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# Understory microclimate and photosynthetic response of saplings in an old-growth eastern hemlock (*Tsuga canadensis* L.) forest[1]

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*Abstract*: I measured microclimate and photosynthesis of eastern hemlock (*Tsuga canadensis* L.) saplings in the understory of an old-growth eastern hemlock forest. About 14% of the canopy trees were deciduous. Daily maximum air temperature in the understory was 3-4°C lower than above the canopy in July through September, but only 1-2°C lower from October through June. Photosynthetic photon flux density (PFD) in the understory was typically less than 20 $\mu$mol m$^{-2}$ s$^{-1}$, or about 1% of full sunlight, and exceeded 200 $\mu$mol m$^{-2}$ s$^{-1}$ during < 1.2% of the daylight hours in July through September. Average PFD was higher in spring, with May having about twice as much total daily PFD as late June and early July. At 22°C, net photosynthesis by hemlock sapling foliage was 0 at ≈10 $\mu$mol m$^{-2}$ s$^{-1}$ PFD and reached light saturation (≈ 5 $\mu$mol m$^{-2}$ s$^{-1}$) at ≈ 350 $\mu$mol m$^{-2}$ s$^{-1}$ PFD. Net photosynthesis near light saturation increased slightly as air temperature changed from 11 to 15°C, but did not change significantly between 15 and 30°C. These microclimatic and physiological measurements indicate that net photosynthesis by hemlock saplings is probably little affected by temperature from late spring through early fall. Late spring is probably the time of greatest photosynthesis by eastern hemlock saplings in hemlock forests with deciduous trees in the canopy.
*Keywords*: *Tsuga canadensis*, hemlock, understory, photosynthesis, PFD.

*Résumé* : J'ai mesuré les conditions microclimatiques et les taux de photosynthèse de gaules de pruche de l'Est (*Tsuga canadensis* L.) poussant en sous-bois dans une vieille prucheraie. Environ 14 % des arbres dominants étaient décidus. La température maximale journalière était de 3 à 4°C plus basse en sous-bois qu'au-dessus de la voûte forestière de juillet à septembre, mais elle était seulement de 1 à 2°C plus basse d'octobre à juin. Le flux de photons photosynthétiques (PFD) en sous-bois était généralement de moins de 20 $\mu$mol m$^{-2}$ s$^{-1}$, ou environ 1 % de la lumière directe et n'excédait 200 $\mu$mol m$^{-2}$ s$^{-1}$ que durant moins 1,2 % de la durée de la photopériode de juillet à septembre. Le PFD moyen était plus élevé au printemps et le PFD journalier total était deux fois plus élevé en mai qu'à la fin juin et au début juillet. À 22°C, le taux de photosynthèse net du feuillage des gaules de pruche était de 0 à un PFD d'environ 10 $\mu$mol m$^{-2}$ s$^{-1}$ et atteignait la saturation en lumière (5 $\mu$mol m$^{-2}$ s$^{-1}$) à un PFD d'environ 350 $\mu$mol m$^{-2}$ s$^{-1}$. Le taux de photosynthèse net en conditions de quasi-saturation en lumière augmentait un peu alors que la température passait de 11 à 15°C, mais ne changeait pas significativement entre 15 et 30°C. Ces mesures microclimatiques et physiologiques indiquent que le taux de photosynthèse net des gaules de pruche est probablement peu affecté par la température, de la fin du printemps jusqu'à début de l'automne. La fin du printemps est probablement le moment où les taux de photosynthèse sont les plus élevés chez les gaules de pruche dans les prucheraies comprenant des arbres décidus dans la voûte forestière.
*Mot-clés* : *Tsuga canadensis*, pruche, sous-bois, photosynthèse, PFD.

## Introduction

Forests dominated by eastern hemlock (*Tsuga canadensis* L.) have long been noted for the dense shade of the understory environment and its cool microclimate (Daubenmire, 1931; Fowells, 1965; Friesner & Potziger, 1936; Moore *et al.*, 1924; Shreve, 1927). The hemlock understory typically has little vegetation when compared to deciduous forests (Rogers, 1980), perhaps because of the low light level. Canham *et al.* (1994) observed that photosynthetically active radiation in the understory of hemlock stands was the lowest of any of nine forest types which they investigated. In spite of this, hemlock saplings occurred in the understory of nearly all the stands sampled by Rogers (1980). Thus, the species is obviously adapted for survival at low light levels.

The ability of hemlock saplings to survive in the understory may also be enhanced by the fact that deciduous trees may form up to 25% of the overstory in hemlock-dominated forests (Rogers, 1980). Given the extremely deep shade cast by hemlocks throughout the year, light reaching the forest floor of mixed hemlock-deciduous forests could be sharply increased when deciduous trees are leafless in late autumn, winter and early spring. If temperature conditions allow photosynthesis during these periods of the year, the higher light levels could greatly increase carbon fixation by hemlock saplings, as well as other evergreen understory species.

The research reported here was conducted in a hemlock stand nearly 200 years old, with a small component of deciduous canopy trees. My first goal was to describe the understory microclimate in terms of air temperature, soil temperature, and photosynthetically active radiation throughout the year. Second, I measured the photosynthetic response of hemlock saplings to temperature and light in order to evaluate their ability to use the light present in the understory at various seasons of the year.

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## Material and methods

### VEGETATION DESCRIPTION

This research was performed in the understory of an old-growth eastern hemlock stand at an elevation of 360 meters in the Harvard Forest in central Massachusetts, U.S.A. (42° 29' N, 72° 11' W). This stand was previously described by Foster *et al.* (1992) and Foster & Zebryk (1993).

Two stands of hemlock saplings were selected for microenvironmental and physiological measurements. These stands were slightly to the north of two large beech trees (*Fagus americana* L.) in the hemlock-dominated canopy. Each sapling stand covered about 25 $m^2$. In each stand I measured the number of saplings over 50 cm tall and the maximum sapling height and diameter, and I also cut five randomly selected saplings plus the tallest sapling from each stand at ground level to determine their ages using annual growth rings. Except for the two beeches, the sapling stands were surrounded by mature hemlocks up to 84 cm in diameter and about 25 m tall. The density, diameter, and basal area of overstory trees as well as sapling density were measured in eight randomly located 10 m × 10 m plots, two within each of four 50 m × 50 m quadrants to the NE, SE, SW, and NW of the center of the sapling stand.

### MICROCLIMATE AND LIGHT ENVIRONMENT

Above-canopy air temperature was measured every 30 seconds at a point 25 m above the ground, near the top of an emergent red spruce tree about 100 m from the study site. In March 1997, the measurement location was moved to 21 m above the ground in a canopy access tower about 12 m from the study site. Understory air temperature was monitored 50 cm above the ground near the center of one of the hemlock sapling stands. Soil temperature was measured at approximately 10 cm soil depth at two locations: beneath the understory air temperature sensor, and 6 m away in a gap between the two stands of hemlock saplings. All temperature measurements were made with shaded 24 ga copper-constantan thermocouples. Average, maximum, and minimum values were calculated every 30 minutes.

Photosynthetic photon flux density (PFD) was measured every 5 seconds at four randomly located points in the hemlock stand. Average, maximum, and minimum values were calculated every 10 minutes. Quantum sensors were leveled on top of stakes 80 to 100 cm above the ground, near the tops of hemlock saplings.

### GAS EXCHANGE MEASUREMENTS, SHOOT WATER POTENTIAL, AND LEAF AREA ESTIMATES

Net photosynthesis (Pn) and stomatal conductance were measured at controlled light intensities during two periods, in early and late summer, using an LI-6200 photosynthesis system (LICOR Inc., Lincoln, Nebraska). The three most recent age classes of mature foliage were each measured separately by using an 0.25-L chamber, and controlled light intensities were supplied by a halogen spotlamp with a dichroic mirror to reduce chamber heating. All Pn measurements were made at chamber temperatures of 20 to 25°C. Early morning and mid-afternoon xylem pressure potentials (*XPP*) of the saplings were measured on the dates of photosynthesis measurements using a pressure bomb. The effects of air temperature on Pn was measured on detached shoots placed in a growth chamber in mid-September. The detached shoots had a free water supply and a PFD of 220 $\mu$mol $m^{-2}$ $s^{-1}$ during photosynthesis measurements. This PFD was sufficient for the hemlock foliage to reach ≈ 90% of light-saturated Pn (see Results section, Figure 5). Leaf areas of shoots on which gas exchange measurements were made were determined by creating photocopies of individual shoots and detached needles, scanning these photocopies, and measuring area of the scanned images using NIH Image computer graphics software (U.S. National Institutes of Health, Bethesda, Maryland).

## Results

### VEGETATION

The two sapling stands where physiological measurements were made contained 61 and 63 saplings over 50 cm tall, respectively, giving a density of about 2.5 saplings per $m^2$ in each stand. The maximum sapling height in each stand was about 1.9 m, the maximum basal diameter was 3.2 cm. Sapling ages, based on a sample of five randomly chosen saplings from each stand plus the tallest sapling in the stand, ranged from 11 to 34 years.

In the area within approximately 50 m of the midpoint between the two stands, the average density of hemlock saplings (> 50 cm in height and < 5 cm dbh) was 1000 ± 273 stems/ha. Within the same area, hemlock trees over 10 cm dbh had a density of 400 ± 52 stems/ha and a basal area of 43.5 ± 6.5 $m^2$/ha. Other species within the sample plots (*Acer rubrum, Acer pensylvanicum, Fraxinus americana, Quercus rubra, Pinus strobus,* and *Picea rubens*) accounted for only 7% of all saplings, 14% of all trees > 10 cm dbh, and 10% of total basal area.

### MICROCLIMATE AND LIGHT ENVIRONMENT

During the summer, air temperature in the stand of hemlock saplings was substantially buffered from warm air temperatures above the forest canopy. Average daily maximum air temperature 50 cm above the ground was about 4°C cooler than above the forest canopy (Figures 1 and 2). The difference decreased to approximately 1°C in late fall and winter, and then rose slightly to about 2°C in spring (Figure 1). Daily minimum air temperatures in the sapling stand and above the forest canopy were very similar at all times of year. Soil temperature at 10 cm depth was buffered from temperature extremes in summer and winter, and showed at most only a few degrees difference between maximum and minimum for each day, although the difference was greater for soil between sapling stands than within a stand (Figures 1 and 2).

Moderation of air and soil temperatures was accompanied by extreme attenuation of light in the hemlock forest understory. During summer and early fall, the light level at the top of the hemlock saplings was less than 20 $\mu$mol $m^{-2}$ $s^{-1}$ PFD, or about 1% of maximum PFD above the forest, during two-thirds of the daylight hours (Figure 3). On a typical sunny day in early summer, PFD at the top of the hemlock sapling canopy was usually below 20 $\mu$mol $m^{-2}$ $s^{-1}$, with only brief periods when PFD rose above 100 $\mu$mol $m^{-2}$ $s^{-1}$

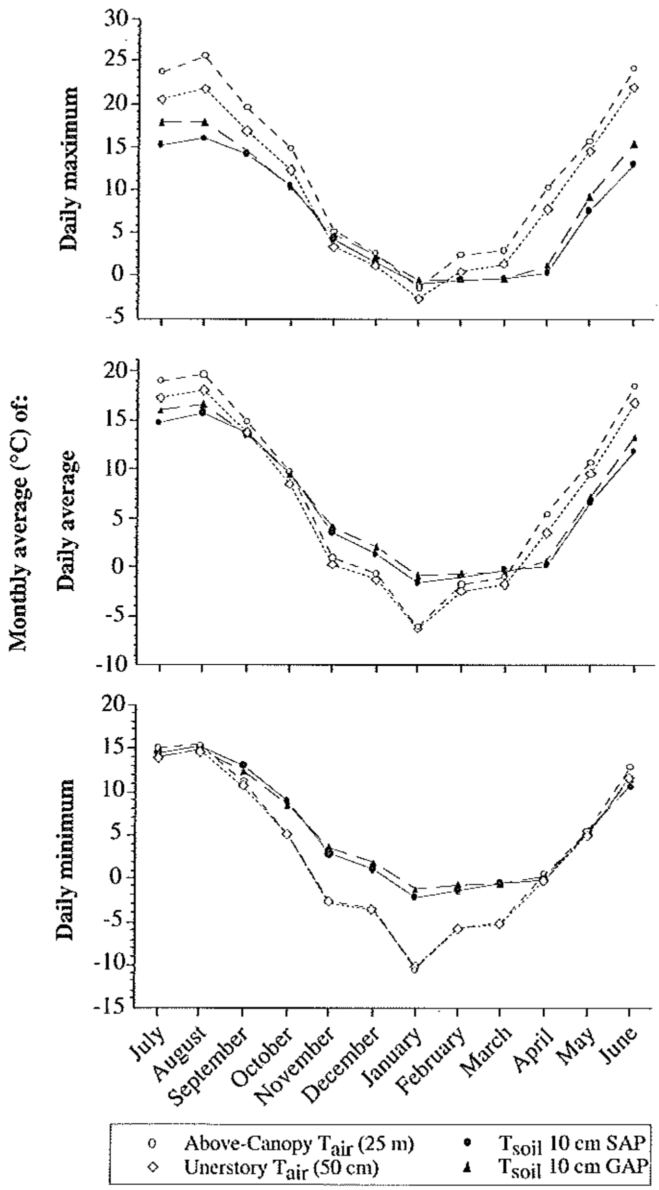


FIGURE 1. Monthly mean values of daily maximum, daily average, and daily minimum temperatures for air above the forest canopy, air within the canopy of a hemlock sapling, and soil beneath and between hemlock sapling stands.

(Figure 4a). On cloudy days, maximum PFD was under 20 $\mu$mol m$^{-2}$ s$^{-1}$ (Figure 5a). These values compare to a typical maximum PFD of approximately 1900 $\mu$mol m$^{-2}$ s$^{-1}$ above the forest canopy in early summer, and agree with the measurements of Canham *et al.* (1994), showing that PFD beneath an eastern hemlock canopy was only about 1% of full sun. This occurred despite the fact that the old-growth hemlocks above the measurement site had a crown depth of only 30-50% of tree height (6-12 m), compared to a crown depth of 95% of tree height in Canham *et al.* (1994). An analysis of all 10-minute mean PFD values at the top of the hemlock sapling canopy showed that PFD exceeded 200 $\mu$mol m$^{-2}$ s$^{-1}$, or about 10% of maximum above-canopy PFD, during only 0.4-1.2% of the daylight hours in July through October (Figure 3).

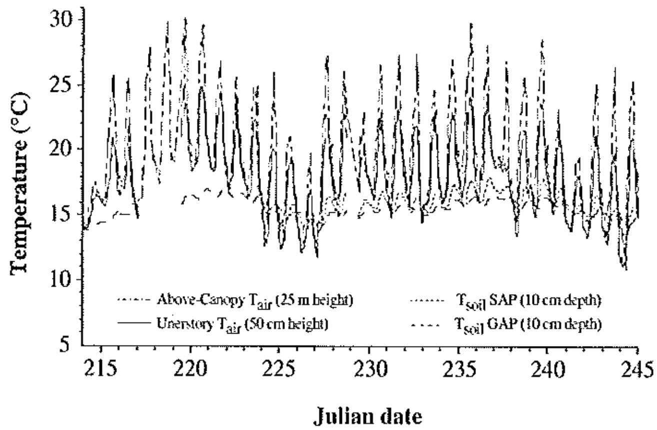


FIGURE 2. Average temperatures calculated every 30 minutes during August 1996 at the locations indicated in the figure, which are further described in the "Material and methods" section. Soil temperature beneath a stand of hemlock saplings ($T_{soil}$SAP) was not measured before Julian day 223, and some data is missing on Julian days 217-219 and 228-229 due to delays in replacing the dataloggers. Data shown in the figure were also used to calculate monthly averages for August in Figure 1.

In spring, substantially more light reached the understory, so that PFD was above 200 $\mu$mol m$^{-2}$ s$^{-1}$ during 2.5-3.5% of the daylight hours in April through June (Figure 3). The greater light levels in spring could also be seen in the daily time-course of PFD reaching the understory on both sunny and cloudy days in spring *versus* summer (Figures 4 and 5). Daily total PFD in the understory was nearly twice as great in May 1997 compared to late June 1996 (Table I).

### GAS EXCHANGE, SHOOT WATER POTENTIAL, AND LEAF AREA

Net photosynthesis by hemlock sapling foliage increased linearly with the logarithm of incident PFD up to about 350 $\mu$mol m$^{-2}$ s$^{-1}$, where Pn became light saturated (Figure 6). Current-year foliage and one- to two-year old foliage responded similarly, with current year foliage reaching a maximum Pn of about 5.5 $\mu$mol m$^{-2}$ s$^{-1}$, and one- and two-year old foliage about 0.5 and 1 $\mu$mol m$^{-2}$ s$^{-1}$ lower, respectively. In growth chamber measurements, varying the air temperature between approximately 15 and 30°C had no detectable effect on Pn, although Pn was slightly lower at 11°C compared to higher temperatures (Figure 7). Early morning average xylem pressure potential (*XPP*), which was assumed to be equal to shoot water potential, varied from -0.2 to -0.5 megapascals (MPa). Mid-afternoon *XPP* on a sunny day in mid-July averaged about -1.2 MPa (Table II).

The age distribution of foliage collected in early October showed that 78% of the foliage was in the three most recent age classes, although some foliage over 4 years old was present (Table III). The average leaf area index of five stands of hemlock saplings was 1.18 with a standard error of 0.22.

## Discussion

### VEGETATION

Some of the deciduous species most common in the hemlock canopy (*Fagus americana*, *Acer pensylvanicum*) were also reported as common by Rogers (1980). *Acer pensylvanicum* was also the second most common species among saplings, as Rogers (1980) found for a number of

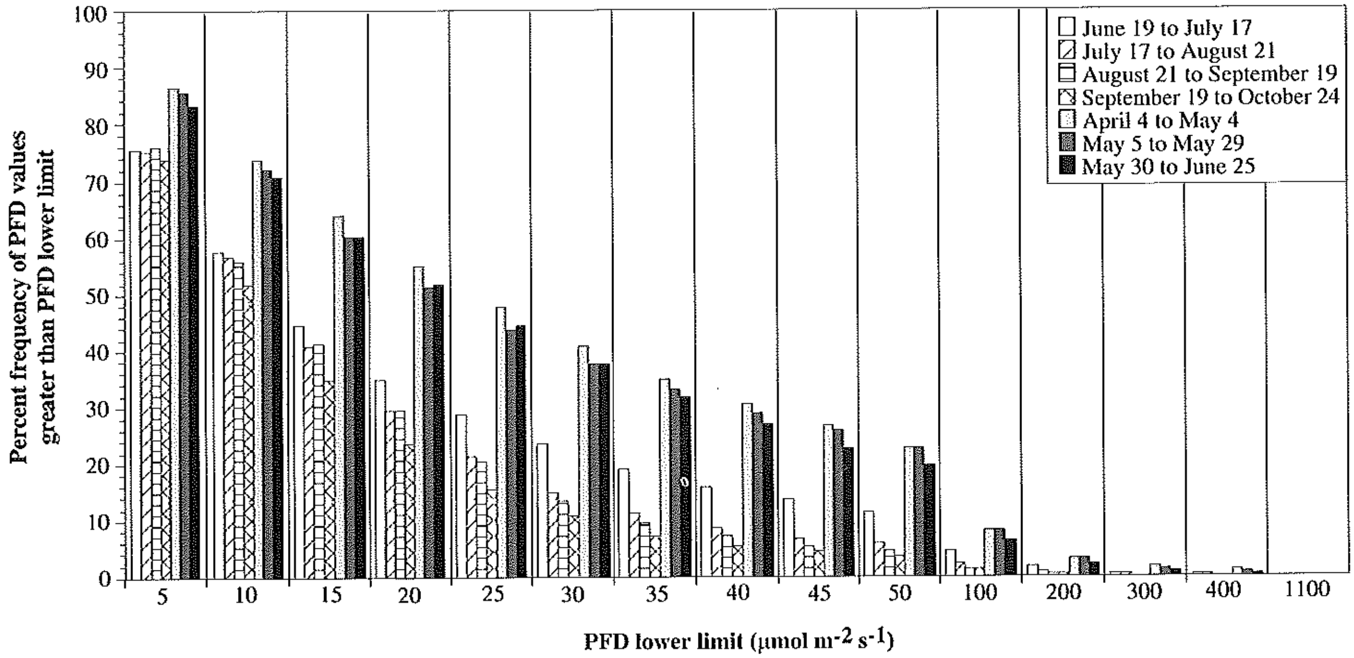


FIGURE 3. Frequency distributions of ten-minute averages for PFD measured every 5 seconds in each of four locations at the top of hemlock sapling canopies. Each bar represents the percent of all average PFD values that were greater than the value indicated at the bottom of the bar. Shading of bars indicates the period of measurements as shown in the figure.

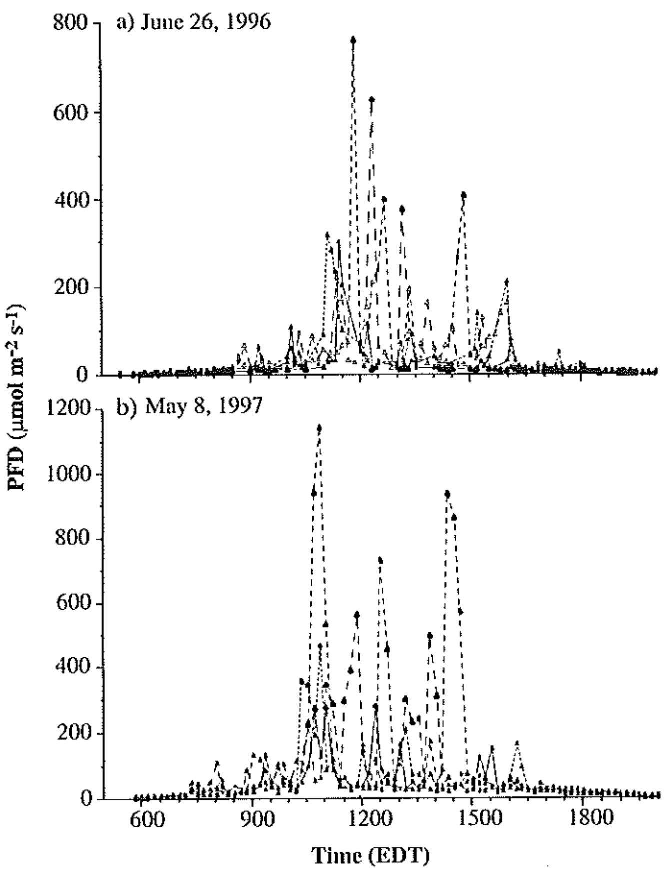


FIGURE 4. Average photosynthetic photon flux density (PFD) measured at four locations near the top of hemlock sapling canopies on sunny days in (a) June 1996 and (b) May 1997. Each quantum sensor measured PFD every 5 seconds; points represent ten-minute averages of these measurements. Measurements at the four locations can be most easily distinguished by solid *versus* dashed lines, and by the length of dots or dashes connecting the points. Note the difference in scale between a and b.

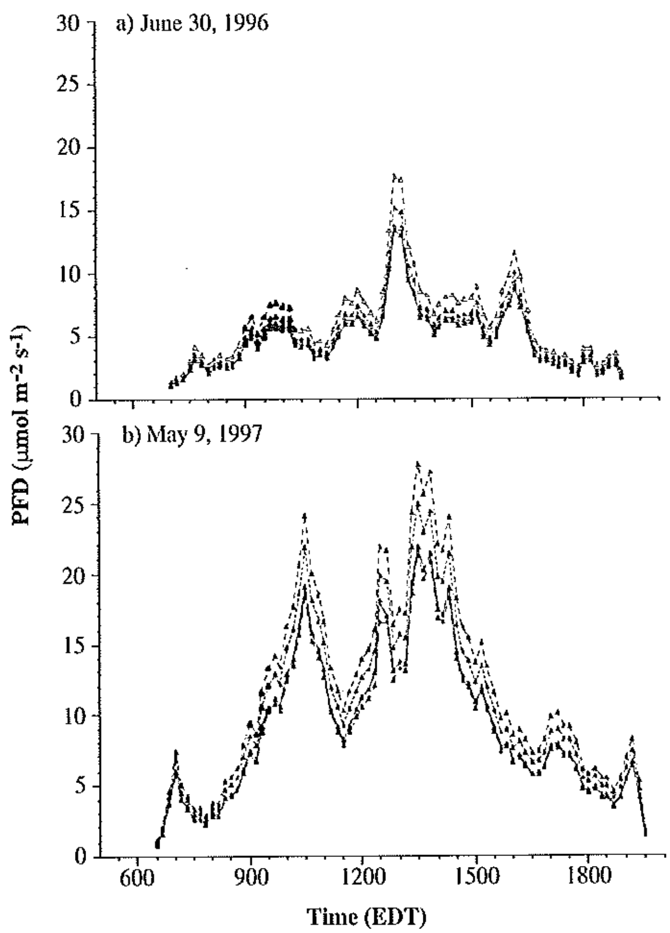


FIGURE 5. Average photosynthetic photon flux density (PFD) measured at four locations near the top of hemlock sapling canopies on heavily overcast days in (a) June 1996 and (b) May 1997. Points indicate ten-minute averages, as in Figure 4.

TABLE I. Average integrated photosynthetic photon flux density (PFD) in moles/m$^2$ at four locations near the tops of hemlock saplings during the periods June 19 to July 3, 1996 and May 5 to May 29, 1997. Maximums and minimums are the highest and lowest averages across all four locations on any day during each period

| | June 19 – July 3, 1996 | May 5 – May 29, 1997 |
|---|---|---|
| Average daily total PFD | 1.13 | 2.23 |
| Maximum | 1.88 | 3.51 |
| Minimum | 0.23 | 0.47 |

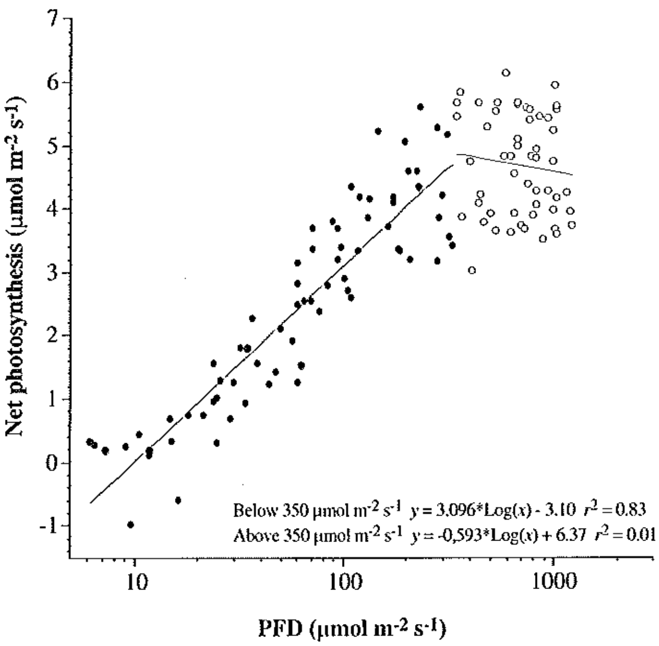


FIGURE 6. Response of net photosynthesis to photosynthetic photon flux density (PFD), as measured with a controlled light source in the field on September 12, 1996. Air temperature in the photosynthesis chamber was 22-24°C. A single average curve for three age classes of foliage (current year, one-year old and two-years old) is shown for simplicity. Responses of the three age classes were very similar, except that maximum Pn and the slope of the response curve declined about 10% with each year of foliage age.

stands. Among tree species, the total deciduous component in both the overstory and understory (14% and 7%, respectively, by tree and sapling density) was also within the range of the hemlock stands studied by Rogers (1980).

### UNDERSTORY MICROCLIMATE

Air temperature in the understory of the hemlock forest averaged about 4°C cooler than the atmosphere above it during the warmest part of summer days (Figures 1 and 2). This contrasts strongly with open environments, in which air temperature is highest close to the soil surface, especially on sunny days (Geiger, 1965).

This cool microclimate was associated with extremely low levels of photosynthetically active radiation in summer. In the late fall and winter (data not shown in Figure 3 because of space limitations), the hemlock saplings continued to receive very low levels of PFD, even after the nearby beech trees became leafless. This was probably a result of a very low solar angle, which caused any direct sun passing through the canopy gaps created by the leafless beeches to reach the understory to the north of the hemlock saplings.

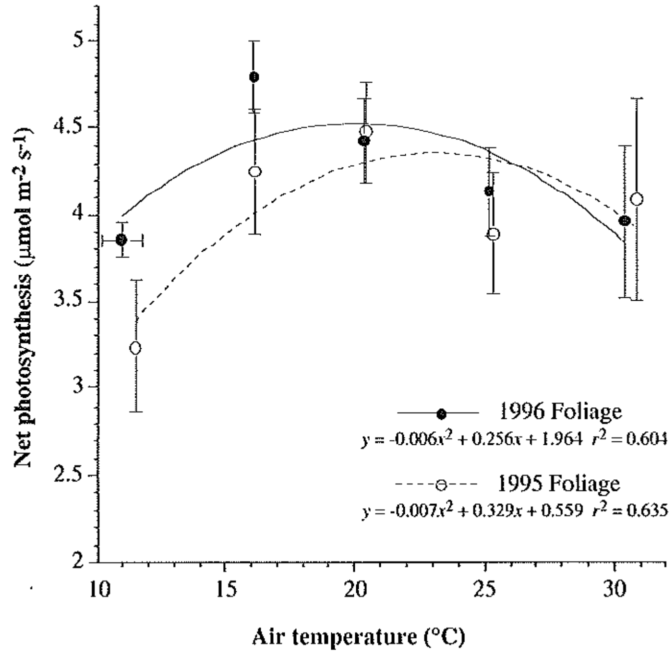


FIGURE 7. Response of net photosynthesis of current and year-old foliage of hemlock saplings to temperature. Measurements were made in a growth chamber and photosynthesis was measured at 220 μmol m$^{-2}$ s$^{-1}$ PFD (net photosynthesis ≈ 90% of light-saturated rate) in mid-September 1996. Wind velocity within the photosynthesis cuvette was about 2 m s$^{-1}$, preventing significant foliar heating above air temperature. Net photosynthesis is expressed on a projected leaf area basis and curves represent best-fit second-degree polynomial regressions; bars indicate standard errors of means. For net photosynthesis, only means at 11°C *versus* 15 and 20°C differed significantly at $p < 0.05$.

TABLE II. Xylem pressure potential (*XPP*) of small hemlock branches containing 2-3 years of growth, harvested in the summer of 1996. Eight branches were measured on each date

| Date | Time (hrs) | Average *XPP* | Maximum | Minimum |
|---|---|---|---|---|
| June 28 | 0630 | -0.32 | -0.20 | -0.45 |
| July 3 | 0800 | -0.33 | -0.25 | -0.45 |
| July 12 | 0800 | -0.34 | -0.25 | -0.50 |
| July 12 | 1530 | -1.22 | -0.90 | -1.70 |
| September 5 | 0645 | -0.23 | -0.20 | -0.30 |
| September 5 | 1745 | -0.65 | -0.55 | -0.90 |

TABLE III. Percentage of total hemlock sapling foliage area present in 1996, which was produced in various years. The sample was composed of a branch tip collected in October 1996 from the upper canopy of each of eight randomly chosen saplings. Two branch tips were randomly selected from each compass direction (N,E,S,W)

| Foliage year | 1996 | 1995 | 1994 | 1993 | ≤ 1992 |
|---|---|---|---|---|---|
| Percent of foliage | 26 | 32 | 22 | 14 | 6 |
| Standard error | 3.1 | 2.6 | 2.7 | 2.0 | 0.8 |

However, in mid- to late spring, the hemlock saplings received the highest illumination of the year (Figure 3), as the sun reached high enough to shine through the leafless beech canopies and directly onto the hemlock saplings. This period was prolonged in 1997 by a very cold May, which delayed leaf development of deciduous trees by two to three weeks compared to an average year (J. O'Keefe, pers. comm.).

The difference in light penetration between summer and late spring can be seen by comparing typical sunny days in late June 1996 and early May 1997 (Figure 4), or typical cloudy days during the same periods (Figure 5). Even on sunny days in late June, periods of PFD above 50 $\mu$mol $m^{-2}$ $s^{-1}$, which might be considered "sunflecks" in this forest, were generally of very brief duration, 10 to 30 minutes at most (Figure 4a). Unfortunately, I did not measure average PFD over intervals shorter than 10 minutes, and therefore I may have missed very short-term sunflecks, which are common in the understory of tropical and temperate deciduous forests (Chazdon, 1988; Pearcy & Pfitsch, 1994). Nevertheless, the data show that in late June, most of the time the light level was very close to the light compensation point of the hemlock saplings, as estimated from the light response curves (Figure 6). On sunny days in early May (Figure 4b), the maximum PFD was higher and PFD was elevated above the background level for longer periods. Even on cloudy days, light reaching the hemlock saplings was much greater in May compared to June (Figure 5b *versus* 5a). These indicate that both more direct and more diffuse illumination reached the saplings in early May than late June, despite the fact that the sun was highest in the sky in late June.

ECOPHYSIOLOGY OF PHOTOSYNTHESIS IN HEMLOCK SAPLINGS

The strong logarithmic response of photosynthesis in the hemlock saplings as PFD increased from 10 to about 350 $\mu$mol $m^{-2}$ $s^{-1}$ suggests that this range is extremely important in the ecology of hemlock saplings. During the summer and fall, the saplings would fix very little carbon without sunflecks to raise PFD above the low background level.

Measurements of incident photosynthetic photon flux and carbon exchange by hemlock saplings indicated that the saplings fixed little or no carbon when they were heavily shaded in summer, but photosynthesis increased rapidly during sunflecks. Sunflecks were infrequent and diffuse radiation was very low in summer, but photosynthetic photon flux from both sources was considerably higher in spring prior to leaf-out of deciduous trees. I observed little variation in photosynthesis over a temperature range of 11-30°C, so hemlock saplings are apparently well equipped to take advantage of sunflecks and higher diffuse PFD levels during April and May. Even though April and May 1997 were much cooler than average (J. O'Keefe, pers. comm.), during April the air temperature was above 10°C 30% of the time between 0900 and 1700 hours EDT. These were the only hours when PFD was sometimes non-limiting for photosynthesis, and temperature limitation was possible. In May, air temperature in the understory was above 10°C during 60% of these hours, and above 15°C during 21% of the same time periods. Considering the fact that there may have been acclimation of the saplings to lower temperatures in April and May compared to September, when temperature responses were measured, cool air temperatures seem unlikely to have been a major limitation to photosynthesis in mid- and late spring.

Another possible limitation to photosynthesis in April and May is low nighttime temperatures. Repeated nighttime temperatures below -2°C can severely limit stomatal conductance and photosynthesis in many north-temperate coniferous species (Smith *et al.*, 1984; Larcher, 1995), as well as in mature hemlock trees (J. Hadley, unpubl. data). However, despite an unusually cool May in 1997, the air temperature in the hemlock understory fell below 0°C only once after April 20, so nighttime frosts should not have limited photosynthesis in late April and May.

I measured the temperature response of photosynthesis in the summer and early fall and not early spring, and the temperature response was measured with near-saturating PFD, rather than at lower PFD levels typical of the hemlock understory. The effect of temperature on photosynthesis in April and May was undoubtedly different than that presented in Figure 6. However, if acclimation occurs at all, photosynthesis at low temperatures would be expected to be greater in early spring than in summer or early fall when air temperatures are consistently warmer. It is also nearly certain that low-light photosynthesis has a more negative response to increasing temperature compared to high-light photosynthesis. This is a consequence of the greater ratio of dark respiration to net photosynthesis when light is comparatively low, and the relatively greater importance of the exponential increase in dark respiration as temperature increases in a low-light environment.

All of these considerations indicate a potential for greater carbon fixation by hemlock saplings in April and May 1997 as compared to the previous summer. This occurred primarily because of the presence of a few deciduous overstory trees, which allowed substantially more light to reach understory saplings in spring than in summer.

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