m
Low <i>A. tsugae</i> population trees (%)	20	48	2
High <i>A. tsugae</i> population trees (%)	31	44	25
	≤9 m	> 9 and ≤15 m	> 15 m
Low <i>A. tsugae</i> population trees (%)	26	42	32
High <i>A. tsugae</i> population trees (%)	38	38	25

Evidence of higher densities higher in the crown is consistent with a congeneric species, the Balsam woolly adelgid (*Adelges piceae* Ratzeburg) (Greenbank 1970; Bryant 1976). The higher light conditions at the top of the crown may explain the pattern of *A. tsugae* densities at both high and low densities of *A. tsugae*. More light and heat at the top of tree crowns may reduce *A. tsugae* survival during warm periods of the year because of desiccation (May 1979). The same higher light and temperature conditions may increase *A. tsugae* survival during cold winters and produce



**Fig. 6.** Confidence intervals (90%) for sistens per 100 new growth needles by branch cardinal direction. The dots represent branch subsamples in both figures ( $n = 206$  branch subsamples, 25 tree samples)

**Table 2.** Percentage of *Adelges tsugae* detections by branch direction. The number of *A. tsugae* detections in each cardinal direction is divided by the total number of detections

Percentage of samples	North	East	South	West
Without <i>A. tsugae</i> sistens	44.7	53.4	61.9	58.1
With <i>A. tsugae</i> sistens	55.3	46.6	38.1	41.9

higher densities in the top of the crown. *Aedalgus cooleyi* Gillette densities are lower in the top most whorl of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) trees because low temperatures there reduce survivorship (Fay and Whitham 1990). Increased light and temperature at the top of the crown could produce these contradictory patterns if the overall density reduction during cold winters was greater than the density reduction caused by high temperatures in the summer.

Lower population *A. tsugae* on the south side of trees may also be related to light and temperature. Sunlight and warmer temperatures on the south side may permit increased predation or desiccate the *A. tsugae* crawlers (M. Montgomery, USDA Forest Service, Hamden, CT, personal communication). The population of scale insects was too low to detect any density differences with crown height or have a significant ecological effect. Even the stand with the densest scale population, an estimated 2.44 per 100 needles, is two orders of magnitude smaller than the 100 *F. externa* per 100 needles which has been documented to cause hemlock decline or death (McClure 1979).

#### 4.2 Implications for monitoring

The variation of *A. tsugae* densities with branch height is unlikely to have a detrimental effect on monitoring *A. tsugae* on trees with high populations (> 20 sistens/100 new needles). However, our results also suggest

that there may be enough variation in distribution of *A. tsugae* within the crown to affect monitoring when *A. tsugae* densities are low. Sampling only branches within reach of the ground from hemlock with low *A. tsugae* populations might give the false impression that no *A. tsugae* were present in the trees.

Sampling the lowest portion of tree crowns in order to measure *A. tsugae* densities is attractive because of its ease. However, even the lowest branches may be out of reach without additional equipment. An additional factor complicating ground-based sampling is the suggestion that stands with low *A. tsugae* populations may have higher *A. tsugae* densities at the top of the crown. Only two of the 13 trees with a low density (<20 sistens/100 new needles) had infestations in the lower crown. Accessing the middle of the crown, i.e. above 7.5 m, increases the likelihood of *A. tsugae* detection even in trees with low populations (table 1). In this study of a forest infested for more than 10 years, samples from 8.5 m and below would have included 20% of the *A. tsugae* detections in low *A. tsugae* population stands (table 1). Based on our results, *A. tsugae* sampling programmes in forests with well-established infestations should include samples from at least 8.5 m and below. In low population stands (<20 sistens/100 new needles), samples from below 5 or 7.5 m may not represent the whole crown, and samples from higher in the crown would help to characterize the infestation. Monitoring new infestations may require a different sampling scheme because new infestations are likely to initially occur at low densities. More research is needed to understand the canopy distribution of sistens at the earliest stages of *A. tsugae* invasion. Further RBS of *A. tsugae* from all three crown strata would justify a lower and mid-crown sampling scheme for *A. tsugae* in other forests where *A. tsugae* densities are high. The data on branch direction offer another possibility for optimizing ground-based sampling. By increasing the selection probably of branches on the north side of the tree, a researcher could increase the likelihood of including sistens on new growth in the sample.

#### 4.3 Randomized branch sampling

The success of this study in documenting the crown distribution of *A. tsugae* shows that RBS is a useful sampling tool in forest entomology. The need to fell trees in order to make estimates of the upper crown is not a drawback of RBS, but rather a result of the need to sample from the upper crown in order to estimate upper crown populations. RBS is flexible enough to permit adaptation to a ground-based sampling and model estimates of the upper crown population. RBS can be also used for multiple objectives, such as the estimation of the number of *A. tsugae* and the number of scale insects.

### 5 Conclusion

The sampling from all crown strata, or at least up to 8.5 m, is time consuming and destructive. However,

without estimates that include at least large portions of the crown, the dynamics of *A. tsugae* populations will remain obscured. It is important to include some whole tree samples in future surveys to examine the crown distribution of *A. tsugae* at low densities, particularly at the front of invasion. Future research should investigate the crown distribution in new infestations, which may increase in density higher in the crown, as the infestations in low population trees did in this study. In addition, research into the density difference between the north and south side of hemlock trees may shed new light on *A. tsugae* control.

There is a whole class of forest pests for which RBS samples could provide crucial information about population densities and distributions. Passively dispersed insects, those that are not drawn to attractants, and those whose attractants are not known at all may fall into this group of insects effectively sampled through an RBS scheme. For example, RBS could be employed to monitor populations of *F. externa* or to improve density estimates of emerald ash borer (*Agrius planipennis* Fairmaire Col., Buprestidae) in trees being destroyed to slow its spread. RBS can fill the need for efficient and statistically sound monitoring caused by more and more invasive insects attacking our forests.

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