

LOW CLOUDS AND CLOUD IMMERSION ENHANCE PHOTOSYNTHESIS IN UNDERSTORY SPECIES OF A SOUTHERN APPALACHIAN SPRUCE–FIR FOREST (USA)¹

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High-altitude forests of the southern Appalachian Mountains (USA) are frequently immersed in clouds, as are many mountain forests. They may be particularly sensitive to predicted increases in cloud base altitude with global warming. However, few studies have addressed the impacts of immersion on incident sunlight and photosynthesis. Understory sunlight (photosynthetically active radiation, PAR) was measured during clear, low cloud, and cloud-immersed conditions at Mount Mitchell and Roan Mountain, NC (USA) along with accompanying photosynthesis in four representative understory species. Understory PAR was substantially less variable on immersed vs. clear days. Photosynthesis became light-saturated between ~ 100 and $400 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ PAR for all species measured, corresponding closely to the sunlight environment measured during immersion. Estimated daily carbon gain was 26% greater on clear days at a more open canopy site but was 22% greater on immersed/cloudy days at a more closed canopy site. F_v/F_m (maximum photosystem II efficiency) in *Abies fraseri* seedlings exposed to 2.5 min full sunlight was significantly reduced (10%), indicating potential reductions in photosynthesis on clear days. In addition, photosynthesis in microsites with canopy cover was nearly 3-fold greater under immersed ($2.6 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$) vs. clear conditions ($0.9 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$). Thus, cloud immersion provided more constant PAR regimes that enhanced photosynthesis, especially in shaded microsites. Future studies are needed to predict the survival of these refugial forests under potential changes in cloud regimes.

Key words: *Abies fraseri*; *Aster divaricatus*; diffuse light; *Eupatorium rugosum*; fog; photoinhibition; *Sambucus pubens*; seedling.

The relic spruce–fir forests of the southern Appalachian Mountains (*Abies fraseri* and *Picea rubens*) spend 30–40% of a typical day in various degrees of cloud immersion (Mohnen, 1992). Most of this immersion occurs at night and at early morning. Early morning is particularly important for daily photosynthetic carbon gain because of the common occurrence of the maximum water status for the day, and the potentially strong impacts of low nighttime temperatures followed by high sunlight levels in the morning (low-temperature photoinhibition; Germino and Smith, 1999, 2000). Cloud immersion also accounted for over 45% of the total annual water input in this forest type (Smathers, 1982). Despite these important relationships, few studies exist in which the ecophysiological effects of cloud immersion in these or other forests have been evaluated (e.g., Letts and Mulligan, 2005). Moreover, future cloud ceilings have been predicted to rise in this and other high mountain environments as the climate changes, resulting in substantially less cloud immersion (Croke et al., 1999; Still et al., 1999; Richardson et al., 2003). In general, forests that are frequently immersed in clouds (i.e., “cloud forests”) may be particularly sensitive to the impacts of climate change worldwide (Foster, 2001) as evidenced by local declines in population sizes and species extinctions already reported (e.g., Pounds et al., 1999).

Little is known about the specific sunlight environments of cloud-immersed plant communities or the corresponding impacts on photosynthetic carbon gain. Both cloud immersion (e.g., fog and mist) and cloud cover can result in major changes

in the incident photon flux density and directional quality (diffuse vs. direct) of sunlight (e.g., Gu et al., 1999; Letts and Mulligan, 2005; Min, 2005). For example, a much greater proportion of sunlight will become diffuse/scattered under the influence of clouds, as opposed to the direct (collimated) sunlight of clear days. However, the variability of this diffuse light regime can vary significantly, along with corresponding impacts on photosynthesis. No studies (to our knowledge) have evaluated the photosynthetic impacts of the diffuse light regime beneath forest overstories during clear or cloud-immersed days. Even on clear days, tree spacing and canopy architecture can generate a broad range of sunlight irradiance in the understory due to penumbral effects (Smith et al., 1989).

Leaf photosynthesis in terrestrial plants often becomes light-saturated at irradiances of about one third to one half of full sunlight (Lambers et al., 1998), and forest researchers now recognize that a more diffuse form of sunlight can lead to major increases in photosynthesis at the plant canopy level (Hollinger et al., 1994; Gu et al., 1999, 2002; Min, 2005). Increases in canopy photosynthesis on a ground area basis have also been attributed to a more homogeneous light distribution within a plant canopy under clouds (Horn, 1971; Norman and Arkebauer, 1991). On a global scale, the unusual stabilization in the atmospheric CO₂ concentration under the plume of the Mount Pinatubo eruption may be another example. The greater penetration of diffuse sunlight into forest canopies (and greater canopy photosynthesis) due to these volcanic aerosols may have increased the global sink for CO₂ absorption (Roderick et al., 2001; Gu et al., 2003). On a smaller scale, Young and Smith (1983) reported that understory plant species of the more open subalpine forests of the south-central Rocky Mountains (USA) generated greater photosynthetic carbon gain during cloudy conditions, at a much lower cost in transpirational water loss. In addition, significant reductions in photosynthesis can develop at sunlight levels above saturation via downregulation

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and/or photoinhibition of photosynthesis in understory species, especially, along with substantial increases in temperature and transpirational costs (see Long et al., 1994; Adir et al., 2003, for reviews).

The purpose of the present study was to measure incident sunlight and corresponding photosynthetic performance for selected understory species in a southern Appalachian spruce–fir forest under both clear-sky and cloudy conditions (both low cloud and cloud-immersed days). Corresponding differences in daily photosynthetic carbon gain were predicted from sunlight measurements and photosynthetic light response curves. In addition, leaf fluorescence was measured to assess potential depressions of photosynthesis due to prolonged exposure to full sunlight.

MATERIALS AND METHODS

Study sites—Two study sites were selected at 1680 and 1908 m a.s.l. (Carver's Gap [CG] and Roan High Knob [RHK], respectively) on an east-facing slope of the Roan Mountain massif (North Carolina, USA, 36°5' N, 82°8' W, 1910 m maximum elevation a.s.l.) in spruce–fir forests [dominant canopy trees were *Abies fraseri* (Pursh) Poir. and *Picea rubens* Sarg. at both sites). As estimated from hemispherical photos, CG was a more closed canopy site and RHK had a more open canopy (13 vs. 19% canopy openness, respectively; see Johnson and Smith, 2005, for more details). One study site was also established at Mount Mitchell, North Carolina, in a spruce–fir forest (USA, 35°54' N, 82°17' W, 2037 m maximum elevation a.s.l.) on an east-facing slope at an altitude of 2015 m and was used with landscape photographs to document immersed and clear days (details described in PAR measurements section).

PAR (photosynthetically active radiation) measurements—The objective of this study was to record PAR levels at actual plant microsites so that the effects on photosynthesis could be evaluated based on differences in measured understory light for cloudy/immersed vs. clear-sky conditions. The purpose was not to characterize the understory light environment of the entire forest community, which would have required many PAR sensors throughout each site and many more days sampled. Photosynthetically active radiation (PAR) was measured instantaneously (no time averages) because in previous studies instantaneous measurements of PAR are much more precise than time-averaged measurements (e.g., Letts et al., 2005). PAR was measured every 10 min for 45 days (19 August to 2 October 2005) at each of the Roan Mountain sites using one PAR sensor (LI-190, LICOR, Lincoln, Nebraska, USA) connected to a voltage amplifier (Model UTA, EME Systems, Berkeley, California, USA) and HOBO data logger (H8 4-channel logger, Onset Computer Corp., Bourne, Massachusetts, USA). PAR sensors were placed in a central location in each site at ground level (i.e., the approximate height of a seedling, 2–3 cm). To compare predictions of PAR from hemispherical photographs to actual PAR measurements, hemispherical photographs of the canopy were taken at seedling heights (for the highest-altitude plot on Roan Mountain, RHK) and were analyzed with HemiView software (version 2.1, Delta T Devices, Cambridge, UK). Using the HemiView software, PAR was predicted at 5-min intervals for an entire day and compared to actual values measured with PAR sensors.

PAR was also measured instantaneously at the Mount Mitchell site every minute for 41 days (6 July to 16 August 2005) using the same sensors/amplifiers/dataloggers as above to (1) compare to landscape photographs to document immersion (ground-level clouds), low clouds (cloud base < ~20 m above the forest canopy, but not contacting the canopy) and clear conditions (clear sky or high, patchy clouds) and (2) to evaluate the effectiveness of 10 min measurement intervals in capturing understory sunlight regimes (i.e., comparing instantaneous measurements every minute to instantaneous measurements every 10 min). Immersion and low clouds were difficult to separate using PAR sensors, even though there were photographs and measurements of PAR for each (periods of immersion and low clouds) from Mt. Mitchell (Fig. 1c). However, clear conditions or clear conditions with high, patchy clouds were easily distinguished from immersion/low cloud conditions. Cloud immersion was documented (DMJ, personal observation) on many of the days measured at Roan Mountain (including 20 August and 10 September).

Mean PAR (means of 4 days) was calculated using instantaneous

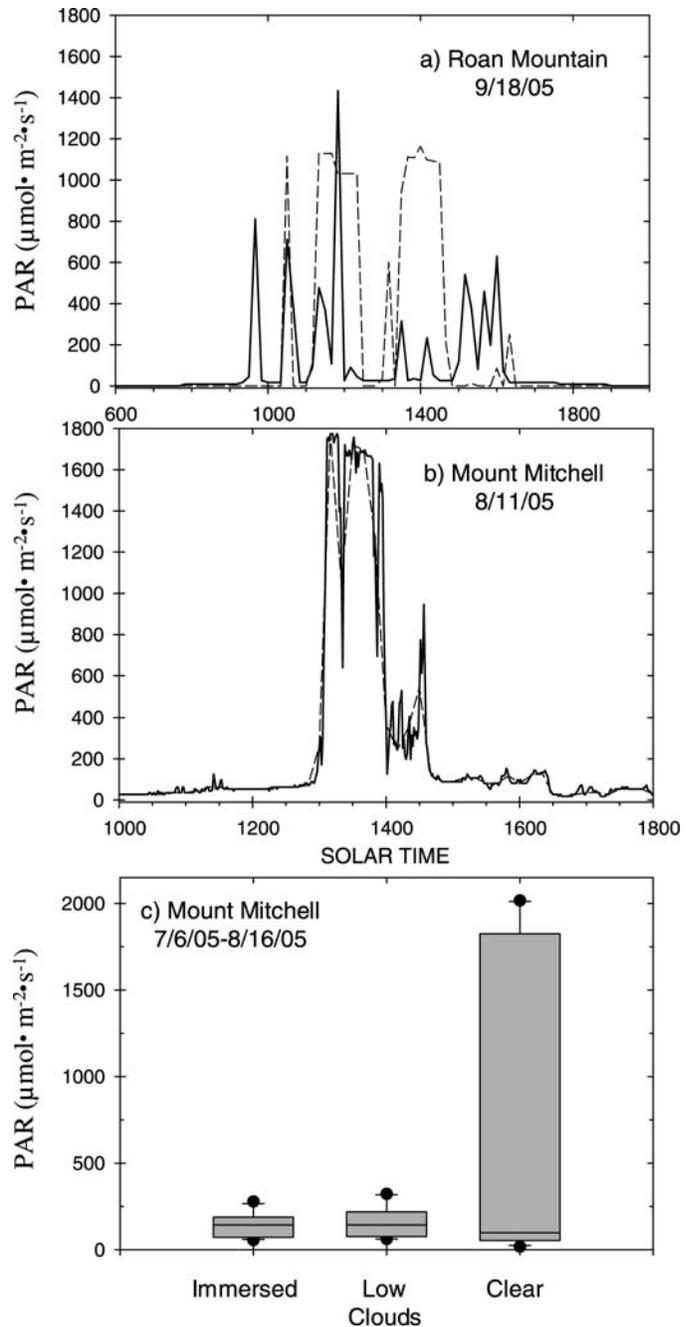


Fig. 1. Sunlight measurements: predicted vs. measured and summary of measurements under clear skies, low clouds, and cloud immersion. (a) Measured (solid line) and predicted clear-day sunlight regime (from hemispherical photographs; dashed line) at Roan Mountain, NC, (b) measured clear-day sunlight regime sampled every minute (solid line) and every 10 min (dashed line) at Mount Mitchell, NC, and (c) summary of photosynthetically active radiation (PAR) measurements from 6 July 2005 to 16 August 2005 (at Mount Mitchell, NC (randomly sampled and documented as immersed, low clouds, or clear sky using landscape photographs, Solar Time, see List 1971). Boxes represent 25th to 75th percentiles, horizontal lines within boxes represent median values, horizontal lines outside of boxes represent 10th and 90th percentiles, and closed circles represent actual range of values of all sampled PAR measurements.

measurements at 10-min intervals from 4 days each with immersed (20, 28 August; 10, 16 September) and clear-sky conditions (21 August; 6, 18, 27 September) at Roan Mountain that were selected for their similarity to previous PAR measurements under documented clear and immersed conditions, personal observations at Roan Mountain, and from personal observations and landscape photographs of Mount Mitchell (Fig. 1c). Mean PAR values were integrated from 0600 to 2000 hours (when there was measurable PAR) to determine the total amount of PAR received at each site. Sunlight regimes for representative clear (6 September) and immersed (20 August) days at Roan Mountain were also plotted to show the impact of averaging (mean PAR values) vs. instantaneous sunlight levels on typical days.

Net photosynthesis and daily carbon gain—Species for photosynthetic measurements were selected to include a variety of common plant types found in the spruce–fir forest understory (conifer tree seedlings, broadleaf shrubs, and herbs). Photosynthetic carbon gain in understory plants (*Abies fraseri*: 2-yr-old seedlings; *Aster divaricatus* L., *Eupatorium rugosum* Houttuyn., and *Sambucus pubens* Michaux.: 2–5-yr-old seedlings) of RHK and CG was estimated by combining instantaneous photosynthetic light response curves and measured PAR values. Individuals ($N = 4–6$ for each PAR value) of *A. divaricatus*, *E. rugosum*, and *S. pubens* were selected in the understory of RHK for light response curves; all light response curve parameters for *A. fraseri* were taken from Johnson and Smith (2005). Leaves were illuminated with different irradiance levels using a blue/red LED light source (6400–02B LED, LICOR). Initially, when leaves were placed in the leaf cuvette, PAR inside the chamber was $200 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. PAR inside the chamber was experimentally increased or decreased to construct light response curves for net photosynthesis. All light response measurements were taken between 1000 and 1400 hours, and each leaf was used for four consecutive measurements at different PAR values. Net CO_2 exchange was measured after each leaf had stabilized, which typically took around 1–2 min. Greater exposure times to each new level of PAR (up to 10 min) did not result in significant changes in photosynthesis ($P = 0.01$). Instantaneous solar radiation measurements (measured every 10 min) were then used to estimate daily carbon from the measured light response curves by integrating photosynthesis (for each instantaneous sunlight measurement) from 0600 to 2000 hours. Net photosynthetic CO_2 flux densities were computed on a total leaf area basis (total leaf area in the chamber; Smith et al., 1991). In all cases, net photosynthesis was measured using a LICOR-6400 portable photosynthesis system (LICOR).

Fluorescence of *A. fraseri* 2-year old seedlings (F_v/F_m , i.e., maximum photosystem II efficiency) was measured at approximately 530–600 (predawn), 1000 and 1330 hours on 13 June and 2 August at RHK. All leaves were dark adapted for 20 min prior to each measurement, which were performed with a PAM fluorimeter (model FMS-2, Hansatech Instruments, Norfolk, UK). Additionally, supplemental light was added to small groups of seedlings (6–10 seedlings) using a halogen spotlight (model Thor-X, Cyclops Solutions, Bedford, Texas, USA). To prevent heating, seedlings were cooled with a small fan, and light from the spotlight was passed through a 2.5-cm piece of acrylic to remove near-infrared radiation. Seedlings were exposed to approximately 500, 1000, or 2000 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ PAR (monitored with a LI-250 handheld PAR sensor, LICOR) for either 1 or 2.5 min.

Sampling and statistics—Statistical analyses were employed using JMP Statistical Analysis Software, version 3.2, (SAS, Cary, North Carolina, USA). Measurements of photosynthesis were averaged for each species ($N = 4–6$ individual measurements at each PAR value for each species; measurements were not repeated on individuals), for a given PAR level, and for time of measurement. The Tukey–Kramer multiple-comparison method (Zar, 1999) was used for evaluating statistical differences between fluorescence measurements under ambient light levels and predawn F_v/F_m values with and without supplemental light as well as PAR measurements from Mount Mitchell. Best-fit regression curves (curvilinear) were used to generate equations for the photosynthetic light response curves for each species.

RESULTS

Measurement and modeling of PAR—Predictions of PAR based on hemispherical photographs had little similarity to actual PAR measurements from the same location (Fig. 1a), although the timing of predicted peaks in PAR in the morning

overlapped with the measured values. Daily mean absolute differences and mean percentage differences between measured and predicted PAR were $107 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ and 26%, respectively. In the afternoon, there was no discernable overlap in measured vs. predicted PAR. However, measurements made every 10 min were similar to those made every 1 min (Fig. 1b). Daily mean absolute differences and mean percentage differences between 1-min and 10-min measurements were $9.7 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ and 1.7%, respectively. It appeared that most of the variation in the 1-min measurement set was captured using 10-min measurement intervals.

Sunlight regimes—Mean PAR values at Mount Mitchell were significantly greater ($P = 0.05$) under documented clear conditions as compared to immersed and low clouds (Fig. 1c), but median PAR was less under clear skies (compared to immersion and low clouds). Mean maximum PAR (mean of four highest sampled values) was significantly greater under clear skies vs. low clouds and immersion (789% greater, $P < 0.01$) and mean minimum PAR (mean of four lowest sampled values) was significantly less under clear conditions (43% less, $P = 0.05$). There were no significant differences in PAR (mean, mean maximum, or mean minimum) between immersed and low cloud conditions.

Cumulative daily understory PAR was 50% greater under clear skies compared to immersed conditions at RHK, but was 18% greater under immersed vs. clear-sky conditions at CG (Table 1). However, when peaks of PAR $> 1000 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ were removed (along with PAR values for the corresponding times on cloudy days) representative day cumulative PAR was $3.1 \text{ mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ under immersion vs. $1.9 \text{ mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ under clear skies at RHK (a 61% difference).

Peaks in maximum sunlight were reduced under immersion, compared to clear days (Fig. 2). At RHK, there were 9 peaks of greater than $200 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ PAR (the approximate light saturation point for the species measured here) for mean clear days, but for mean immersed days, there were only 3 peaks greater than $200 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Intensity of peaks in sunlight was reduced by approximately 76% and 45% (Fig. 2) at RHK and CG, respectively, under immersion.

Not only was peak sunlight intensity reduced during immersion, but PAR values were also less variable. Cloud immersion resulted in more time during a mean day when PAR values were between 100 and $400 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at both RHK and CG (Table 2). Between 1000 and 1700 hours at RHK, mean PAR for immersed and clear days remained between 51 and $283 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ and 34 and $651 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, respectively (Fig. 2a). Representative-day PAR at RHK varied from 18 to $1253 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ and 53 to $405 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ on clear and immersed days, respectively (Fig. 2c). Afternoon mean PAR on immersed days at CG remained between 70 and $120 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, whereas much of the clear day PAR values were below $50 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (Figs. 2b, 2d).

Photosynthesis—Photosynthetic light response curves for *A. fraseri*, *A. divaricatus*, *E. rugosum*, and *S. pubens* all saturated between 100 and $400 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (Fig. 3; Light response curves for *A. fraseri* from Johnson and Smith, 2005). Maximum light-saturated photosynthesis values ranged from approximately $2.0–3.2 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Predicted carbon gain for these species (as well as for *A. fraseri* seedlings) was 26% higher at RHK on clear days vs. cloudy days but was 22%

TABLE 1. Study site, cumulative daily photosynthetically active radiation (PAR) (for mean clear and immersed days) and the percentage of immersed days over the 45-d measurement period. RHK = Roan High Knob and CG = Carver's Gap.

Site	Cumulative clear-day PAR ($\text{mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$)	Cumulative immersed-day PAR ($\text{mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$)	Days with immersion (%)
RHK	5.22	3.48	67% (30/45)
CG	1.82	2.15	71% (32/45)

TABLE 2. The percentage of time between 0600 and 2000 hours on a mean clear or immersed day when PAR was between 100 and 400 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at each site. RHK = Roan High Knob and CG = Carver's Gap.

Site	Immersed days at 100–400 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (%)	Clear days at 100–400 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (%)	Increase in time with PAR at 100–400 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ on immersed day (%)
RHK	44	33	+33
CG	9.8	6.6	+48

higher at CG on immersed days than on clear days (Table 3). Photosynthesis in areas shaded by canopy was greater during immersion than during clear conditions. For example, integrated carbon gain for *A. fraseri* seedlings was 1.9 times greater for immersed conditions vs. clear conditions between 1200 and 1800 hours at CG (13.0 vs. 6.8 $\text{mmol} \cdot \text{m}^{-2}$) and 2.9 times greater for immersed conditions vs. clear conditions between 1230 and 1330 at RHK (2.6 vs. 0.9 $\text{mmol} \cdot \text{m}^{-2}$).

Both simulated high-sunlight conditions (Fig. 4a) and naturally occurring sun patches (Fig. 4b, 4c) resulted in reduced F_v/F_m in seedlings of *A. fraseri*. A 2.5-min exposure to 2000 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ PAR resulted in a 9.5% decrease in F_v/F_m ($P = 0.0051$). Also, on a clear day when measured PAR at 1000 hours was above 1200 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, a significant decrease (approximately 6% decrease from predawn values, $P = 0.0014$) in F_v/F_m values was observed in the same seedlings,

but no changes in F_v/F_m values were measured during an immersed day over the same time period.

DISCUSSION

Previous studies addressing cloud immersion in the southern Appalachians have focused primarily on the potentially negative impacts of increased exposure to pollutants via increases in surface deposition. Polluted cloudwater can be damaging in these forests because of the extremely low pH, plus high sulfate and nitrate concentrations found in Appalachian cloudwater (e.g., Mohnen, 1992; Thornton et al., 1994). However, little work has addressed the potentially strong influence of clouds on the understory sunlight environment and corresponding plant ecophysiology (e.g.,

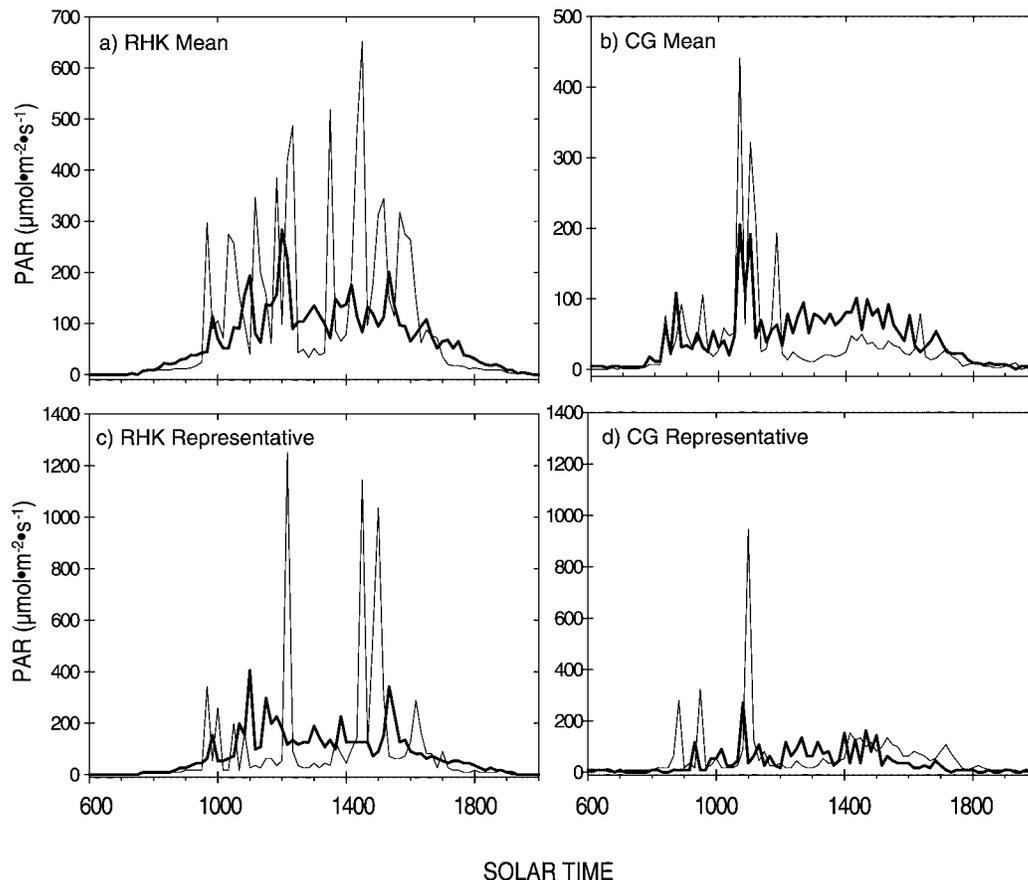


Fig. 2. Mean photosynthetically active radiation (PAR) (mean of 4 days; a, b) and actual PAR for a representative day (c, d) measured instantaneously every 10 min for clear (light line) and cloud-immersed days (heavy line) at Roan High Knob (RHK; a, c) and Carver's Gap (CG; b, d).

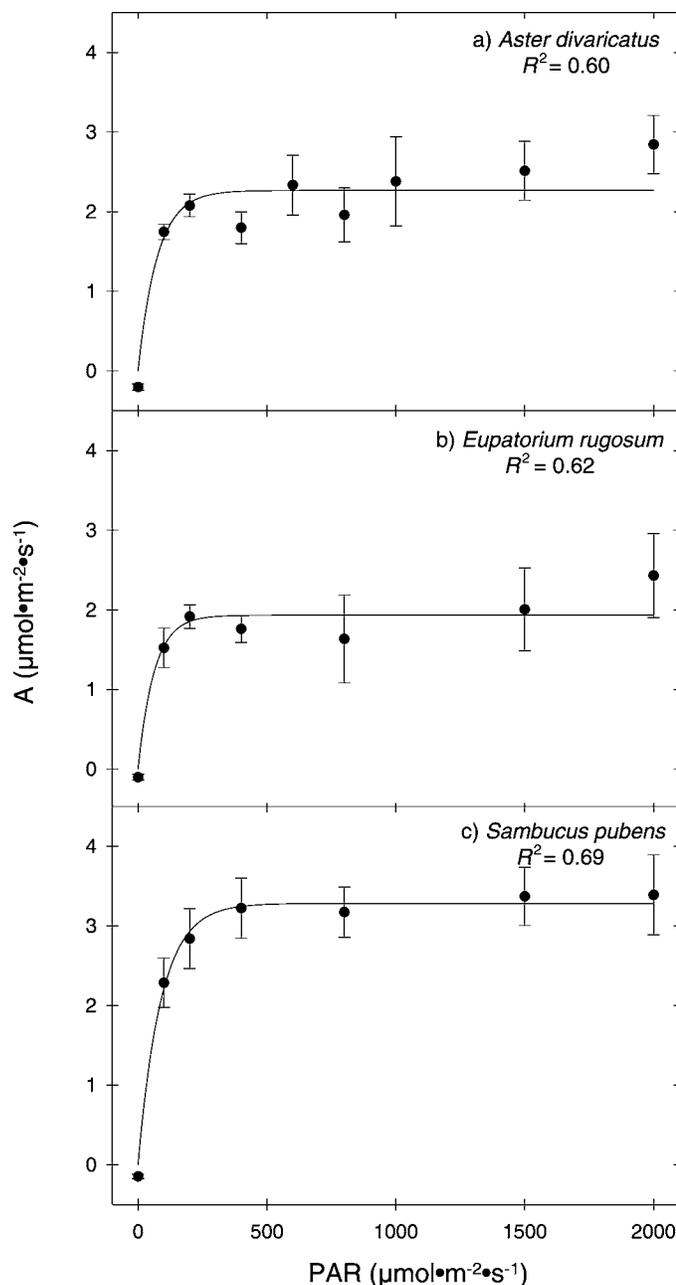


Fig. 3. Photosynthetic light response curves (instantaneous) of (a) *Aster divaricatus*, (b) *Eupatorium rugosum*, and (c) *Sambucus pubens* measured during midday (1100 to 1400 hours) at the Roan High Knob site (see Table 1 for equation parameters). Points represent means of 4–6 replicates, and error bars are standard errors.

photosynthesis and transpiration). Only one group (to our knowledge) has attempted to analyze the interaction between cloud immersion and understory plant photosynthesis (Letts and Mulligan, 2005), and they concluded that leaf surface wetness and reduced PAR under clouds caused reductions in photosynthesis in understory species of a tropical cloud forest. However, PAR measured in deforested (open) areas was compared with photosynthesis in forested (closed) areas. Therefore, the study did not directly address the effects of cloud immersion on photosynthesis in understory species.

TABLE 3. Light response equation parameters and predicted daily photosynthetic carbon gain (PCG) on clear vs. immersed days. All equations of form $y = a(1 - e^{-bx})$; all parameters for *Abies fraseri* are from Johnson and Smith (2005). PCG units are $\text{mmol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$. RHK = Roan High Knob and CG = Carver's Gap.

Species	<i>a</i>	<i>b</i>	RHK PCG	RHK PCG	CG PCG	CG PCG
			Clear	Immersed	Clear	Immersed
<i>Aster divaricatus</i>	2.27	0.0013	12.8	9.5	4.9	6.1
<i>Abies fraseri</i>	2.49	0.012	27.4	26.4	16.0	18.8
<i>Eupatorium rugosum</i>	1.93	0.0016	12.9	9.8	5.0	6.2
<i>Sambucus pubens</i>	3.28	0.0011	16.1	11.8	6.1	7.5

During either cloud cover or cloud immersion, reductions in sunlight intensity would be expected in open forests or deforested areas, whereas increases in intensity, due to the greater penetration of diffuse light, might be expected in more closed forest types.

Understory sunlight—The degree of canopy openness (i.e., gapiness) and leaf area index have been used as a measure of sunlight penetration into plant canopies for over 50 years (Lemmon, 1956; Evans and Coombe, 1959; Machado and Reich, 1999). Although photographic estimates of openness in certain forest types, this technique was inadequate for accurate estimates of understory PAR and corresponding photosynthesis in the understory species studied here. Sunlight regimes computed from hemispherical photographs produced estimates of photosynthetic carbon gain that were substantially higher (up to 107% greater) than predicted from actual understory PAR measurements. In contrast, instantaneous PAR measurements taken at 10-min intervals generated a much more accurate estimate of the variability of sunlight values, with an accuracy equivalent to that using 1-min measurement intervals.

In general, clouds alter the intensity, spectral quality, and directional character (i.e., diffuse vs. direct) of sunlight. Clouds typically increase the diffuse component of sunlight, enabling greater penetration (lower attenuation coefficients) into canopies and understories compared with direct-beam sunlight (see Campbell and Norman, 1998). In previous studies of the interaction of clouds, sunlight penetration, and canopy photosynthesis, diffuse light from clouds not only increased canopy penetration, but also canopy photosynthesis per unit ground area (e.g., Roderick et al., 2001; Gu et al., 2003; Min, 2005) and radiation use efficiency (moles of CO_2 per moles of PAR-wavelength photons, e.g., Hollinger et al., 1994). However, Graham et al. (2003) found that by adding light under cloudy conditions, photosynthesis in a tropical tree species increased, and Letts and Mulligan (2005) predicted that decreases in PAR, due to cloudiness, would result in reduced plant photosynthesis in a tropical forest. The variation in photosynthetic responses to cloudiness and immersion is likely due to differences in forest structure (i.e., open or closed forests) and cloud type (optically thick vs. thin, see Min, 2005). Cloudiness, and particularly cloud immersion, can provide benefits other than increased diffuse light, including cooler leaf temperatures and reduced leaf-to-air vapor deficit, both of which decrease transpiration (Gu et al., 2002). In the present study, immersion and low clouds resulted in similar understory sunlight regimes with less variation, reduced irradiance levels during sunlight peaks, and increased length of time near

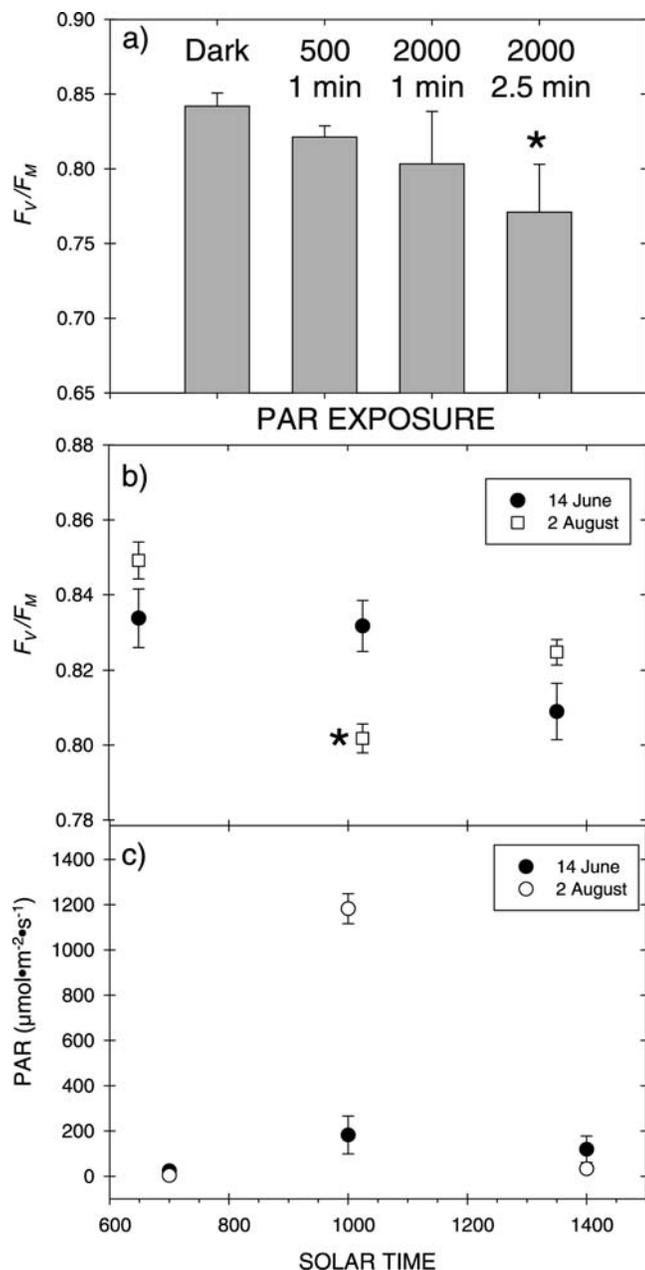


Fig. 4. F_v/F_m (maximum photosystem II efficiency) values for *Abies fraseri* 2-yr-old seedlings (a) predawn with supplemental light (asterisk indicates significantly different from no light control, $P = 0.0051$), (b) throughout a clear (2 August, open squares) and an immersed morning and early afternoon (14 June, immersed until approximately 1100, closed circles) (* indicates significantly different from predawn measurement, $P = 0.0014$), and (c) corresponding PAR. Points represent means of 4–6 replicates, and error bars are standard errors.

photosynthetic optima (nearer to the photosynthetic light saturation point, Figs. 2, 3) as compared to clear conditions. Measured understory PAR on a representative immersed day remained between 53 and 405 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, whereas PAR varied from 18 to 1253 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ on a representative clear day (Fig. 2c) at the highest altitude site. In addition, cumulative PAR within the optimal range for photosynthesis

(i.e., with peaks of PAR > 1000 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ removed) at the highest altitude site was 61% greater on immersed days.

Cloud effects on photosynthesis—Photosynthesis in all three measured species had light saturation points between 100 and 400 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ PAR, typical for shade species (e.g., Naidu and Delucia, 1998). Photosynthesis in first-year (germinant) seedlings of *Abies fraseri* at the same location (Roan Mountain) also saturated at PAR values < 400 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (Johnson and Smith, 2005). In the present study, PAR values measured during immersion at the high altitude sites corresponded to either points along the initial slope of the light response curve or the light saturation point for these species. Moreover, these PAR values are optimal for photosynthesis because they result in the greatest quantum yield (Lambers et al., 1998, carbon fixed per photons absorbed), they are well below values that would result in photoinhibition, and they do not result in higher leaf temperatures and increased transpiration at the same degree of stomatal opening. Also, the more homogenous values of sunlight under immersion prevents the acclimation period (i.e., induction, Chazdon and Pearcy, 1986) experienced by shade plants when exposed to sun patches. Thus, not only does sunlight under cloud immersion penetrate deeper into the understory than direct light during clear-sky conditions but actual values of PAR are more optimal for carbon capture. In fact, *A. fraseri* seedlings at CG (greater canopy cover) were predicted to fix 22% more carbon on cloudy days, while seedlings at RHK (less canopy cover) were predicted to fix 26% less carbon on cloudy days than clear days. Seedlings in areas directly shaded by the canopy were also predicted to fix much more carbon during immersion than during clear conditions (2.9 times more carbon gain for a 1-h interval at RHK and 1.9 times more carbon gain for a 6-h interval at CG). Similarly, afternoon cloudiness was predicted to increase carbon gain by 41–69% in understory seedlings of *Abies lasiocarpa* and *Picea engelmannii* (Johnson et al., 2004). Carbon gain has been strongly associated with survival in young seedlings of *A. fraseri* in the southern Appalachians (Johnson and Smith, 2005), as well as in *A. lasiocarpa* and *P. engelmannii* in the south central Rocky Mountains (Germino and Smith, 1999).

Although clear and immersed conditions resulted in similar amounts of predicted daily carbon gain, the effects of photoinhibition, temperature, and water status were not taken into consideration here, and all may be influenced strongly by immersion. For example, depressions in F_v/F_m have been observed in shade-adapted plants that were suddenly exposed to high sunlight (e.g., Houter and Pons, 2005). In the present study, approximately half to full sunlight exposure (for as little as 2.5 min) resulted in depressed fluorescence in seedlings of *A. fraseri*, although no depression in fluorescence was observed (over the same time period) under cloud immersion. It is also possible that measured PAR values under immersed conditions were artificially low because only the upper hemisphere was measured, and thus a portion of diffuse light (lower hemisphere) was not measured. Also, no depression in photosynthesis was seen at the highest PAR values on the light response curves, most likely due to the brief duration of the high-intensity light (approximately 60 s). Cloud immersion may also result in leaf wetness (Letts and Mulligan, 2005), which could reduce carbon gain due to the limited diffusion of CO_2 in water (Nobel, 2005). Leaf wetness during cloud

immersion has been observed in the species measured in the current study (D. M. Johnson and W. K. Smith, unpublished data). However, many plant species in areas with frequent leaf wetting have strategies for surface water repulsion (Brewer et al., 1991; Brewer and Smith, 1997). In fact, water beading on hydrophobic leaf surfaces can result in reduced transpiration (saturated boundary layer) and increased photosynthetic carbon gain (i.e., greater stomatal opening at low leaf-to-air vapor pressure deficits, Smith and McClean, 1989). More work is needed to determine the overall impacts of cloud immersion on leaf surface wetness and gas exchange in this and other cloud-immersed systems.

Absorptance values for diffuse light incident on leaves are not available in the literature. One unpublished study found that diffuse light was both reflected and transmitted more than direct-beam light in certain species (C. R. Brodersen and T. C. Vogelmann, University of Vermont, unpublished data). However, the large proportion of oblique rays in diffuse/scattered light should result in greater reflection from a horizontal, laminar leaf surface than for a more cylindrical leaf shape such as a conifer needle. Although considerable research has focused on sunflecks/sunpatches, leaf display, and light interception (e.g., Chazdon, 1995), little work has dealt with diffuse light interception, especially during cloudiness or immersion. To our knowledge, no complete set of experimental measurements has been published for leaves irradiated with diffuse vs. direct-beam light, despite the fact that some crop and forest canopies have been found to photosynthesize more under diffuse sunlight (as compared to direct sunlight).

More data are needed to characterize the understory light environment in different forest types and under different cloud types during above-canopy clouds and cloud-immersed conditions. The ability to quantify the altitude of the cloud base is required for accurate measurements of the effects of cloud base height and different cloud types on understory light and plant physiology. Changes in cloud base height has already been correlated with population declines in tropical cloud forests (Pounds et al., 1999) and these data may be critical for predicting potential changes in plant community composition with future changes in cloud frequency.

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