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Source: Arctic, Antarctic, and Alpine Research, 46(2) : 371-378

Published By: Institute of Arctic and Alpine Research (INSTAAR),
University of Colorado

URL: <https://doi.org/10.1657/1938-4246-46.2.371>

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Dynamic Cloud Regimes, Incident Sunlight, and Leaf Temperatures in *Espeletia grandiflora* and *Chusquea tessellata*, Two Representative Species of the Andean Páramo, Colombia

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Abstract

The alpine páramo of Chingaza National Park, Colombia, has a highly variable cloud regime typical of many tropical alpine areas. Yet, little information is available regarding the effects of such dynamic sunlight regimes on alpine temperatures. A close association between changes in incident sunlight and corresponding air (T_a) and leaf (T_l) temperatures occurred in two dominant species with strongly contrasting leaf form and whole-plant architecture. Spikes in sunlight incidence of $>3000 \mu\text{mol m}^{-2} \text{s}^{-1}$ occurred during cloud cover and corresponded to increases in T_l of $4\text{--}5^\circ\text{C}$ in a 1-min-interval in both species. Although T_l was predominately above T_a , during the day, depressions below T_a of over 6°C occurred during cloudy conditions when photosynthetic photon flux density (PPFD_s) was $<400 \mu\text{mol m}^{-2} \text{s}^{-1}$. The greatest frequency (69%) of changes in incident sunlight (PPFD_s ; over 2-min intervals) was less than $100 \mu\text{mol m}^{-2} \text{s}^{-1}$, although changes $>1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ occurred for 2.4% of the day, including a maximum change of $1512 \mu\text{mol m}^{-2} \text{s}^{-1}$. These data may be valuable for predicting the ecophysiological impact of climate warming and associated changes in future cloud regimes experienced by tropical alpine species.

DOI: <http://dx.doi.org/10.1657/1938-4246-46.2.371>

Introduction

Alpine plants have often been characterized adaptively as being short in stature so that leaf temperatures can be more tightly coupled to the protective boundary layer microclimate of the soil surface. This coupling results in lower wind speeds and greater departures from air temperature due to heating by solar radiation during the daytime or cooling due to long-wave radiation exchange with clear skies at night (Grace, 1977; Smith and Young, 1987; Jordan and Smith, 1994; Körner, 2007, 2012). However, considerable variation in plant temperatures can occur due to microsite differences at ground level (Salisbury and Spomer, 1964; Cernusca, 1976; Moser et al., 1977; Fetene et al., 1997; Scherrer and Körner, 2010; Larcher, 2012), as well as plant stature regardless of microsite (Körner et al., 1983; Gauslaa, 1984; Diemer, 1996; Taschler and Neuner, 2004) and leaf size (Grace, 1977). In general, plants with smaller leaves and taller plants exposed to higher wind speeds are more coupled to air temperature and less to radiational heat exchange due to enhanced convective heat exchange.

Although clouds can be a frequent occurrence in mountain ecosystems (Moser et al., 1977; Johnson and Smith, 2008; Berry and Smith, 2012), few comparisons of their specific influence on air and leaf temperatures have been reported. One study measured sunlight levels and leaf temperatures at a lower and higher elevation site in New Guinea (Körner et al., 1983). Several other studies have reported the influence of plant stature and form on temperatures of various plant parts at higher elevations, although only under sunny conditions (e.g., Salisbury and Spomer, 1964; Körner and DeMoraes, 1979; Körner and Cochrane, 1983, 1985; Fetene et al., 1997; Körner, 2003; Cui et al., 2004; Larcher, 2012). Similar to the present study, one study reported temperature differences between two herbaceous perennial species of the Ecuadorian Andes, one a flat rosette habit with dark leaves and the other an erect-leaved species with pubescent leaves (Diemer, 1996). Another similar study in the

Qinghai-Tibet plateau reported differences in leaf temperatures based on leaf and whole-plant structure and reported significant photoinhibition of photosynthesis beginning at a sunlight incidence about $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ in both species, which appeared exacerbated by higher leaf temperatures (Cui et al., 2004). It has also been recognized that large-leaved herbs of mountain areas around the world, including the equatorial areas of the Andes, can be substantially warmer than air temperature (Grace, 1977). The more compact leaf crown closer to the ground (e.g., cushion plants) appeared to generate the greatest departures from air temperature during both day and night due to lower wind speeds and less convective heat exchange (Kleier and Rundel, 2009).

The aim of our study was to evaluate the influence of a highly variable cloud regime and corresponding effects on leaf and air temperatures in two common páramo species of this northern Andean region. Diurnal air and leaf temperatures, plus incident sunlight levels, were compared under highly dynamic cloud conditions that are characteristic of this alpine páramo region, as well as other tropical alpine systems.

These data will serve to initiate the development of an empirical model for evaluating the influence of such a variable cloud regime on photosynthesis and water relations, as well as potential effects of altered cloud regimes due to continued global warming (Eastman and Warren, 2013).

Materials and Methods

SITES AND SPECIES

Chingaza National Park (CNP) is located on the Eastern Cordillera in Colombia, less than 70 km east of Bogotá, and páramo ecosystems in CNP have been classified as humid (Cleef, 1981; Sarmiento, 1986). The park comprises more than 50,000 hectares ranging in altitude from ~800 to ~4000 m and contains an esti-

mated plant biodiversity of over 2000 species (Parque Nacional Natural Chingaza, 2005–2009). Above ~3200 m, the vegetation of the park changes from high-elevation mountain forests to the alpine páramos where more than 350 plant species occur within a mosaic of natural glacial lakes.

Chingaza has a unimodal monthly precipitation regime, with a wet season lasting from April through November and a short dry season from December to late February or early March (Sarmiento, 1986). However, El Niño (ENSO) years can lead to extreme drought seasons such as occurred in late 2009 and early 2010, in contrast to 2012 when the dry season was less than two months and rainfall was frequent by early February (A. Sanchez, J. M. Posada, and W. K. Smith, unpublished data; NOAA, 2013). Mean annual air temperatures at CNP range between ~6 and 10.5 °C but are most variable during the dry season, with maximums greater than 20 °C and nighttime minimums several degrees below freezing; during the wet season nighttime temperatures rarely go below freezing (Tol and Cleef, 1994; de los Ángeles et al., 2002). The annual maximum and minimum precipitation are highly variable, ranging between 1690 and 3320 mm, with an annual mean of around 2000 mm (Tol and Cleef, 1994; de los Ángeles et al., 2002).

We chose three páramo sites located around Laguna Seca, at 3557, 3568, and 3696 m of altitude; the sites were located at 4°41'7"N, 73°45'59"W; 4°41'12"N, 73°46'21"W; 4°41'27"N, 73°48'6"W, respectively. We considered these sites representative of the páramo of this region in terms of topography, species composition, and climate (Parque Nacional Natural Chingaza, 2005–2009). Two species of this páramo were chosen for study: *Espeletia grandiflora* Bonpl. (Asteraceae) and *Chusquea tessellata* Munro (Poaceae). Both species are dominant members of the CNP páramo community and grow sympatrically. *Espeletia grandiflora* (Asteraceae) is a caulescent rosette endemic of the Eastern Andes of Colombia that can grow to 4–5 m in height with thick leaves that are covered with a dense, white pubescence on both adaxial (top) and abaxial (bottom) leaf surfaces (Fig. 1; Smith and Koch, 1935; Fagua and Gonzalez, 2007). *Chusquea tessellata* (Poaceae) is a dwarf bamboo with a broad distribution that extends from Venezuela to northwestern Bolivia; it can grow to more than 3 m in height and has glabrous leaves on both adaxial and abaxial sides

(Tol and Cleef, 1994; Clark, 2003). Both species had relatively laminar and upright leaf orientations—in *E. grandiflora*, the third and fourth whorls have angles of ~65°–75° (leaf angle varies depending on the specific location of individual leaves within the rosette) and *Chusquea tessellata* of ~70°–80° from horizontal (Fig. 1). Thus, these species had contrasting leaf form and whole-plant architecture.

INCIDENT SUNLIGHT, AIR AND LEAF TEMPERATURES

To associate the high variability in sunlight at CNP, photosynthetic photon flux density (PPFD, 0.4–0.7 μm) incident on adaxial leaf surfaces and corresponding abaxial leaf temperatures were measured for both species. In addition, air temperature (T_a) and PPFD incident on a horizontal plane measured at 1.5 m above ground at the site ($PPFD_s$) were collected only meters away from measurement plants. Incident $PPFD_s$ was measured with a quantum sensor (model LI-190s, LiCor, Lincoln, Nebraska) placed in an open area with an unobstructed view of the sky. Measurements were continuous beginning ~0.5 hr after sunrise and ~0.5 hr prior to sunset. Three individuals per species were measured simultaneously at each of the three sites and three leaves per individual were recorded continuously for a total of 11 days ($N = 9$ total individuals and 27 total leaves per species). Individual plants were approximately 0.5–1.0 m tall and selected leaves appeared healthy and fully mature. Leaf temperatures (T_l) were measured using fine-wire (36 ASU gauge), copper-constantan thermocouples, while sunlight incident on individual leaves ($PPFD_l$) was measured using GaAsP light sensors (G1118 Hamamatsu). The PPFD leaf sensors and thermocouples were connected to a Campbell multiplexer (AM16/32B and AMT25, respectively, Campbell Scientific, Utah) and recorded by a Campbell datalogger (model CR-1000, Campbell Scientific, Utah). All leaf sensors were logged every minute. All $PPFD_l$ sensors and thermocouples were placed at the same locations on sampled leaves, approximately in the center of the leaf, midway between the tip and base. Thermocouples were placed on the abaxial (bottom) side, while PPFD sensors were placed on the adaxial (top) side of the leaf. Air temperatures were recorded using three Thermochron iButtons (model DS1921G) located 1.5 m aboveground, shielded



FIGURE 1. Study species *E. grandiflora* (left) and *C. tessellata* (right) at natural locations in the field.

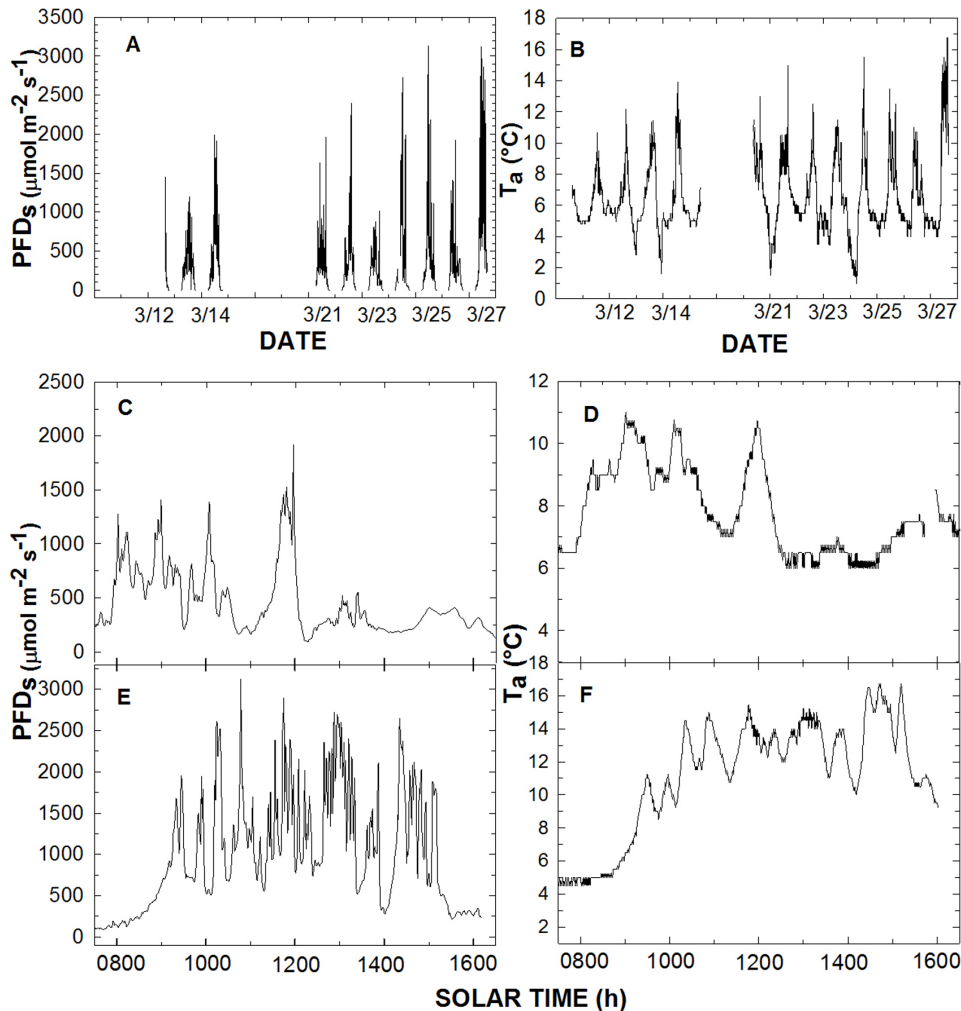


FIGURE 2. Instantaneous photon flux density (PFD_s) incident on a horizontal plane (PFD_s and T_a , respectively) during the study period (A, B), plus hourly values for the coldest (C, D) and warmest (E, F) days measured (3/26/12 and 3/27/12, respectively).

from direct sunlight and the cold night sky using a 20-cm-diameter circular shield painted with 3M reflective white paint and positioned 5 cm above the sensors. These sensors were located within 3 m of the study plants.

Results

SITE PFD_s AND AIR TEMPERATURE (T_a)

There was considerable variation in measured PFD_s between all measurement days, ranging from a maximum instantaneous PFD_s value of over 3000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and a lowest maximum of $\sim 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 2, part A). Greater variability in PFD occurred on the warmest day with the greatest PFD_s values occurring as single, higher-intensity episodes that lasted only minutes or less (Fig. 2, part E). For example, in a one-minute interval, PFD_s changed from 2200 to 3200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and from near 3200 to 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, then back to 2500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ over a 5-minute interval. On a cooler day, PFD_s declined from near 1900 to 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$, also over a 5-minute interval (Fig. 2, part C). Thus, differences between the coldest and warmest days during the measurement days showed distinct shifts in maximum values, but a prolonged, low morning PFD on the warm day (due to cloud immersion) (Fig. 2, part E).

For daily comparisons of both PFD_s and T_a , times and days with high PFD values also corresponded to days with warmer T_a

(Fig. 2). A maximum daily T_a of between 11 and 12 $^{\circ}\text{C}$ occurred on cooler days compared to maximums of ca. 17–18 $^{\circ}\text{C}$ on warmer days, and both types of days occurred throughout the study period. Most days had multiple temperature peaks throughout both morning and afternoon, especially for the warm days (Fig. 2, part F). In general, there was an increase in T_a during early morning on the cooler days that led to higher air temperatures in the morning than afternoon (Fig. 2, part D), although warmer days showed a somewhat opposite trend (e.g., Fig. 2, part F).

During an average day, a bell-shaped curve of hourly PFD_s measurements occurred, with maximum mean PFD_s near 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at midday, increasing and decreasing almost linearly from 0600 h and 1800 h, respectively (Fig. 3, part A). A near linear increase in PFD_s occurred between 0600 and 1200 h compared to a more delayed decline from 1200 to 1800 h. Thus, afternoon PFD_s values tended to be higher overall than morning values (Fig. 3, part A). The greatest duration (percentage of daytime) of specific PFD_s values was for values $< 100 \mu\text{mol m}^{-2} \text{s}^{-1}$ (20.4%) followed by the total duration of all flux densities of between 100 and 350 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (37.6%, Fig. 3, part B). A precipitous decrease in the intensity and daily duration of incident PFD began at about 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Also, $PFD < 400 \mu\text{mol m}^{-2} \text{s}^{-1}$ occurred 67.3% of the time during the day while $PFD > 500 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $PFD > 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ occurred for 28.6% and 9.4% of the time, respectively (Fig. 3, part B).

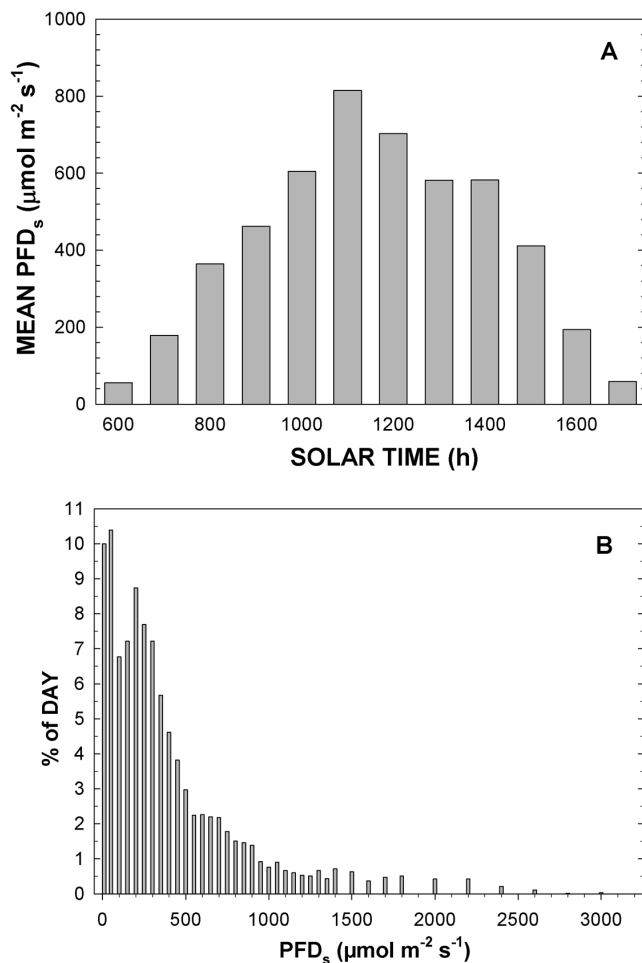


FIGURE 3. (A). Mean hourly PFD measured at the central location (PFD_s) for all sampling days and (B) mean percent of daylight hours when indicated values (intervals) of PFD_s occurred. PFD Intervals were 50 to 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and then 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Greatest values at 2800–2900 and at more than 3000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ had a frequency of 0.02% and 0.03%, respectively.

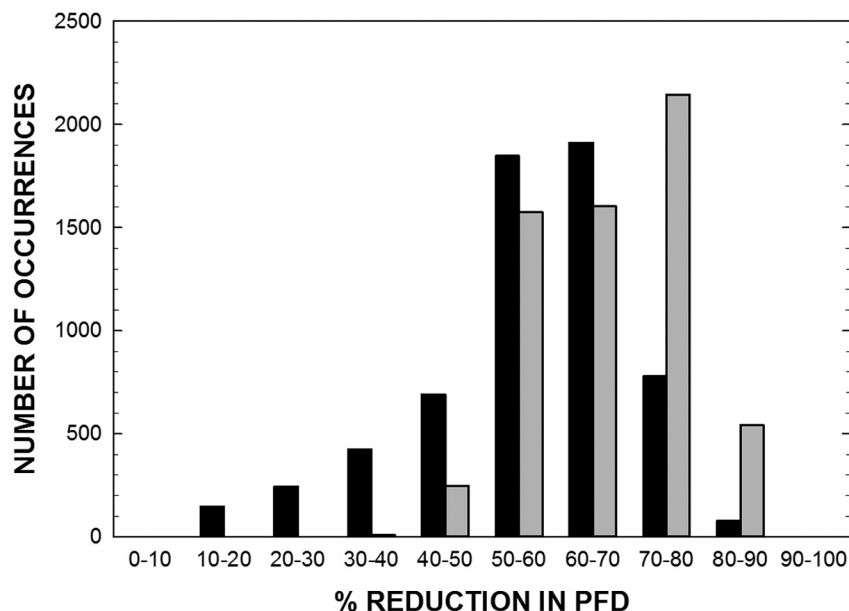


FIGURE 5. Estimating leaf orientation effects on PFD_l using comparisons with the horizontal PFD_s sensor located at the central site location. The number of percent reductions in PFD due to a nonhorizontal leaf orientation were calculated as the percent difference between PFD_s and PFD_l , i.e. $[(PFD_s - PFD_l)/(PFD_s) \times 100]$ for *Espeletia grandiflora* (black) and *Chusquea tessellata* (gray) for all corresponding PFD measurements. Number of occurrences were pooled from data on nine leaves from three individuals per species measured over 11 days.

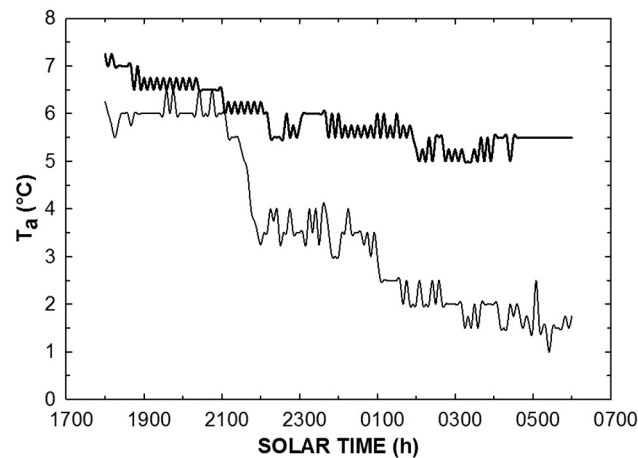


FIGURE 4. Nighttime air temperatures for the coldest (light line; 3/24/12) and warmest night (bold line; 3/23/12) during the study period.

Minimum nighttime T_a also varied, with the coldest night (mostly clear night skies) T_a of about 1 $^{\circ}\text{C}$ and the warmest night (overcast night) near 5 $^{\circ}\text{C}$ (Fig. 4). During the coldest night, temperatures decreased gradually, reaching minima at near 0530 h and also decreased gradually during the warmest night where the lowest T_a recorded occurred between 0200 and 0400 h. There was >3 $^{\circ}\text{C}$ difference between daily maxima and minima (T_a) during the warmest night compared to a 5 $^{\circ}\text{C}$ difference during the coldest night (Fig. 4).

PFD_L AND LEAF TEMPERATURE

The inclined leaf orientation in both species substantially reduced incident PFD_l compared to the centrally located, horizontal PFD_s sensor (PFD_s). This was especially true for *C. tessellata* where PFD_s was $\sim 70\%$ – 80% greater than PFD_l incident on leaves (PFD_l), while for *E. grandiflora* this value was mostly between 50% and 70% (Fig. 5).

Leaf temperature (T_l) and PFD_l for *E. grandiflora* and *C. tessellata* paralleled one another, with low T_l values corresponding to

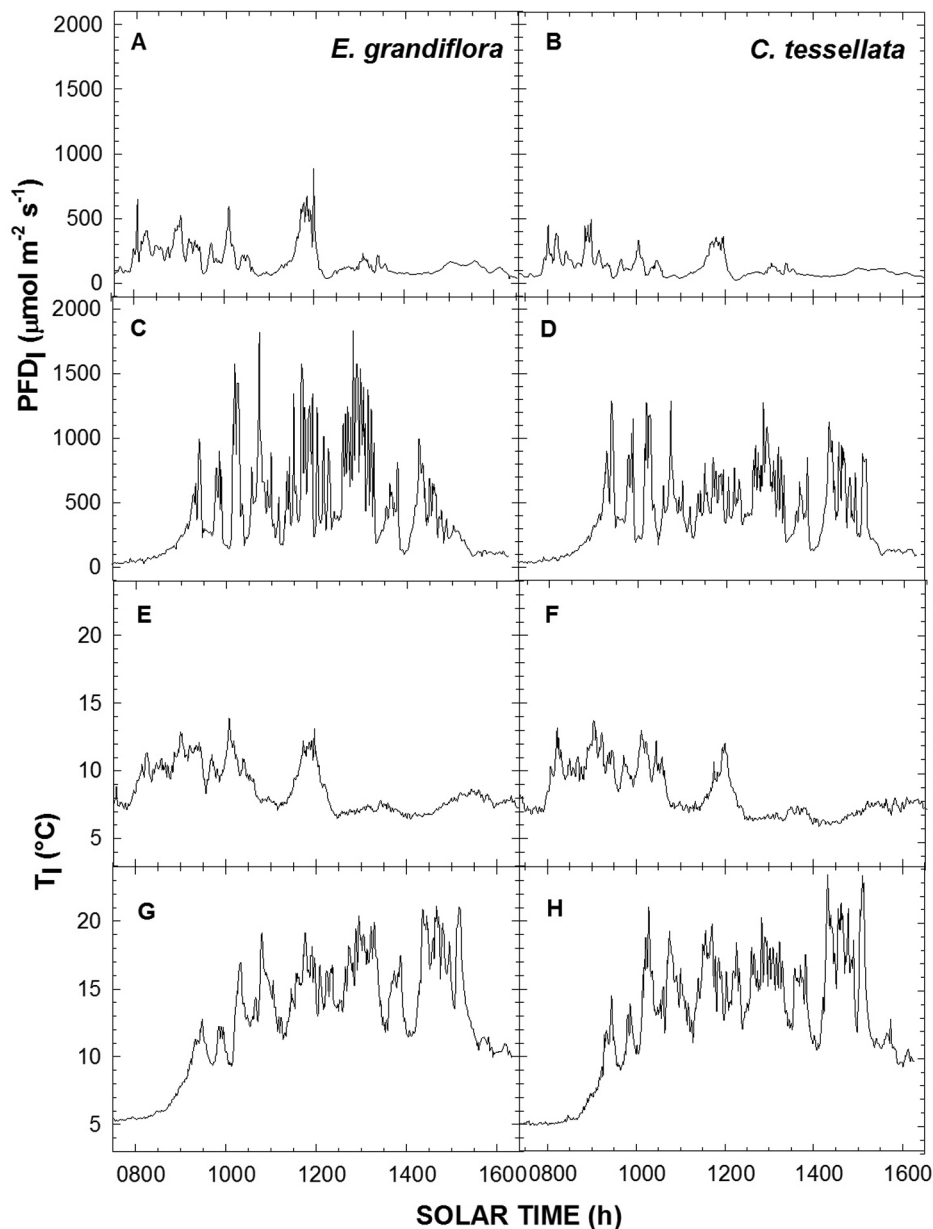


FIGURE 6. Hourly variation in PFD_i and T_i in *E. grandiflora* and *C. tessellata* leaves on the coldest (A and B; E and F; 3/26/12) and warmest day (C and D; G and H; 3/27/12).

a low PFD_i (Fig. 5). Both species had similar PFD_i and T_i patterns, although the incident PFD values were higher in *E. grandiflora*, with a difference with *C. tessellata* of up to $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 6, parts A and C); *Chusquea* never experienced values over $1300 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 6, parts B and D). Leaf temperatures on both species were similar on cold days, with both species reaching maximums of near 14°C (Fig. 6, parts E and F), while on warmer days *C. tessellata* had higher T_i by about 3°C than *E. grandiflora* during the afternoon (Fig. 6, parts G and H).

Considering differences between T_i and T_a , both *E. grandiflora* and *C. tessellata* maintained average T_i values above T_a , especially during the day (Fig. 7). However, maximum $T_i - T_a$ differences (ΔT) were over 12°C (Fig. 7, part B), while $T_i < T_a$ was more frequent in *C. tessellata* and up to -5.7°C for both species, and for all T_a (Fig. 7, part C). Temporally, morning ΔT in both species showed steep linear increases, although *C. tessellata* warmed more slowly

(Fig. 7, part A). In contrast, *C. tessellata* cooled more slowly in the afternoon, and both species showed less linear decreases during the afternoon compared to morning increases.

Discussion

SITE PFD AND AIR TEMPERATURES

Data describing the influence of cloud dynamics on air and leaf temperatures in high elevation alpine zones are rare in the literature, especially for equatorial alpine areas (see review by Körner, 2002; Pellicciotti et al., 2011). Our páramo study site, northern Andes, was characterized by high levels of incident sunlight, along with high temporal variability due to cloud patterns that ranged from high cirrus clouds to full cloud immersion (A. Sanchez, J. M. Posada, and W. K. Smith, unpublished data). At high elevations, in-

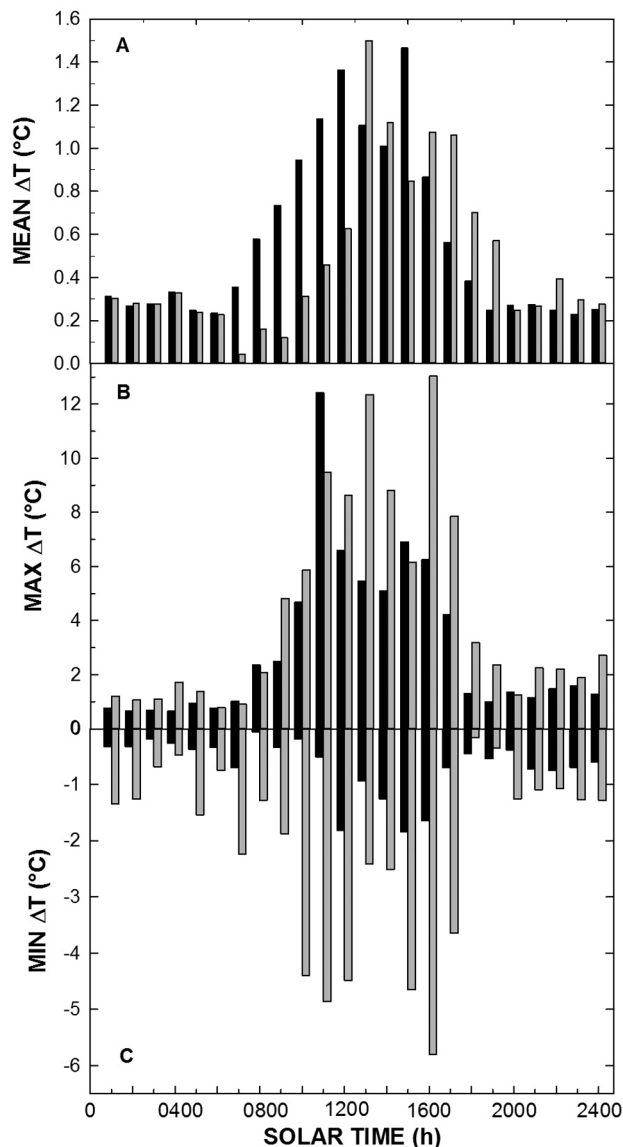


FIGURE 6. (A) Hourly mean, (B) maximum, and (C) minimum temperature differences between the leaf (T_l) and air temperature (T_a) for *E. grandiflora* (black) and *C. tessellata* (gray) measured over the entire study period, i.e. $\Delta T = T_l - T_a$.

creased levels of insolation during clear skies are well known (e.g., Smith and Geller, 1980; Bader et al., 2007; Körner, 2007). However, as reported for other tropical alpine areas (Diemer, 1996), lower levels of incident sunlight ($<400 \mu\text{mol m}^{-2} \text{s}^{-1}$) may dominate the frequency distribution of sunlight levels due to clouds and fog, although maximum, much higher values may occur intermittently. Specifically, Diemer (1996) reported that over 50% of incident sunlight values were below about $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ with maximum values of $>2400 \mu\text{mol m}^{-2} \text{s}^{-1}$ occurring for less than 2% of the total day in an Ecuadorian Andes site, similar to our data (Fig. 3). PFD values of over $3000 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 2), well above the Solar Constant (an average of 1361 W m^{-2} or approximately $2790 \mu\text{mol m}^{-2} \text{s}^{-1}$; Percy, 1989), have been reported elsewhere and are associated with specific cloud patterns (Gu et al., 2001; Dye et al., 2009).

Although rapid changes in PFD levels (Fig. 6) have been associated with both photosynthetic induction (Percy and Way, 2012)

and photoinhibitory effects (e.g., Germino and Smith, 1999; Cui et al., 2004), these associations have yet to be studied comprehensively (see Smith and Berry, 2013, for recent review). In both species studied here, inclined leaf orientations reduced incident PFD compared to the horizontal-sensor PFD_s by more than 50%–60%. This is a potentially important architectural trait that avoids high PFD, as well as the potentially stressful, short transition times from low to high PFD, e.g., from <400 to over $3000 \mu\text{mol m}^{-2} \text{s}^{-1}$. The lower values of PFD_l relative to the horizontal sensor (PFD_s) in *C. tessellata* indicate a greater decline in PFD interception due to a more inclined leaf orientation, approximately 70%–80% lower compared to ~50% in *E. grandiflora* (Fig. 5).

Comparisons of the warmest and coldest days during the sampling period showed considerably greater T_a values along with a greater number of PFD_s values above approximately $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ on the warmest day of the sampling period. The warmest day also had a shift to higher T_a , in correspondence with PFD_s above about $400\text{--}500 \mu\text{mol m}^{-2} \text{s}^{-1}$. Thus, solar heating appeared to have had a significant impact on T_a during both the afternoon and morning (Fig. 2).

LEAF PFD AND TEMPERATURES

Leaf temperature patterns relative to PFD_l and T_a were similar between the two species, despite contrasting differences in whole-plant architecture and individual leaf form. Thus, in terms of PFD effects on T_l , leaf orientation similarities seemed to override differences in leaf morphology such as the dense pubescence found in *E. grandiflora*. Based upon differences in leaf form and plant architecture, the slightly more horizontal leaf inclination in *E. grandiflora* should have also led to greater nighttime sky exposure and, thus, colder minimum temperatures. However, thicker leaves and a denser leaf pubescence could lead to less T_l variability (Jordan and Smith, 1994; Meinzer et al., 1994).

Some studies have pointed to the importance of nighttime minimum air temperatures in the alpine as dictating the functional beginning and end of the growth season, plus the frequent occurrence of low-temperature photoinhibition of photosynthesis following near-freezing nights even during summer (Hamerlynck and Smith, 1994; Germino and Smith, 1999, 2000; Johnson and Smith, 2005). Because minimum air temperatures often occur at or near sunrise (Fig. 4), minimum leaf temperatures could occur almost simultaneously with relatively high sunlight exposure (Fig. 2, part C). In addition, the accumulation of cold air settling next to the ground, enhanced by wind-sheltered, yet sky-exposed microsites, can also contribute to minimum leaf temperatures at night that are well below air temperature (e.g., Fig. 7; Jordan and Smith, 1995; Germino and Smith, 1999). Moreover, cloud cover and leaf orientation away from the sky can act to curtail both leaf warming during the day and cooling during the night by minimizing the radiational heat exchange that uncouples leaves from air temperature.

Conclusions

The results presented here show a tight coupling between a highly variable PFD regime and corresponding air and leaf temperatures for two dominant species of this northern Andes páramo, despite having contrasting leaf morphology, leaf form, and whole-plant architecture. Rapid changes in PFD levels of over $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ occurred over time intervals of minutes or less, especially on warmer days. Leaf orientation reduced both PFD_l and leaf tem-

perature, and seemed to outweigh contrasting differences in leaf morphology (heavy pubescence in *E. grandiflora*) and whole-plant architecture (upright rosette versus multiple erect stems, Fig. 1) between the two species. This information could be critical for anticipating functional responses of native species to potential changes in future cloud regimes under current scenarios of climate warming.

Acknowledgments

The authors would like to thank Camilo Rey for his help in the field and calibration of all instruments, and Chingaza National Park (CNP) for providing logistical support and permits for this research. This project was funded partially by the Center for Energy, Environment, and Sustainability (CEES) at Wake Forest University and the National Science Foundation, U.S.A. (IOS-1122092).

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MS accepted December 2013