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RESEARCH

Microclimatic Variation Within Sleeve Cages Used in Ecological Studies

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ABSTRACT. Sleeve cages for enclosing or excluding arthropods are essential components of field studies evaluating trophic interactions. Microclimatic variation in sleeve cages was evaluated to characterize its potential effects on subsequent long-term experiments. Two sleeve cage materials, polyester and nylon, and two cage sizes, 400 and 6000 cm^2, were tested on eastern hemlock, *Tsuga canadensis* (L.) Carrière. Temperature and relative humidity inside and outside cages, and the cost and durability of the cage materials, were compared. Long-term effects of the sleeve cages were observed by measuring new growth on *T. canadensis* branches. The ultimate goal was to identify a material that minimizes bag-induced microclimatic variation. Bagged branches whose microclimates mimic those of surrounding unbagged branches should have minimal effects on plant growth and may prove ideal venues for assessing herbivore and predator behavior under natural conditions. No differences were found in temperature or humidity between caging materials. Small cages had higher average temperatures than large cages, especially in the winter, but this difference was confounded by the fact that small cages were positioned higher in trees than large cages. Differences in plant growth were detected. Eastern hemlock branches enclosed within polyester cages produced fewer new growth tips than uncaged controls. Both polyester and nylon cages reduced the length of new shoot growth relative to uncaged branches. In spite of higher costs, nylon cages were superior to polyester with respect to durability and ease of handling.

Key Words: enclosure, cage, herbivore exclusion, hemlock, *Tsuga canadensis*

Maintaining realistic experimental conditions in which to evaluate trophic interactions in ecological research is problematic. Enclosures and exclosures are used routinely in evaluating such interactions in marine (Quinn and Keough 1993, Silliman and Bertness 2002), lotic (Flecker and Allan 1984, Johnson et al. 1985, Dudgeon 1993), and terrestrial systems (Opperman and Merlender 2000, Webster et al. 2005). The use of cages to enclose insects on plants is an efficient way to assess herbivore population dynamics (Krause and Raffa 1996; Robison et al. 1998; Adams and Rieske 2001, 2003; Parsons et al. 2005), evaluate host plant suitability (Haines et al. 2003, Rieske 2004, Talsma et al. 2008), and evaluate natural enemy interactions (Smith and De Bach 1942, Luck et al. 1988, Rosenheim 2001), including predation (Story et al. 2012) and parasitism (Amarasekare et al. 2009). In eastern North American forests, field cages have been used to study the hemlock woolly adelgid, *Adelges tsugae* Annand, an invasive pest of eastern hemlock, *Tsuga canadensis* (L.) Carrière. Enclosures and exclosures provide a means of measuring predatory rates of natural enemies (Wallace and Hain 2000) and potential biological control agents of the adelgid (McClure and Cheah 1999; Butin et al. 2003; Lamb et al. 2005, 2006; Flowers et al. 2006; Hakeem et al. 2011). The use of cage studies to evaluate interactions between predator, herbivore, and host plant is an effective approach to investigating population dynamics, but it is not without drawbacks. These limitations may include inconsistencies in observations due to different spatial scales, and alterations in insect behavior, physiology, or morphology. Butin et al. (2003), for example, note that cages may enhance insect survival by providing protection from rain and wind, while McClure and Cheah (1990) question whether cages affect experimental results by moderating branch microclimate.

Sleeve cages can alter microclimates by shading, altering light intensity, temperature, and humidity, and reducing wind speed (Smith and De Bach 1942, Luck et al. 1988). Polyester material can increase within-cage temperatures and reduce solar radiation by up to 76% and wind speed by up to 85% (Rougier and Silvain 1982). Polyester exclusion cages have also been reported to lower ambient temperature by 0.4°C while increasing relative humidity (Chambers et al. 1983), whereas other studies report no temperature or humidity effects relative to ambient conditions (Hand and Keaster 1967). These variable findings make it difficult to predict the effects and importance of caging with respect to plant performance, herbivory, natural enemy effectiveness, and associated trophic interactions. These issues are particularly relevant when evaluating such relationships with sedentary, slowly developing, or long-lived herbivores. Clearly, the circumstances in which a sleeve cage is used, including the nature of the caged subjects, the length of time and season deployed, and the types of caging materials utilized, will influence its effects on the system under study.

The microclimatic variation in sleeve cages was evaluated to characterize potential effects on subsequent experiments. Two types of sleeve cage material in two sizes were tested on branches of the coniferous *T. canadensis*. The temperature and relative humidity inside and outside sleeve cages, and also the cost and durability of the cage materials, were compared. Long-term effects of the sleeve cages were observed by measuring new growth on *T. canadensis* branches. The ultimate goal was to identify a material that minimizes bag-induced microclimatic variation and does not affect outcome of longer term experiments utilizing sleeve cages.

Materials and Methods

Sleeve cages were constructed in two sizes, 10 by 40 cm and 60 by 100 cm, from standard white polyester voile (Hancock Fabrics, Lexington, KY) and from white nylon mesh (70 µm thread diameter and 161 µm mesh opening, Dynamesh, West Chicago, IL) sewn on three sides using polyester thread to form a bag. Five healthy eastern hemlock trees (~2.5 m) were selected from a hemlock garden at the University of Kentucky's Spindletop Research Farm (Fayette Co., KY). Three small branches (~35 cm) were chosen from the top third of each tree and three large branches (~1 m) were chosen mid-height, all facing northwest. Selected branches were caged on 5 November 2010, and one small and one large branch per tree remained open and

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uncaged. Thus, each tree had a polyester caged branch, a nylon caged branch, and an uncaged control branch of both small and large sizes. Sleeve cages were slipped over the terminal end of each selected branch and closed with thin wire at the basal end of the branch.

Temperature data loggers (iButtons, Maxim Integrated Products, Sunnyvale, CA) were placed in small plastic water-proof bags secured to caged branches with thin wire in the middle of each sleeve cage. Temperatures were recorded at 3 h intervals 5 November 2010 to 4 February 2011, and 9 June 2011 to 6 July 2011. In November 2010, relative humidity was measured with three Indoor/Outdoor Hygro-Thermometers (Extech Instruments Corp., Nashua, NH) installed on each tree for 48 h. One experimental tree was randomly selected and the hygrothermometer sensor was placed on the middle of a preselected branch, either inside the cage or open to ambient conditions on a control branch. Readings were taken for 48 h and were completed for the large set of cages on all five trees before moving to the small branches.

Cages were visually inspected every 2 d for the first 30 d, intermittently for the next 4 mo, and a final time following cage removal. Cage condition was rated based on the following system: 1) no damage or change in condition; 2) fabric worn, loose threads; 3) small holes or tears less than 5 mm; 4) holes or tears greater than 5 mm, no longer able to contain small insects.

Cages remained in place for 18 mo (5 November 2010–7 May 2012). At the time of cage removal, each small branch was visually observed and all branch tips, considered potential sites for new growth, were counted. Sites of new growth were counted and their length measured with calipers. After removing large cages, each large branch was marked at the terminal 50 and 25 cm. All branch tips and sites of new growth were counted on the terminal 50 cm, and all new growth was measured on the terminal 25 cm. Each branch was photographed with a reference grid and all cages were inspected for damage.

Statistical Analyses

Three weeks of temperature data were selected to represent fall, winter, and summer seasons (Table 1). For each season, average daily temperature readings were compared across cage material and cage size using a repeated measures analysis of variance (SAS 9.2, Cary, NC). Minimum and maximum temperature and relative humidity readings collected from the hygrothermometers were compared across cage treatment using analysis of variance and blocking by tree. All but three maximum relative humidity readings were 99%, so this dependent variable was excluded from the analysis. The percentage of new growth on each branch was calculated by dividing the number of tips with new growth by the total number of branch tips. Arcsine square root transformed percent growth data and the average length of the new growth were analyzed with ANOVA, blocking by tree. The independent variables were cage size and cage material, and the interaction between the two was tested. Cage condition was compared across material and cage size at nine time points using a repeated measures analysis of variance.

The cost of material per cage was calculated based on the October 2010 retail price of the polyester voile (US$1.82/m^2; US$4.97 per linear yard of 118-inch wide material, in Lexington, KY) and the online bulk purchase price of the nylon mesh (US$4.62/m^2; US$4.84 per linear yard of 45-inch wide material). The costs of thread were considered negligible, and labor costs were not calculated.

Results

There was no difference in the average daily within–cage temperature between polyester and nylon cages and uncaged control branches within seasons (Table 2). Maximum daily temperature occurred at 1500 hours (3:00 p.m. eastern time) for each season, and the minimum temperature occurred at 0600 hours in the fall and summer, and at 0900 hours in the winter (Fig. 1). Average daily within–cage temperature did vary with cage size (Table 2). Temperatures were higher inside small cages compared to large cages at each time interval for each season (Fig. 2). There was no interaction between cage size and cage material with respect to average daily temperatures within seasons (Table 2).

Table 1. Temperature data from selected 1-wk periods representing fall, winter, and summer seasons, used to evaluate microclimatic variation within sleeve cages enclosing eastern hemlock branches

Season	Dates	Mean daily temperature (°C)	
		Maximum	Minimum
Fall	6 Nov. 2010–12 Nov. 2010	9.75	0.44
Winter	17 Jan. 2011–23 Jan. 2011	5.5	−14.4
Summer	29 June 2011–5 July 2011	29.1	19.7

Table 2. Effects of sleeve cage construction material (polyester and nylon) and size (400 and 6000 cm^2) on average within-cage temperatures of enclosed eastern hemlock branches relative to uncaged control branches across three seasons. Small cages were located in the upper third of the tree, while large cages were placed mid-height

Season	Material	Size	Size × Material
Fall	$F_{2,24} = 2.18$; $P = 0.14$	$F_{1,24} = 4.50$; $P = 0.04$	$F_{2,24} = 0.08$; $P = 0.92$
Winter	$F_{2,24} = 0.29$; $P = 0.75$	$F_{1,24} = 23.2$; $P < 0.001$	$F_{2,24} = 0.19$; $P = 0.82$
Summer	$F_{2,24} = 0.62$; $P = 0.55$	$F_{1,24} = 8.80$; $P = 0.01$	$F_{2,24} = 1.06$; $P = 0.36$

Data from the hygrothermometers showed no difference in maximum ($F = 0.97$; df = 6, 23; $P = 0.38$) or minimum ($F = 0.21$; df = 6, 23; $P = 0.88$) temperatures between cage materials and controls. Minimum relative humidity also did not differ between polyester, nylon, and uncaged control branches ($F = 0.51$; df = 6, 23; $P = 0.61$), and maximum relative humidity reached 99% for all branch treatments and was not analyzed.

After 18 mo, only three hemlock branches showed signs of poor health, indicated by fading foliage, but branch decline was independent of cage material or cage size. The percent of caged branch tips with new growth varied among cage treatments ($F = 5.91$; df = 2, 12; $P = 0.02$) but was greater than 85% for all treatments. Uncaged control branches had a significantly greater proportion of new growth than polyester caged branches. The proportion of new growth on branches in nylon cages was not different from either uncaged control branches or polyester caged branches (Fig. 3). Branches in small cages had a higher average proportion of new growth than those in large cages (0.93 ± 0.02 and 0.87 ± 0.03) respectively, $F = 9.04$; df = 1, 12; $P = 0.01$), but there was no interaction between the size of the cage and the material used ($F = 2.92$; df = 2, 12; $P = 0.09$).

The average length of new growth also varied by cage treatment ($F = 15.02$; df = 2, 12; $P = 0.001$). Uncaged control branches had significantly longer growth tips than caged branches, but there was no difference in the average length of new growth between nylon and polyester cages (Fig. 4). On an average, length of new growth was greater on branches in large cages compared to branches in small cages ($F = 9.20$; df = 1, 12; $P = 0.01$) with respective means of 22.7 ± 1.9 and 18.5 ± 1.1 mm. There was no interaction between cage size and material ($F = 0.77$; df = 2, 12; $P = 0.49$) with respect to average length of new growth.

Degradation of the cages over the 18-mo evaluation period differed by size and by caging material. While large polyester cages showed signs of wear and tear after just 5 d and had small holes after 75 d, small polyester cages showed less damage (Table 3). There was a significant interaction between cage size and material ($F = 9.38$; df = 1, 16; $P = 0.007$). Nylon material was more resilient and there were no visible signs of damage on small or large nylon cages after 4 mo. However, after 18 mo, both polyester and nylon cages had discernible damage, with small holes near corners and with frayed edges. Neither type of cage

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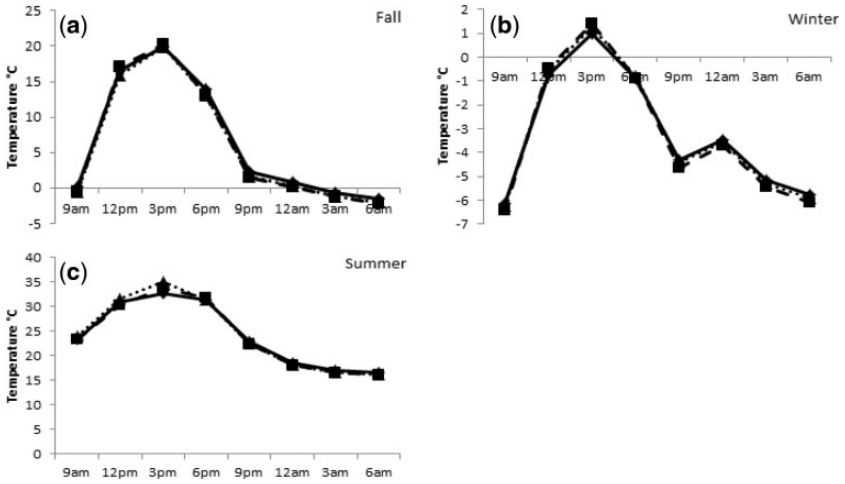


Fig. 1. Average temperature at 3 h intervals over 7 d on eastern hemlock branches in sleeve cages of polyester (- - -■- - -) and nylon (· · ·▲· · ·), relative to uncaged branches (—◆—), during (a) fall (6–12 Nov. 2010), (b) winter (17–23 Jan. 2011), and (c) summer (29 June–5 July 2011).

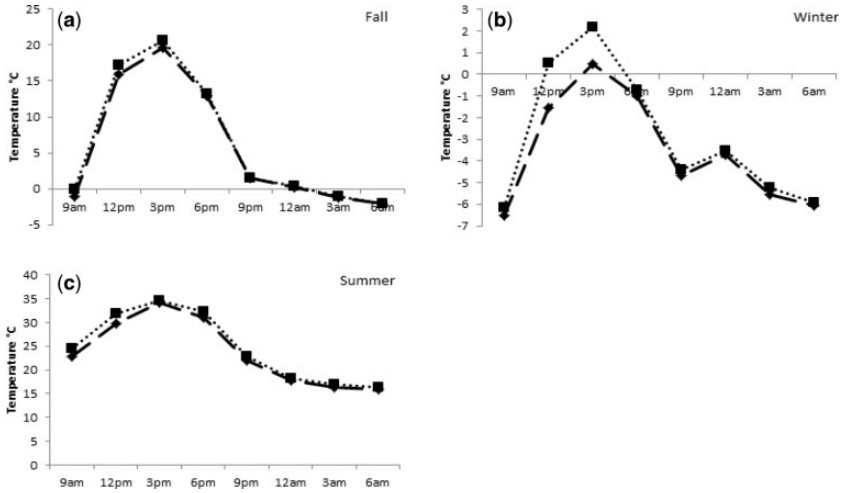


Fig. 2. Average temperature at 3 h intervals in small (400 cm^2) (· · ·■· · ·) and large (6000 cm^2) (- - -◆- - -) sleeve cages on eastern hemlock branches over 7 d during (a) fall (6–12 Nov. 2010), (b) winter (17–23 Jan. 2011), and (c) summer (29 June–5 July 2011).

would have been effective at containing or excluding smaller arthropods over long term.

Discussion

Sleeve cages are standard tools for evaluating trophic interactions under field conditions and minimizing within-cage microclimatic effects is essential for realistic evaluations of tritrophic interactions and natural enemy efficacy. The data showed that exclusion sleeve cages of polyester and nylon had only a minimal abiotic impact on the microhabitat of eastern hemlock branches. Temperature and relative humidity within cages made of either material did not differ from ambient control branches, but within-cage light penetration was not measured. These results are consistent with Lamb et al. (2005); they placed dataloggers inside and outside a sleeve cage on one hemlock branch at three sites and found no difference in temperature. Average temperatures were higher inside small cages relative to large cages; these differences were most evident during the winter and may be attributable to cage position. The smaller cages were located in the upper third of the canopy and, therefore, subjected to more direct sunlight and greater radiant energy. Of necessity, the small cages also enclosed smaller branches and therefore less foliage, reducing the modulating effects of foliar metabolism. Potential effects of the host plant itself in modulating temperature and humidity fluctuations cannot be discounted; within-cage microclimatic variation may be greater in plants with different morphology, physiology, or growth form.

Caging did affect *T. canadensis* growth; the proportion of new branch tips was lower on branches caged in polyester relative to uncaged controls, and the length of *T. canadensis* new growth was negatively affected by both cage material and cage size. These results contrast with a previous study measuring microclimatic effects inside cages on *Malus domestica* Borkh. (Fam. Rosaceae), a woody fruit tree (Lawson et al. 1994), which found that tree growth was not affected by cages, and that tree performance, as measured by shoot growth, increased inside cages relative to controls. However, Lawson et al. (1994) were utilizing whole-tree enclosures on a fast-growing fruit tree, whereas we utilized branch sleeve cages on a slow-growing conifer. While there was no direct change in microclimate due to caging material, alterations in host plant quantity were evident. These alterations in plant performance could affect herbivore performance, directly through decreases in available resources, or indirectly by influencing plant physiology and host plant quality (Price et al. 1980, Scriber and Slansky 1981). The hemlock woolly adelgid prefers to settle and feed

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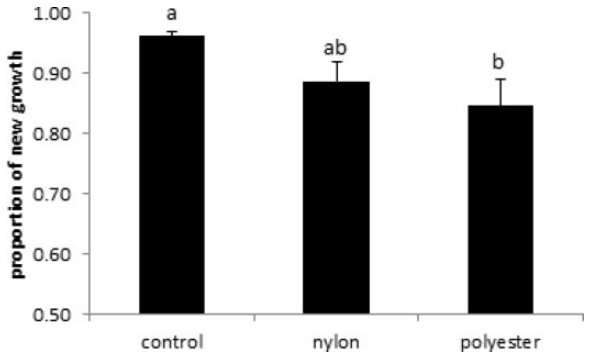


Fig. 3. Proportion of eastern hemlock branch tips with new growth varies with cage treatment ($F = 5.91$; df = 2, 12; $P = 0.02$). Control treatments were uncaged, and nylon and polyester cages were installed 18 mo before growth measurements.

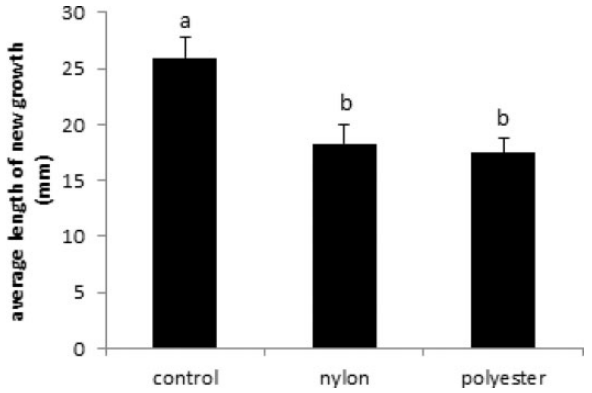


Fig. 4. The average length of new growth on eastern hemlock branches varies across cage treatment ($F = 15.02$; df = 2, 12; $P = 0.001$). Control treatments were uncaged, and nylon and polyester cages were installed 18 mo before growth measurements.

on new hemlock tissue (Young et al. 1995), so decreased *T. canadensis* plant health negatively affects *A. tsugae* performance (McClure 1991). The effects of alterations in plant quality should not be discounted.

These experiments were conducted over a relatively long period (18 mo) on eastern hemlock, an extremely slow-growing, shade-tolerant conifer. Long-term caging studies are useful to evaluate host plant suitability for sedentary herbivores or predator–prey dynamics through several generations. The data indicate, however, that large polyester cages lose their ability to effectively hold/exclude insects after 75 d. Smaller polyester cages and cages made from nylon material are more durable and may be effective enclosures/exclosures for up to 18 mo. Lamb et al. (2005) used nylon sleeve cages on eastern hemlock branches in experiments lasting 5–6 mo, but Lamb et al. (2006) used polyester cages when data was collected just 10 d after caging. Both studies used appropriate caging materials for their respective experimental durations, and likely experienced minimal caging effects. Wallace and Hain (2000) performed field cage experiments on *T. canadensis* lasting 75–95 d but no mention is made of cage material. This information is necessary to evaluate the effectiveness of cages as true exclosures.

T. canadensis growth was affected by cages after 18 mo, but shorter term caging experiments may show no detectable effect on host plant quality. Similarly, effects on deciduous or herbaceous plants, or on more rapidly growing species, may differ. Lack of data in this study for the spring season is unfortunate, since spring is a crucial period for many insect–plant systems and an especially critical time for emergence and settlement of *A. tsugae* progrediens nymphs on eastern hemlock. However, the adelgid is bivoltine in North America, and data collection coincided well for development of the sistens generation.

Table 3. Degradation of polyester and nylon sleeve cages of two sizes installed on eastern hemlock branches for 18 mo. Cage degradation differed by size ($F = 8.73$; df = 1, 16; $P = 0.01$) and by material ($F = 13.74$; df = 1, 16; $P = 0.002$), with a significant size × material interaction ($F = 9.38$; df = 1, 16; $P = 0.007$)

			Degradation rating[1]								
			Days after cage installation								
Material	Size[2]	Cost per cage[3]	5	10	15	20	30	45	75	120	540
Polyester	Small	0.07	1	1	1	1	1.2	1.2	1.2	1.2	3
	Large	1.09	1.4	1.6	2.2	2.8	2.8	2.8	3	3.6	3.6
Nylon	Small	0.19	1	1	1	1	1	1	1	1	2.6
	Large	2.77	1	1	1	1	1	1	1	1	2.4

[1]Degradation rating ($n = 5$) – 1: no damage or change in condition, 2: fabric worn, loose threads, 3: small holes or tears < 5 mm, 4: holes or tears > 5 mm, no longer able to contain small insects.
[2]Small: 10 by 40 cm; Large: 60 by 100 cm.
[3]Materials only, US$ per m^2.

Polyester cages were found to be more prone to degradation than their nylon counterparts; they were also more difficult to construct and manipulate in the field. The softer threads of the polyester material made the fabric limp and difficult to hold in place when sewing the cages and inserting them on branches. While nylon caging material is ~2.5 times more expensive, it is also more resilient to damage and UV degradation, and has minimal effects on within-cage microclimate and plant growth. The data in this study suggest that nylon mesh is more resilient in long-term studies and its use in cage exclusion studies minimizes impacts on plant performance which could potentially affect herbivore and predator behavior (Price et al. 1980, Scriber and Slansky 1981), thus effectively facilitating studies evaluating trophic interactions.

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