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Cloud immersion alters microclimate, photosynthesis and water relations in *Rhododendron catawbiense* and *Abies fraseri* seedlings in the southern Appalachian Mountains, USA

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Summary The high altitude spruce–fir (*Abies fraseri* (Pursh) Poiret.–*Picea rubens* Sarg.) forests of the southern Appalachian Mountains, USA, experience frequent cloud immersion. Recent studies indicate that cloud bases may have risen over the past 30 years, resulting in less frequent forest cloud immersion, and that further increases in cloud base height are likely in the event of continued climate warming. To assess the impact of this trend on the regeneration of high altitude spruce–fir forests and the migration of plant communities, in particular the encroachment of spruce–fir forests and *Rhododendron catawbiense* Michx. islands into adjacent grass bald communities, we investigated effects of cloud immersion on photosynthetic parameters of seedlings of *Abies fraseri* and *R. catawbiense* in a grass bald site and *A. fraseri* in a forest understory. Although photosynthetic photon flux was 4.2 to 19.4-fold greater during clear conditions, cloud immersion had no effect on photosynthesis in *A. fraseri* at either site, whereas it reduced photosynthesis of *R. catawbiense* by about 40%. However, cloud immersion increased mean leaf fluorescence by 7.1 to 12.8% in both species at both sites. Cloud immersion increased mean relative humidity from 65 to 96%, reduced transpiration by 95% and reduced mean leaf-to-air temperature difference from 6.6 to 0.5 °C.

Keywords: altitude, climate change, diffuse light, fog, photoinhibition, transpiration.

Introduction

Many high mountains of the southern Appalachians are mosaics of spruce–fir (*Abies fraseri* (Pursh) Poiret.–*Picea rubens* Sarg.) forests, northern hardwood forests and grass bald communities (Whittaker 1956, Mark 1958). The highest altitude spruce–fir forests experience cloud immersion on two days out of three and during 30–40% of all summertime hours (Mohnen 1992, Baumgardner et al. 2003). On the slopes of these mountains, the transition from lower-altitude hardwood forests to spruce–fir forests has been associated with the mean altitude of cloud base (Braun 1964). Cloud immersion occurs most often in early morning, and contributes about 45% of the annual water input through canopy interception (Smathers 1982).

Few studies have evaluated the effects of cloud immersion on the ecophysiology of forests (e.g., Motzer et al. 2005, Letts and Mulligan 2005). It has been predicted that cloud ceilings in mountain regions will rise in the event of climate warming (Croke et al. 1999, Still et al. 1999, Richardson et al. 2003). The consequent reduction in cloud immersion will likely affect the reproduction of high altitude forests and the migration of plant communities (Foster 2001), as has been reported in tropical cloud forests, where reduced cloud immersion due to recent climate warming has resulted in population decline or extinction of some species (Pounds et al. 1999).

Past studies on the ecophysiological effects of cloudiness and cloud immersion have focused on adult trees (e.g., Gu et al. 2002, Burgess and Dawson 2004, Min 2005). However, impacts on seedling establishment may be more important in assessing how changing climate will affect forest regeneration and the encroachment of forest species into montane grass balds, where they may displace endemic and rare plant species (Sullivan and Pittillo 1988, Weigl and Knowles 1999).

Both cloud immersion (e.g., fog and mist) and cloud cover can result in major changes in the incident photon flux and directional quality (diffuse versus direct) of sunlight (Gu et al. 1999, Letts and Mulligan 2005, Min 2005). An increase in the proportion of diffuse sunlight has been correlated with increased photosynthetic carbon gain in certain forest types (Min 2005, Johnson and Smith 2006). Cloud immersion can also result in other microclimatic changes, including a reduction in leaf temperatures (T_l) and leaf-to-air vapor pressure deficit (LAVD) (Gu et al. 2002).

Our objective was to measure photosynthesis (A), transpiration (E) and associated microclimatic parameters (solar irradiance, temperature and humidity) in *Abies fraseri* (Pursh) Poiret. (evergreen conifer) and *Rhododendron catawbiense* Michx. (evergreen broadleaf) seedlings in a southern Appalachian spruce-fir forest and an adjacent grass bald community under clear skies and during cloud immersion. Leaf fluorescence was measured to assess effects of cloud immersion on photosynthetic capacity. We hypothesized that photosynthesis of understory seedlings would be greater (because of increased sunlight penetration) and photosynthesis in establishing seedlings in grass balds would be reduced during cloud immersion. Leaf temperature (T_l) and E were expected to be lower in both the forest understory and adjacent grass bald during cloud immersion, leading to increased water-use efficiency (WUE).

Materials and methods

Study sites

Spruce–fir forests, northern hardwood forests and grass bald communities are the dominant vegetation types in high altitude areas of Roan Mountain, NC, USA (Mark 1958). Spruce–fir forests dominate the highest altitudes and are composed of canopy trees *Abies fraseri* and *Picea rubens,* associated shrubs and small trees (*Sambucus pubens* Michx. and *Rhododendron catawbiense*), various understory ferns (*Athyrium filix-femina* (L.) Roth, *Dryopteris campyloptera* Clarkson and *Dryopteris intermedia* (Muhl. ex Willd.) A. Gray) and herbs (*Aster divaricatus* L., *Eupatorium rugosum* Houtt. and *Oxalis montana* Raf.) (Whittaker 1956). Grass bald communities occur on mountain top areas surrounded by spruce–fir stands and are composed primarily of the grass, *Danthonia compressa* Austin with isolated islands of *Rubus* spp., the shrubs *Alnus crispa* (Aiton) Pursh and *R. catawbiense,* as well as *P. rubens* and *A. fraseri* islands (Mark 1958).

Two study sites with an area of approximately 20 m^2 were selected on an east-facing slope of the Roan Mountain massif (36° 5′ N, 82° 8′ W, 1910 m a.s.l.); one in a spruce–fir forest (FS), the other in a contiguous grass bald–forest ecotone (GB). The GB site had little canopy cover and received about 5.5 times more cumulative daily sunlight than the FS site (32.1 and 6.4 mol m^{-2} day^{-1}, respectively; Figure 1).

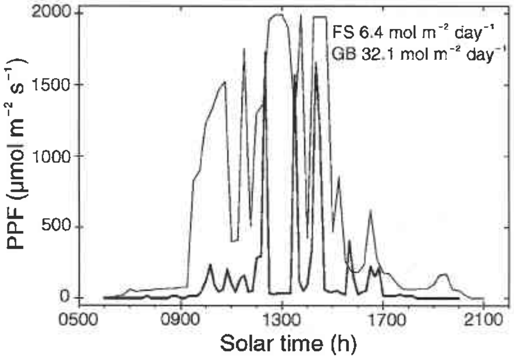

Figure 1. Representative course of solar irradiance on a clear-day at the grass bald (GB, thin line) and forest (FS, thick line) sites. Values are cumulative daily photosynthetic photon flux (PPF) for each site.

Photosynthesis, water relations and microclimate

Photosynthetic carbon assimilation rate (A), leaf fluorescence (variable/maximum; F_v/F_m, maximum photosystem II (PSII) efficiency), T_l and water status (Ψ, stem xylem pressure potential) were measured in 3–5-year-old seedlings of *Abies fraseri* (at both FS and GB) and *Rhododendron catawbiense* (at GB only). Photosynthetic photon flux (PPF) on a horizontal surface (LI-190 PAR sensor, Li-Cor Lincoln, NE), air temperature (T_a) and relative humidity were also measured.

Measurements were made on six days in the summer of 2006, including periods during four of those days (May 30, June 15, June 29 and July 15) that were chosen as representative of clear and cloud-immersed conditions. Mean above-canopy PPF during clear and cloud-immersed periods was 976 and 146 µmol m^{-2} s^{-1}, respectively. Cumulative daily PPF at GB and FS, was recorded every 10 min for 4 days (June 15–18) with a Li-Cor LI-190 PAR sensor connected to an amplifier (Model UTA, EME Systems, Berkeley, CA) and a data logger (HOBO H8, Onset Computer, Bourne, MA) (Figure 1).

Photosynthesis, T_l, T_a and air vapor pressure were measured at 0800, 1000, 1200 and 1400 h on each measurement date. Seedlings were selected randomly for each measurement, some seedlings being measured more than once during the season. Net photosynthetic CO$_2$ fluxes were computed on a leaf area basis. For *R. catawbiense*, the area of leaf in the chamber was measured with a leaf area meter (DT Area Meter, Delta-T Devices). The area of *A. fraseri* needles was estimated from the length and diameter (from cross section) of 25 randomly selected needles. The number of needles per unit of stem length and the computed needle areas were used to estimate total needle area in the cuvette during each photosynthesis measurement. Photosynthesis was measured with a Li-Cor LI-6400 portable photosynthesis system with a 6400-05 leaf chamber, which allows for natural illumination of leaves (i.e., both adaxial and abaxial surfaces as well as direct and diffuse components). Wet leaves were blotted with tissue paper before the gas exchange measurement, and vapor pressure of ambient air was recorded before each gas exchange measurement. Leaf temperature was measured with an infrared thermometer (Raynger ST80, Raytek, Santa Cruz, CA) and T_a was measured with a fine-wire thermocouple (contained within the LI-6400-05 leaf chamber). Variable fluorescence and F_m of seedlings were measured at about 0530–0600 (predawn), 1000 and 1400–1500 h with a PAM fluorimeter (Model FMS-2, Hansatech Instruments, Norfolk, U.K.). All leaves were dark adapted for 20 min before measurement, and subsequently received a 2 s light pulse (3 mmol m^{-2} s^{-1}).

Stem xylem pressure potential was measured between 0530 and 0600 h (predawn, Ψ_{pd}) and between 1400 and 1500 h (midday, Ψ_m) on each measurement date with a Scholander-type pressure chamber (Model 1000, PMS Instrument Company, Corvallis, OR). Gas exchange and Ψ measurements were made on adjacent (within 3 m) seedlings.

Transpiration could not be measured accurately during periods of cloud immersion because water accumulated on leaf surfaces (Smith and McClean 1989). Therefore, E before chamber enclosure was estimated based on the vapor pressure of the ambient air, the vapor pressure estimated for leaf intracellular spaces (calculated from T_l and assuming 100% relative humidity within the leaf), and an estimated leaf conductance of 150 mmol m^{-2} s^{-1} based on measurements with dry leaves on clear days at the same time of day. To calculate WUE when E was 0 mmol m^{-2} s^{-1} because of cloud immersion, E were set to 0.1 mmol m^{-2} s^{-1}.

Sampling and statistics

Effects of site, species and cloud immersion on measured variables were evaluated by analysis of variance (ANOVA). Where treatment effects were significant, the Tukey–Kramer multiple-comparison method (Zar 1999) was used to determine the significance of differences among means.

Results

Solar irradiance, photosynthesis and leaf fluorescence

At both sites, cloud immersion reduced mean PPF by a factor of 4.2 to 19.4 (Figures 2 and 3b). Although A differed significantly between species, site and condition (clear versus immersed, Table 1), not all pairwise comparisons differed significantly (Table 2). The effect of cloud immersion on A of *A. fraseri* was not significant at either FS or GB (Table 1, Figure 4a). However, when data for clear and cloud-immersed conditions were combined, mean A of *A. fraseri* at GB was 2.6 to 9.5 times greater than at FS. The photosynthetic rate of *R. catawbiense* was 2.3 times that of *A. fraseri* during clear periods, but there was no difference between species during cloud immersion. Although F_v/F_m did not differ significantly between species, it was 7.3% greater at FS than at GB and was increased 7.1–12.8% by cloud immersion in both species at both sites (Tables 1 and 2, Figures 3c and 4b).

Water status and transpiration

Predawn xylem pressure potential of *R. catawbiense* was nearly constant on all measurement dates (Figure 5). Afternoon Ψ_{pd} of *R. catawbiense* and both Ψ_{pd} and Ψ_m of *A. fraseri* tended to increase throughout the season, although they were most negative on the completely clear day of May 30, and least negative on the completely cloud-immersed day of July 15.

Under clear conditions, E of *R. catawbiense* was higher than that of *A. fraseri* (Table 2). Otherwise, E did not differ significantly between species and sites (Table 1). In contrast, E was 83–95% lower during cloud immersion than during clear periods in both species. Median and mean E during cloud immersion were 0 and 1.6 mmol m^{-2} s^{-1}, respectively (Figure 6a), whereas the corresponding values under clear conditions were 3.9–8.3 mmol and 7.2 mmol m^{-2} s^{-1}. Mean water-use efficiency (A/E) was less than 1.0 µmol $mmol^{-1}$ (Figure 6b) in both species and at both sites during clear conditions, but was greater during cloud immersion (1.5, 7.4 and 4.1 µmol $mmol^{-1}$ in *A. fraseri* at FS, *A. fraseri* at GB, and *R. catawbiense* at GB, respectively).

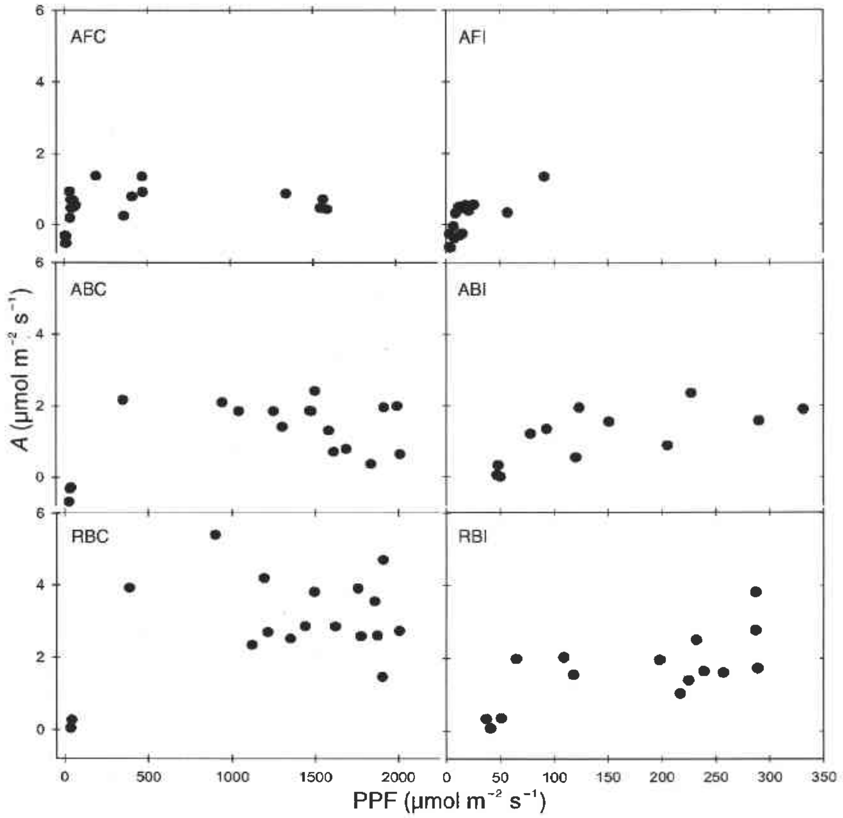

Figure 2. Incident photosynthetic photon flux (PPF) and net photosynthesis (A) at each site during clear and cloud-immersed conditions for *Rhododendron catawbiense* and *Abies fraseri* seedlings. Observation codes: *Abies fraseri* (A); *Rhododendron catawbiense* (R); forest site (F); grass bald (B); clear conditions (C); and cloud immersed (I).

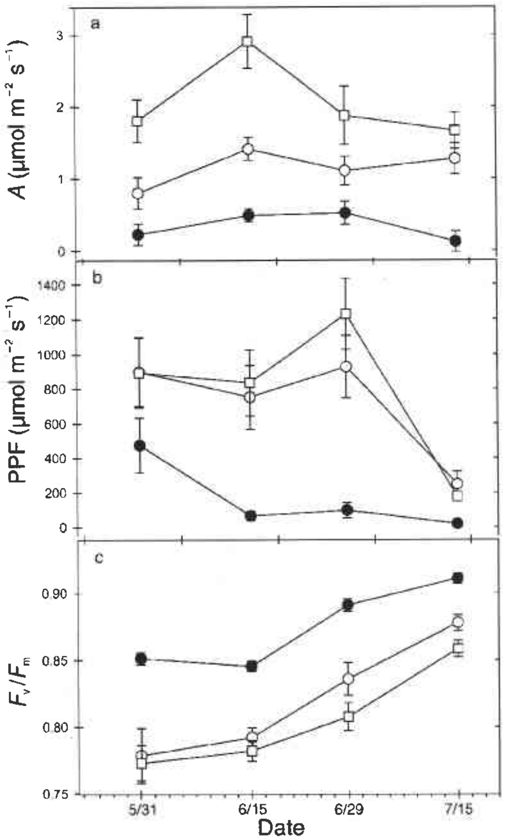

Figure 3. Mean daily (a) photosynthesis (A), (b) incident photosynthetic photon flux (PPF) and (c) leaf fluorescence (F_v/F_m) for *Rhododendron catawbiense* and *Abies fraseri* seedlings during summer 2006 at the forest (●) and grass bald (○) site and *R. catawbiense* at the bald site (□). Measurements were made on four dates: May 31 was clear, on June 15 and June 29 the sites were partly immersed in cloud and on July 15 they were immersed in cloud throughout the day.

Leaf and air temperatures, and leaf-to-air vapor pressure deficit

Mean T_l was 5.5 °C lower at FS than at GB on clear days, and 6.6 °C lower in both species and at both sites during cloud immersion than during clear periods Figure 7a). Leaf temperature of *R. catawbiense* was 1.7 °C higher than that of *A. fraseri* at GB and 3.6 °C higher at FS, although the difference was significant only at FS during clear conditions.

Leaf-to-air temperature differences (LATD) were small in both species at both sites under both clear and cloud-immersed

Table 1. Results of analysis of variance (P values) for effects all factors (Overall), site (forest versus grass bald) species (*Rhododendron catawbiense* versus. *Abies fraseri*) and conditions (clear versus cloud immersed) on: A, mean daily photosynthetic carbon assimilation; leaf fluorescence (F_v/F_m); transpiration rate (E); and leaf temperature (T_l). Differences in leaf-to-air temperature were not significant.

Effect	A	F_v/F_m	E	T_l
Overall	< 0.001	< 0.001	< 0.001	< 0.001
Site	< 0.001	< 0.001	ns	0.02
Species	< 0.001	ns	ns	ns
Condition	0.008	< 0.001	< 0.001	< 0.001

Table 2. Mean photosynthetic carbon fixation rate (A, μmol m^{-2} s^{-1}), leaf fluorescence (F_v/F_m), transpiration rate (E, mmol m^{-2} s^{-1}) and leaf temperature (T_l, °C). Values are means for all observation dates. Different letters within a column indicate significant differences (P = 0.05, Tukey-Kramer multiple comparison). Observation codes: *Abies fraseri* (A); *Rhododendron catawbiense* (R); forest site (F); grass bald (B); clear conditions (C); and cloud immersed (I). Abbreviation: SD = mean standard deviation.

Observation	A	F_v/F_m	E	T_l
AFC	0.47 a	0.85 a	7.98 a	22.8 a
ABC	1.23 b	0.78 b	8.15 a	27.0 b
RBC	2.77 c	0.77 b	5.53 b	29.0 b
AFI	0.12 a	0.91 c	0.86 c	19.5 c
ABI	1.14 b	0.88 ac	0.39 c	19.1 c
RBI	1.67 b	0.86 a	0.95 c	20.4 c
SD	0.53	0.03	1.98	2.1

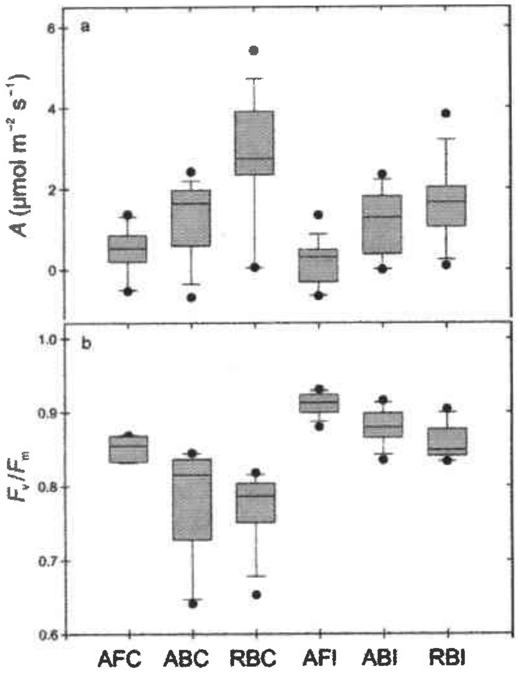

Figure 4. Summary of (a) photosynthesis (A) and (b) leaf fluorescence (F_v/F_m) measurements. Observation codes: *Abies fraseri* (A); *Rhododendron catawbiense* (R); forest site (F); grass bald (B); clear conditions (C); and cloud immersed (I). Boxes include the 25th to 75th percentiles, horizontal lines within boxes represent median values, horizontal lines outside of boxes represent 10th and 90th percentiles, and closed circles represent actual range of sampled measurements.

est soils of Roan Mountain typically do not experience significant drying during the summer (Mark 1958) and regional rainfall in the summer of 2006 was about 92% of mean summer rainfall (data from the State Climate Office of North Carolina, http://www.nc-climate.ncsu.edu).

Leaf and air temperatures

Compared with clear conditions, cloud cover can result in lower T_l (e.g., Leuschner 2000) which would also reduce the driving force for E (LAVD, Nobel 2005). Cloud immersion resulted in reduced T_l and leaf-to-air pressure deficits in both our study species. In addition, T_l was tightly coupled to T_a during cloud immersion compared with clear-sky periods. Reductions in daytime T_l and LATD, along with increases in nighttime T_l (a strong consequence of cloudiness and immersion) may prevent either high- or low-temperature photoinhibition, which may be a characteristic of many high altitude environments (Germino and Smith 2000). Photoinhibition has been linked to reductions in seedling carbon gain and survival in high altitude systems (Germino et al. 2002) and could contribute to changes in seedling establishment patterns and community composition in the event of climate change and the associated changes in cloud-immersion regimes (Still et al. 1999).

In conclusion, changes in cloud base height have been correlated with population declines in tropical cloud forests (Pounds et al. 1999). Thus, data relating microclimate to plant physiology under cloudy and cloud-immersion conditions may be critical for predicting the effects of changes in cloud patterns on plant community composition and distribution.

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