Changes in protective influences and competitive costs of *Abies balsamea* on *Tsuga canadensis* growth during sapling maturation

By Maximillian Manayan

Mentor: Bethany Blakely

Abstract:

Eastern hemlock (*Tsuga canadensis*) was a dominant plant in the northern hardwoods forest, but was greatly reduced in number due to a variety of factors. There is evidence of hemlock recruiting in gaps and growing in association with balsam fir (*Abies Balsamea*), which serves as a protective influence by dissuading deer browse. We predicted that hemlock growing in association with balsam fir would have more growth success on average (H1) due to reduction of deer browse, and that there would be competitive costs on hemlock by its close association with balsam fir (H2). The research was conducted at the University of Notre Dame Environmental Research Center in the Upper Peninsula of Michigan (46.227893, -89.523743). We decided to measure growth success by recording height, and niche separation by recording sapling distance from the center of the canopy gap. The data set indicated balsam fir association had an effect on hemlock sapling growth up until a certain threshold height, then ceased to influence hemlock growth. There was no linear relationship between sapling height and sapling placement in the gap, contradicting the notion of niche separation. The gaps analyzed suggested that association with balsam fir after the threshold height may exert competitive effects on hemlock growth due to competition for shared resources.

Introduction:

Since the industrialization of the planet, humans have done irreparable damage to the environment on both global and local scales (Wilbanks and Kates 1999). Locally, more than 99% of the old-growth Eastern Deciduous Forest has been clear-cut due to deforestation and urbanization (Carson 2017). Moreover, introduction of invasive species by humans has led to a drastic decrease in numbers of six major tree species, including the Eastern hemlock (Carson 2017). Eastern hemlock (*Tsuga canadensis*) was a once dominant tree in the Upper Great Lakes region. After heavy logging in the 19th and 20th centuries, Eastern hemlock has shown poor recruitment and continues to struggle to recover in the area (Rooney et al. 2000).

Poor recruitment in Eastern hemlock could be due to over-browsing by white-tailed deer (*Odocoileus virginanus*) compounded with the parasiticism of the invasive hemlock woolly adelgid (*Adelges tsugae*), both of which have been observed in the Upper Great Lakes region (Paradis 2008). Moreover, poor regeneration of hemlock could be due to interspecific competition with the dominant woody, deciduous trees (Rhemtulla 2009). The presence of neighboring deciduous trees leads to thick leaf mats on the forest floor that accumulates seasonally. These leaf mats impeding Hemlock seedlings from reaching the soil below, preventing seedlings from acquiring moisture and nutrients needed for germination (Kostel et al. 2005). An interaction of climate, land conditions, and disturbance have created unfavorable conditions for hemlock regeneration in the Northern Great Lakes Region (Mladenoff 1993).

Although there are clear implications of interspecific competition with broadleaf deciduous trees, hemlock has been found recruiting in close association with needleleaf coniferous trees, such as balsam fir (*Abies balsamea*). In canopy gaps that contain balsam fir populations, hemlock populations have shown recruitment (Hett and Loucks 1976). Specifically, hemlock saplings that grow in association with balsam fir can be nearly three times denser and twice as tall as unassociated hemlock saplings (Borgmann et al. 1998). Canopy gaps are created when a form of natural disturbance results in an opening of the canopy. The resulting gap dynamics differ noticeably from the surrounding forest, due to the drastic increase of sunlight and temperature. The opening of the canopy may allow shorter plants to access the necessary sunlight to grow and facilitates the inhabitation of different competing species that may be less shade-tolerant (Urban et al. 1991). Balsam fir is often found in association with hemlock and serves as a protective influence. Balsam fir is unpalatable to deer, a primary predator of hemlock, and may reduce browsing of neighboring hemlock populations (Borgmann et al. 1998). Whether balsam seedlings physically shield hemlock from deer browsing or discourages deer from browsing in balsam-dominated gaps, balsam fir allows hemlock seedlings to mature in areas where they are found in close association. However, balsam fir may also be hindering hemlock recruitment by competing for light and nutrients in the canopy gaps (Martin, Unpublished). Close association and competition between the two species may result in niche separation in the gap. Balsam fir may have a competitive advantage in the center of the gap where light is abundant, while hemlock saplings may have a competitive advantage near the gap edge because they are a shade tolerant plant (Ward 2004). We hypothesize that hemlock found growing in association with balsam fir will be taller than unassociated hemlock saplings (H1) because balsam fir acts as a protective agent against deer browse. We also hypothesize (H2) that balsam fir and hemlock compete for resources in canopy gaps, and niche separation will be apparent in the distribution of hemlock saplings towards the outside of the gap.

Materials and Methods:

This study was conducted at the University of Notre Dame Environmental Research Center (UNDERC) located in the Upper Peninsula of Michigan (46.227893, -89.523743). The UNDERC site is part of the northern hardwoods forest in the Eastern Deciduous Forest. The landscape consists of a mixture of coniferous trees and deciduous hardwoods interspersed with lakes and wetlands.

We located fifteen canopy gaps that had different ratios of hemlock (*Tsuga canadensis*) saplings to balsam fir (*Abies balsamea*) saplings. Three stands were assessed (Table 1), each stand with five gaps. In order to define the gap, we ran twine around the surrounding trees and enclosed the “Expanded gap,” displayed in Figure 5 (Runkle 1992). Open sky above the canopy gap was recorded by standing at the center of the gap and using an inclinometer in each direction along the long and short axes (Phattaralerphong 2006). We then measured the length of the encircling twine to establish gap circumference (m). Gap shape, axes lengths, and surrounding environment were also noted. Within each gap, we recorded both a general ratio of balsam fir to hemlock saplings and the number of hemlock found at each site. General association between the two species was recorded in gaps where balsam fir and hemlock saplings were observed growing in association with each other. Association was defined by branch overlap between a hemlock sapling and a balsam fir sapling. To test for niche separation, we recorded the distance of each sapling from the center of the gap. We also recorded measurements of balsam fir saplings with heights between 30 cm – 400 cm and hemlock saplings between 0 cm – 400 cm, and whether hemlock saplings were associated with balsam fir saplings.

Once the data was recorded, we began with general descriptive statistical tests. This included t-tests on average height (cm) of balsam fir versus average height (cm) of hemlock at gap level, stand level, and total combined data. T-tests were also run on height (cm) of hemlocks associated with balsam fir versus hemlocks not associated with balsam fir at the three levels.

In order to test for niche separation, regression analysis was performed on sapling height (cm) versus distance from the gap center (m) for both species. If niche separation were present, general trends of increasing or decreasing heights would be seen from the gap center to gap edge, and would be opposite for both sapling species.

We also obtained the mean height of hemlock saplings and divided the measurements into two subsets: hemlocks shorter than the mean height, and hemlocks taller than the mean height. A t-test was run for each of these subsets to test for a relationship between sapling height and association with balsam fir. To test for a relationship between hemlock height class and association, a Chi-square test was run for both the small subset and the large subset.

Results:

In general, we found hemlock saplings were taller than balsam fir saplings [95% CI, (113.15 cm, 88.22 cm), $p = 1.461e^{-08}$] (Figure 1). The t-test comparing height of total associated hemlocks versus total non-associated hemlocks indicated that non-associated hemlocks are taller on average [95% CI, (104.01 cm, 125.18 cm), p = 0.002819] (Figure 2). We observed no relationship between height and distance from gap center for hemlock saplings ($R^2 = 0.00661$, p = 0.1252). Similarly, balsam fir sapling height and distance from gap center were unrelated ($R^2 = 0.004734$, p = 0.1406).

In the short subset, hemlock saplings associated with balsam fir were shown to be taller on average than saplings not associated [95% CI, (71.69 cm, 62.22 cm), p = 0.0347]. There was a direct relationship between height and association for the short subset ($X^2 = 22.891$, $p = 1.714e^{-06}$). The tall subset of saplings showed no relationship between height and association ($X^2 = 2.329$, p = 0.127). On average, non-associated hemlocks were taller than their associated counterparts in the absence of a relationship [95% CI, (168.19 cm, 173.67 cm), p = 0.5115].

Discussion:

Clear-cutting and other human activities have left a large portion of the Eastern Deciduous Forest as a mature second-growth forest (Carson 2017). Previous old-growth dominants, such as the American chestnut (*Castanea dentate*), have been completely devastated due to human-introduced pathogens and altered disturbance regimes (Barakat *et al*. 2009). Removal of deer predators such as the gray wolf has led to a large increase of white-tailed deer, which presents potential threats to hemlock forests due to deer browse (Côté *et al*. 2004; Anderson and Loucks 1979). Further, hemlock saplings have struggled to recruit in woody, deciduous-dominated forests that have replaced many of the clear-cut coniferous stands (Anderson and Loucks 1979).

Due to the gradual rise in both white-tailed deer and deciduous hardwoods, hemlock saplings of the Upper Great Lakes area are recruiting in association with balsam fir as a means of protection. In the fifteen gaps measured, hemlock favored balsam fir association during the initial stages of sapling development. However, we found balsam fir association may actually be a detriment to hemlock growth after a certain height threshold. Balsam fir association plays a protective role against deer browse until the threshold height is met, after which balsam fir may exert a competitive influence on hemlocks that are large and no longer need protection from deer browse.

Small hemlock seedlings are more likely to experience mortality due to deer browse. It was surprising to find that the average height of balsam fir was shorter than the average height of hemlocks. However, the taller average height of hemlock can be attributed to deer browse. In general, deer browse on the smaller saplings would decrease the number of hemlocks in the short subset through mortality, boosting the average height of hemlocks. Similarly, hemlocks may be shorter when associated with balsam fir because the short, unassociated hemlock saplings lack protection from deer browse. Balsam fir acts as a protective influence when associated with hemlock because it is unpalatable to deer. The unappetizing nature of balsam fir could discourage foraging on associated hemlocks.

Although balsam fir association would increase the chance of survival in short hemlock saplings, it may also hinder hemlock sapling maturation because the close proximity limits resources such as space, light, and nutrients. An unassociated hemlock sapling whose growth has surpassed the risk of mortality would have access to more resources in the absence of competition from neighboring saplings, which would allow for more favorable conditions and promote a higher growth rate.

We found small hemlocks are more likely to be associated than not. Moreover, associated saplings are generally taller in the small subset. The shorter hemlocks are most likely associated because growing in close proximity with balsam fir offers protection, particularly from deer browse. Hemlock saplings may establish equally in association or not, but are more likely to survive in association. Association with balsam fir may present optimal growing conditions to a certain height threshold, most likely around the mean height of hemlocks. Past this height, competitive costs from growing in association with balsam fir may begin to outweigh the benefits of protection from deer browse. Nearly two-thirds of the short subset were associated, and the associated hemlocks were taller on average (Figure 3). This may be attributed to the height threshold and the probability that these associated hemlocks of the short subset are better protected at shorter heights.

For the large subset of hemlocks, height was unaffected by association with balsam fir. Association is likely not as important of protective influence, due to the size of the hemlocks relative to the portion of the tree browsed by deer. A larger hemlock would be able to withstand the same amount of deer browse that would destroy a smaller sapling. We also found less large hemlocks were associated with balsam fir than unassociated. This supports the threshold notion and that if an unassociated short hemlock happens to survive until the threshold height, the sapling's height is not hindered by competition for resources. Thus, the sapling has a better chance of survival past when it passes the threshold.

We found no support for either of the original hypotheses. Hypothesis 1, which stated associated hemlock would be taller than unassociated hemlock, was directly contradicted by the dataset. Moreover, there was no evidence of niche separation throughout the gap. The regression analysis showed that distance from the gap center had no affect on the height of either species. This suggests there is no significant niche separation between balsam fir and hemlock. Sapling height is scattered throughout the gaps, meaning they can grow in a range of abiotic conditions. Other environmental factors such as sunlight and soil moisture have little effect on where hemlock and balsam fir grow in the gap.

Although we did not support either of the initial hypotheses, we did find that the relationship between hemlock and balsam fir changes as saplings age. When a small hemlock sapling is associated, balsam fir facilitates survival and growth. Once the threshold height is reached, however, balsam fir may become more of a hindrance to growth due to competition of resources. We found no evidence that either species is outcompeting the other at this point; only that balsam fir may exert a competitive influence. If hemlock were outcompeting balsam fir at this stage, we would see a more direct relationship between non-association and hemlock height ($p<0.05$). Due to the absence of relationship, balsam fir association may not even negatively affect hemlock height. The lack of balsam fir association may just be more favorable and lead to optimal growth of hemlock saplings. If competition at larger sapling sizes is not too strong, it may be outweighed by protection at a smaller stage, leading to a net benefit for hemlock recruitment. Upon further study of the relationship between these two species, we may find that the once dominant Eastern hemlock is rising in numbers by recruiting in gaps with balsam fir.

Acknowledgements:

This research was supported by the University of Notre Dame and the Bernard J. Hank Endowment Fund. I would like to thank my mentor, Bethany Blakely, for the extensive guidance into forest ecology and field research. I would also like to thank Angela Pantell, Emily Ramirez, Katheryn Barnhart, Sam Sutton, and Renee Dollard for their help with both the field and statistical sides of this research. I would like to thank UNDERC technician Patrick Larson, and TAs Hannah Legatzke, Bethany Hoster, and Claire Goodfellow for their timely help regardless of circumstance. Finally, I would to thank Dr. Gary Belovsky, Dr. Michael Cramer, and Sherry DePoy for the wonderful opportunity and experience they provided.

Literature Cited:

Anderson, R.C., Loucks, O.L. 1979. White-tailed deer (Odocoileus virginianus) influence on structure and composition of Tsuga canadensis forests. *Journal of Applied Ecology*, 16, 855-861.

Barakat, A., DiLoreto, D., Zhang, Y. *et al*. 2009. Comparison of the transcriptomes of American chestnut (*Castanea dentata*) and Chinese chestnut (*Castanea mollissima*) in response to the chestnut blight infection. *BMC Plant Biology*, 9:51.

Borgmann, K., Waller, D., Rooney, T. 1998. Does Balsam Fir (Abies balsamea) Facilitate the Recruitment of Eastern Hemlock (Tsuga Canadensis)? *The American Midland Naturalist,* 141(2): 391-397.

Carson, W. 2017. On the causes and consequences of region-wide changes in the browsing and disturbance regimes within the Eastern Deciduous Forest Biome [Powerpoint slides]. Retrieved from http://environment.harvard.edu/events/2017-03-24-150000/harvard-forest-seminar

Côté, S., Rooney, T., Tremblay, J. *et al*. 2004. Ecological Impacts of Deer Over Abundance. *Annual Review of Ecology, Evolution, and Systematics*, 35: 113-147.

Hett, J., & Loucks, O. 1976. Age structure models of balsam fir and eastern hemlock. *Journal of Ecology*, 64(3), 1029-1044.

Kostel-Hughes, F., Young, T., & Wehr, J. 2005. Effects of leaf litter depth on the emergence and seedling growth of deciduous forest tree species in relation to seed size. Journal of the Torrey Botanical Society, 132, 50-61.

Mladenoff, D. J. 1993. Eastern hemlock regeneration and deer browsing in the northern great lakes region: A re-examination and model simulation. *Conservation Biology*, 7, 889-9000.

Paradis, A., Elkinton, J., Hayhoe, K., Buonaccorsi, J. 2008. Role of winter temperature and climate change on survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America. *Mitigation and Adaption Strategies for Global Change*, 541-554.

Phattaralerphong, J., Sathornkich, J., Sinoquet, H. 2006. A photographic gap fraction method for estimating leaf area of isolated trees: assessment with 3D digitized plants. *Tree Physiology*, 26, 1123-1136.

Rhemtulla, J. M., Mladenoff, D. J., Clayton, M. K. 2009. Legacies of historical land use on regional forest composition and structure in Wisconsin, USA (mid-1800s–1930s–2000s). Ecological Applications, 19(4): 1061-1078.

Rooney, T., McCormick, R., Solheim, S., Waller, D. 2000. Regional variation in recruitment of hemlock seedlings and saplings in the Upper Great Lakes, USA. *Ecological Adaptations: Ecological Society of America*, 1119- 1132.

Runkle, J. R. 1992. Guidelines and Sample Protocol for Sampling Forest Gaps, *USDA Forest Service*.

Urban, D.L., Bonan, G.B., Smith, T.M., Shugart, H.H. 1991. Spatial applications of gap models. *Forest Ecology and Management*, 95-110.

Ward, J., Montgomery, M., Cheah, C. *et al*. 2004. Eastern Hemlock Forests: Guidelines to Minimize the Impacts of Hemlock Woolly Adelgid. *US Forest Service*, 27.

Wilbanks, T. J., Kates, R. W. 1999. Global Change in Local Places: How Scale Matters. *Climatic Change*, 43:3, 601-628.

Tables and Figures:

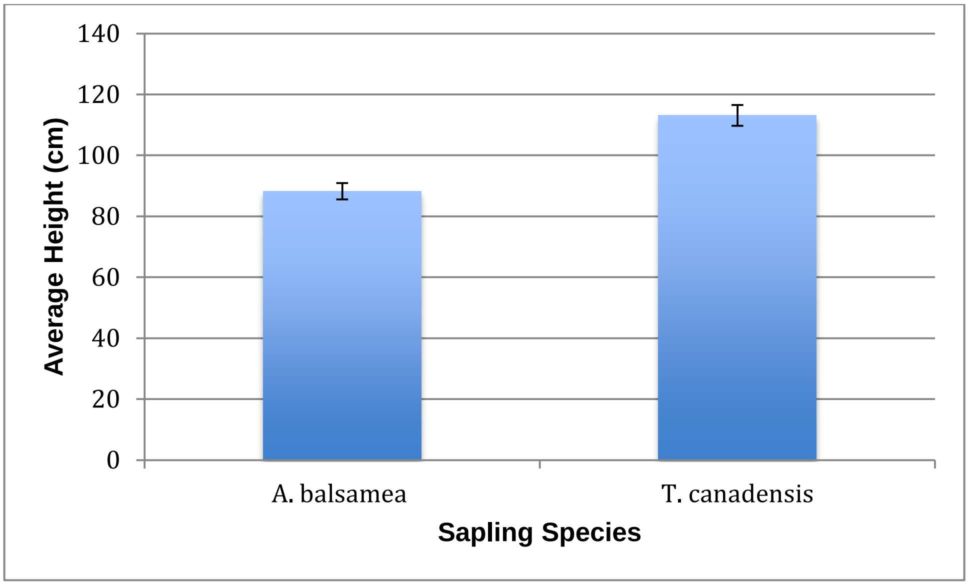

Figure 1. Average heights of *A. balsamea* (88.22±2.66 cm) and *T. canadensis* (113.15±3.43 cm) [n = 817, p = 1.461e^{-08}].

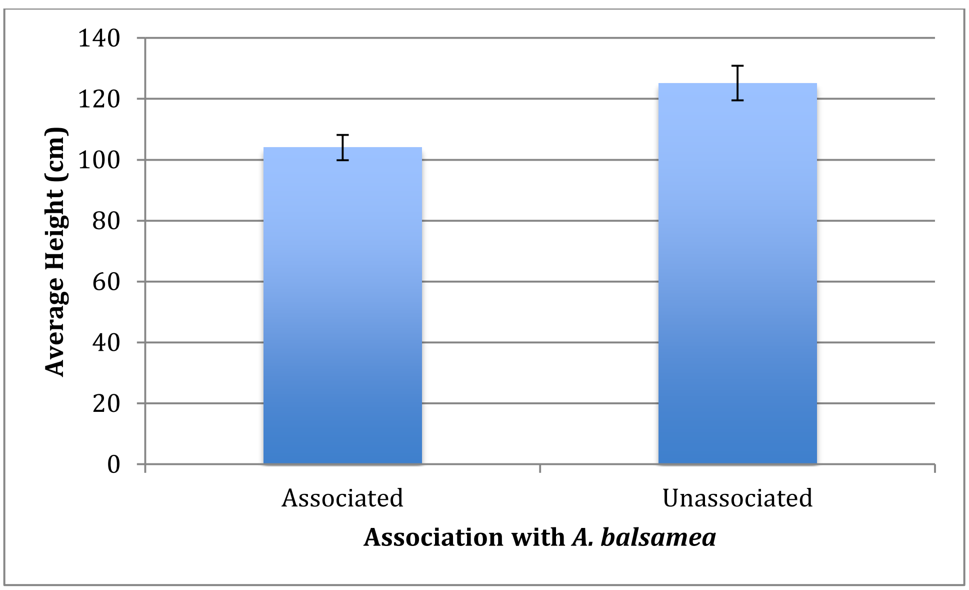

Figure 2. Average heights of associated *T. canadensis* (104.01±4.12 cm) and unassociated *T. canadensis* (125.18±5.67 cm) [n = 357, p = 0.002819].

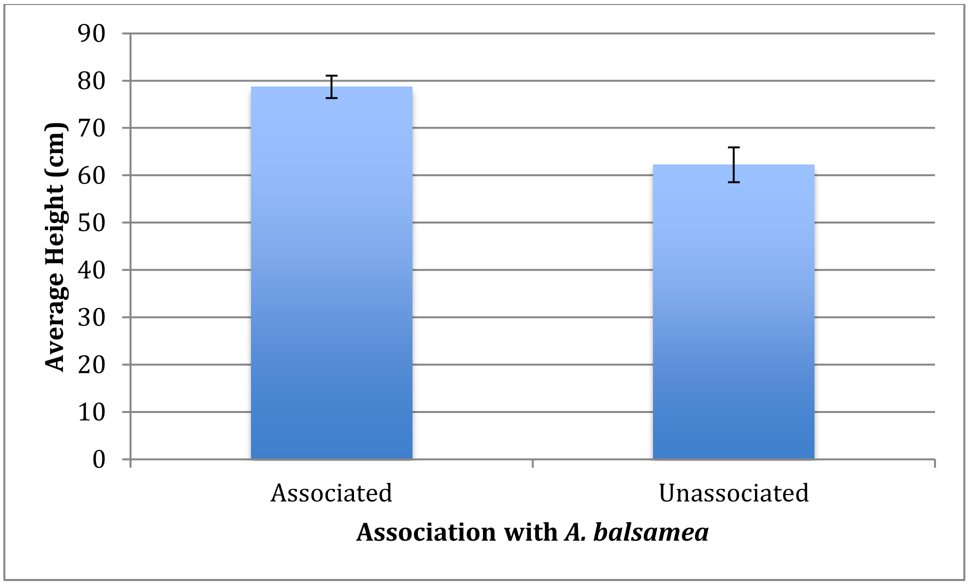

Figure 3. The average heights of associated *T. canadensis* (71.69±2.38 cm) and unassociated *T. canadensis* (62.22±3.71 cm) for the short subset [n = 202, p = 0.0347].

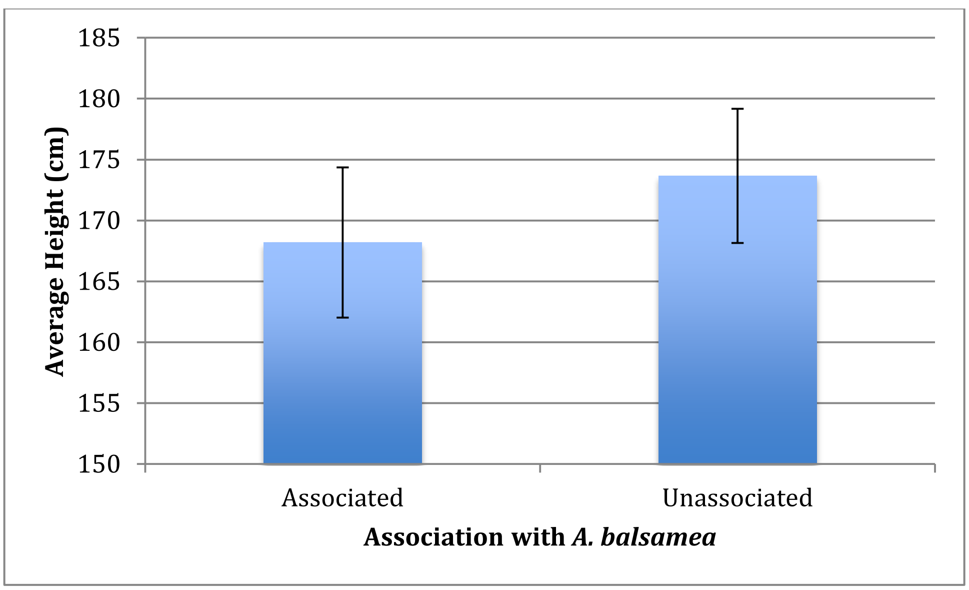

Figure 4. The average heights of associated *T. canadensis* (168.19±6.16 cm) and unassociated *T. canadensis* (173.67±5.51 cm) for the large subset [n = 155, p = 0.5115].

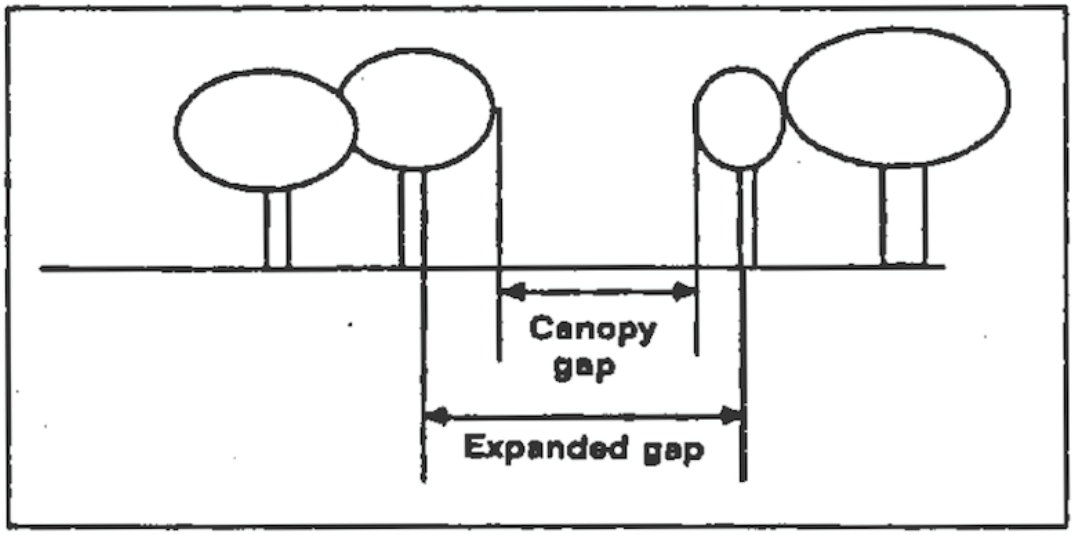

Figure 5. The above figure shows two definitions of measuring canopy gaps by J. R. Runkle. This study only looked at saplings in the "Expanded gap."

Stand (Coordinates)	Number of Hemlock Saplings	Number of Balsam Fir Saplings	Average Height of Associated Hemlock Saplings	Average Height of Unassociated Hemlock Saplings
Naked Kitty (46 13.0926, 89 31.1412)	96	257	74.04 cm	74.16 cm
Crampton (46 12.4494, 89 28.30974)	98	16	189.67 cm	163.66 cm
Plum (46 13.0182, 89 29.48616)	163	187	96.83 cm	119.70 cm

Table 1. This table displays the general count of each species and average heights of hemlock by association of each stand.