

Introduction

The debate over the mechanistic factors that limit the altitudinal limit of forest trees to specific elevations, and no higher, has been a continuing source of controversy for over a century (see Tranquillini 1979 and Arno 1984 for reviews). Environmental effects on both photosynthetic carbon gain and respiratory-driven growth processes have been used to evaluate limitations at the alpine treeline. Most of these earlier studies have focused on correlations between treeline altitudes worldwide and associated mean minimum annual temperatures. According to these more traditional ideas, trees are unable to assimilate enough carbon for survival above certain altitudes. However, Körner (1998, 1999) proposed that low soil temperatures coupled with drought stress inhibit the carbon processing abilities at treeline, not their capabilities for carbon gain via photosynthesis. Körner's hypothesis about the altitudinal extent of treelines suggests that it is not limitation to photosynthetic carbon gain at high elevation, but the processing of fixed carbon into growth via respiratory physiology. A more recent study suggests that increasing non-structural carbon pools without significant growth is caused by carbon source availability exceeding demand (Körner 2003). Extremely cold soil temperatures at night may also as inhibit the processing of photosynthate produced during the day, thus preventing the expected growth from a given amount of carbon gained (Körner 1998). These cold soil temperatures were also proposed as being generated by the large size and shading of mature trees at treeline, preventing their growth at higher elevation. In contrast, Smith et al. (2003) have proposed that the elevational extent of treelines is due fundamentally to the inability of conifer tree seedlings to establish above existing treelines, and may have little to do with factors influencing mature tree growth. To date,

there have been no studies of alpine treeline conifers comparing photosynthetic carbon gain over entire annual growth periods. Furthermore, if carbon limitations are apparent, little is known about which abiotic factors may limit photosynthetic carbon gain at different times of summer and how they compare quantitatively.

Abiotic factors (solar radiation, water, and temperature) may be most limiting to the photosynthetic carbon gain of these timberline tree species (Smith et al. 2003). Particularly important during the 2002 growing season was the small amount of previous winter's snowpack, an early warm period in spring, and resulting low water availability in the following summer. As a result, 2002 was one of the driest years on record, with the mountains of Southeastern Wyoming receiving approximately 45% of normal winter precipitation, leading to widespread drought and fire in the region (National Atmospheric Deposition Program WY00 site (N 41° 23', W 106° 16', 3284 m elevation). The period from April to September 2002 was the seventh driest on record, with approximately 150mm for the state average precipitation, since NOAA (National Oceanic and Atmospheric Administration) began recording in 1895 (NOAA Drought Information Center). The dry winter was only slightly attenuated by modest rainfall throughout the spring and following months in 2002. This extremely dry condition allowed for a unique opportunity to observe the physiological response of *P. engelmannii* and *A. lasiocarpa* to low water availability under otherwise relatively normal light and temperature conditions.

The most general hypothesis here is that the photosynthetic carbon gain of these timberline tree species is limited more as elevation and exposure increase across the treeline ecotone. In addition, a secondary hypothesis is proposed that temperature, water, and sunlight limitations will generate different degrees of limitation at different times of

the summer growth period, depending on position in the ecotone. Thus, the purpose of the present investigation was to produce an observational, correlative data set that would provide circumstantial evidence testing the above hypotheses for an episodically dry year. These types of episodic stresses may become more frequent and intense under several current scenarios of future climate change (Brown and McLachlan 2002).

Materials and methods

In the south-central Rocky Mountains, USA, contiguous subalpine forest is well established at ca. 2300 m, emerging from mixed shortgrass prairie interspersed with riparian forest. This subalpine forest consists primarily of a mixture of *Picea engelmannii*, *Abies lasiocarpa*, *Pinus contorta*, *Pinus flexilis*, and *Populus tremuloides*. With increasing elevation tree species composition changes to two co-dominants, *A. lasiocarpa* and *P. engelmannii*, while *P. flexilis*, *P. contorta*, and *P. tremuloides* become rare. From this point upward, the continuous forest merges into the well documented ribbon forest formed by strong prevailing wind effects on snow deposition (Billings and Mark 1957). Within this treeline ecotone spruce and fir become tightly grouped into tree “islands” with surrounding alpine tundra. Further increases in elevation and wind exposure brings an ever changing and highly variable environment. The treeline ecotone is formed in this region, and with higher altitude the spruce and fir become stunted in growth and are reduced, ultimately, to the isolated krummholz mats at the furthest altitudinal extent these two species (Figure 1). This change in distribution and growth form is

Alpine Treeline

15
m

Seedling/Sapling * Forest Trees

Abundance
← Wind Direction

Timberline

Treeline

Intact Forest

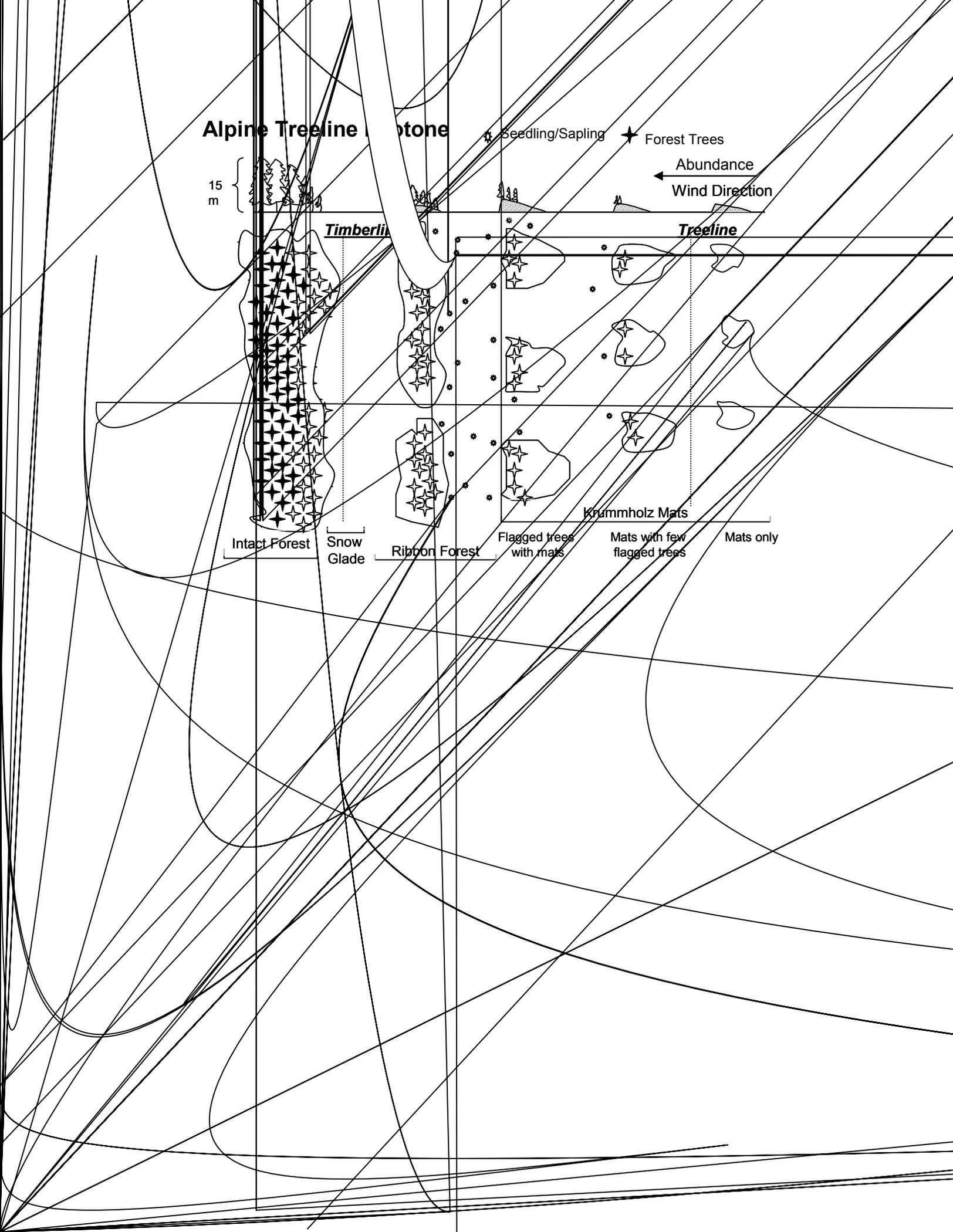
Snow
Glade

Ribbon Forest

Flagged trees
with mats

Krummholz Mats
Mats with few
flagged trees

Mats only



highly variable, depending on wind patterns, slope, snow deposition, sky exposure, and multiple stress factors encountered by these trees (Smith et al. 2003).

Photosynthetic carbon gain and water status of mature cone-bearing trees of *Picea engelmannii* Parry ex. Englem. and *Abies lasiocarpa* [Hook.] Nutt. were monitored throughout the summer of 2002. Three study sites, one in a continuous spruce-fir forest, one near the center of the alpine treeline ecotone (alpine meadow interspersed with tree islands), and one at the most extreme edge of the alpine treeline, were located in the Medicine Bow Mountains of southeastern Wyoming. Abiotic factors (sunlight, temperature, and water status) were characterized for each site and compared to quantitative variations in shoot-level photosynthesis throughout the summer of 2002.

Study sites

The subalpine forest thins to ribbon forest, and eventually to flagged tree islands and krummholz mats, with increasing elevation across the treeline ecotone. Mature trees group together in these islands and exhibit a denser and more windswept appearance with the procession toward the treeline limit, while inter-island distance spatially increases. (Daubenmire 1954; Wardle 1968; Smith et al. 2003). *Picea engelmannii* and *Abies lasiocarpa* are the two codominant conifer species that form the timberline and treeline boundaries of the south-central Rocky Mountains, USA. Other associated species include *Pinus flexilis*, *P. contorta*, shrubs (*Salix spp.* and *Ribes coloradense*), and many herbaceous species such as *Caltha leptosepala*, *Helianthella quinquenervis* and *Erythronium grandiflorum* (Billings 1969; Peet 1988).

Three study sites (approximately 20 m x 20 m) were selected for comparison in the treeline ecotone of the Snowy Range of the Medicine Bow Mountains in southern Wyoming, USA (N 41° 20', W 106° 13'). One site was located within in a continuous mixed *A. lasiocarpa*, *P. engelmannii* subalpine forest (FS) at 2965 m elevation. The second site was composed of a mosaic of tree (both *A. lasiocarpa* and *P. engelmannii*) islands within an alpine meadow located near the center of the upper treeline ecotone (TS) at 3198 m. The third site was located at the farthest extent of a recognizable alpine treeline (AS) at 3,256 m where krummholz mats formed tree islands spaced tens of meters apart in the surrounding alpine tundra. All three sites were located on east-southeast (ca. 106° for FS, ca. 114° for TS, and ca. 118° for AS) slopes (< 10° for both all sites).

Photosynthesis and water status

Photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) in mature trees (5 m to 10 m in height at FS and TS, and <2 m in height at AS, and 25 years to 150 years in age) was monitored via gas-exchange measurements throughout the summer at all sites approximately every three weeks (June 22, 23, and 26; July 12, 13, and 17; July 30, 31 and August 2; August 17, 18, and 19; September 20, 21, and 22). Measurements were taken at five times per day at approximately 0900, 1100, 1400, 1600 and 1800 hours (solar time, List 1971). Each sampling consisted of ten individual south facing sun shoot measurements, five for *A. lasiocarpa* and five for *P. engelmannii*, from three to five individual trees for each species.

Daily mean photosynthesis (A) was calculated by averaging all photosynthesis measurements for each species during a day. Integrated daily photosynthesis (A_{int}) was computed by averaging photosynthesis values for each time period (900, 1100, 1400, 1600 and 1800 hours), multiplying by the amount of time in each interval (in seconds), and summing for the entire day. Integrated annual photosynthetic carbon gain (A_{net}) was determined for each species by integrating the area under the curves for the plotted A values for all sample days during the summer.

Photosynthesis of the selected conifer shoots was measured using a Li-6200 model portable photosynthesis system (LICOR Inc., Lincoln, NE) for south-facing, previous-year needle cohorts (1-yr old) in the shoot's natural orientation to the sun. Photosynthesis was computed on a total leaf area basis by calculating the average number of needles per cm of stem within the sample cuvette and multiplying needle area by stem length. Based on shoot samples, 34.0 cm² and 30.4 cm² of total needle area occurred per 10 cm of stem length in *P. engelmannii* and *A. lasiocarpa*, respectively (similar to results of Thompson and Leyton 1971; Hadley and Smith 1987; Smith et al. 1991). Photosynthesis, when expressed on a silhouette leaf area basis (comparable to horizontal broadleaves), was approximately three to four times greater for both species, as previously reported in Smith et al. (1991).

Xylem water potential (ψ) was measured using a Scholander-type pressure bomb (model 1000, PMS Instrument Co., Corvallis OR) at intervals throughout the season at all sites. Measurements were taken at two-week intervals between 1400 and 1500 solar time during each day from 6/10/2002 to 9/22/2002. Stems were cut with a razor blade and the cut portion was immediately covered with petroleum jelly, placed into air-tight freezer

bags on ice until measurements were completed, approximately one hour later. Field measurements of ψ were taken within minutes of excision, and compared to those of shoots transferred to the lab. No significant changes in water status occurred due to transfer and storage time during the period of measurement.

T_{leaf}, T_{air}, PAR, and precipitation

Photosynthetically active radiation (*PAR*, 0.3 – 0.7 μm wavelengths), air temperature (T_{air}), and soil temperature (T_{soil}) were measured at each site in areas representative of and within 100m of the study sites. *PAR*, T_{air} , and T_{soil} levels were recorded every 10 minutes for a total of 67 days (June 26-July 1, July 5-July 24, August 2-August 8, August 15-August 25, August 31-September 22). *PAR* levels were measured using LICOR Li-190 *PAR* sensors oriented horizontally at 1 m height, T_{air} using two fine-wire (0.02 mm diameter) copper-constantan thermocouples (Omega Engineering, Stamford, CT) at 1 m height and shielded from direct solar radiation, and T_{soil} using three thermistors (Type T, 20 gauge) buried at 15 cm depths (Omega Engineering, Stamford, CT). All sensors were connected to dataloggers (model 21x, Campbell Scientific, Logan, UT). *PAR* levels were also monitored during photosynthetic measurements via the Li-6200 sensor head with attached Li-190 *PAR* sensor oriented in the same plane as the primary axis of the measurement shoot. *PAR* regime nomenclature (e.g. sunflecks versus sunpatches) follows Smith et al. (1989). Needle temperatures (T_{leaf}) were monitored via the fine wire thermocouple incorporated in the Li-6200 sensor head cuvette at each physiological measurement described above.

Weekly precipitation data were taken from the National Atmospheric Deposition Program WY00 site (N 41° 23', W 106° 16', 3284 m elevation), located less than 1 km from research sites. Rainfall was measured daily using an Alter-shielded Belfort rain gauge and summed weekly.

Calculations

Photosynthesis (A), stomatal conductance (g_s), transpiration (E), internal CO₂ (C_i) concentration, and water use efficiency (WUE) were calculated from the measurement values acquired from the Li-6200. Photosynthesis and other physiological parameters were calculated according to equations used in von Caemmerer and Farquhar (1981). The equation used for photosynthesis is based on changes during the measurement period of CO₂ concentration (c_i and c_f), length of the measurement (t_i and t_f), total leaf area (a), temperature (T_a), and the volume (v) of the cuvette, as in $A = [v (c_i - c_f) 0.000529 \text{ Pa}] / [(t_f - t_i) a (T_a + 273)]$. Stomatal conductance (g_s) is calculated based on the inverse of the resistance to the flow of water vapor through stomatal openings, or $g_s = [a (t_f - t_i) ((q_s[T_L]) - H_f q_s[T_a])] / v ((H_f q_s[T_a f]) - (H_i q_s[T_a i]))$, where a refers to the leaf area, t_f and t_i are initial and final times of the measurements, T_a and T_L are air and leaf temperatures, H is the relative humidity, and $q_s[T]$ is the saturation vapor pressure at temperature T . Transpiration (E) is calculated as $E = (v/a)(dq/dt)$, where v is volume, a is area, q is the water vapor concentration, dur

and diffusion coefficients of CO₂ and H₂O in air, primarily in the boundary air layer above the leaf surface.

RESULTS

Seasonal trends

Mean photosynthetically active radiation (*PAR*) was greatest at AS, followed by TS and FS, except for the first measurement period (6/22, 23, and 26) where TS measurements occurred at higher *PAR* levels (Figure 2). Integrated *PAR* was 3920, 5077, and 5188 mol m⁻² growing season⁻¹ for FS, TS, and AS respectively (Figure 3), based on data from cuvette-level *PAR* sensor on the Li-6200 used for gas exchange measurements described below. Sunny days were characterized by clear skies with minimal cloud occurrence during physiological measurement periods. *PAR* sensors in an open, non-shaded location received an average of 1.23 mol m⁻² day⁻¹ of *PAR* on a representative sunny day, 7/15/2002 (Figure 4), while on cloudy days the *PAR* sensors received an average of 0.59 mol m⁻² day⁻¹ of *PAR* (Figure 5). Cloudy days were characterized by intermittent cloud occurrence, where there were significant reductions in *PAR* reception. FS air temperatures (T_{air}) and leaf temperatures (T_{leaf}) showed an increase from 6/22, 23, 26 to 7/12, 13, 17, followed by a general decrease throughout the rest of the summer (Figure 6). T_{leaf} was greater than T_{air} at all sites throughout the season. Soil temperature (T_{soil}) at FS showed a general increase throughout the season with a sharp decline during the 9/20 measurement. T_{soil} at TS decreased throughout the season while T_{soil} at AS peaked during the 8/2 measurement, followed by decreasing values until the end of the season (Figure 6). Representative early season (7/13/2002) diurnal soil

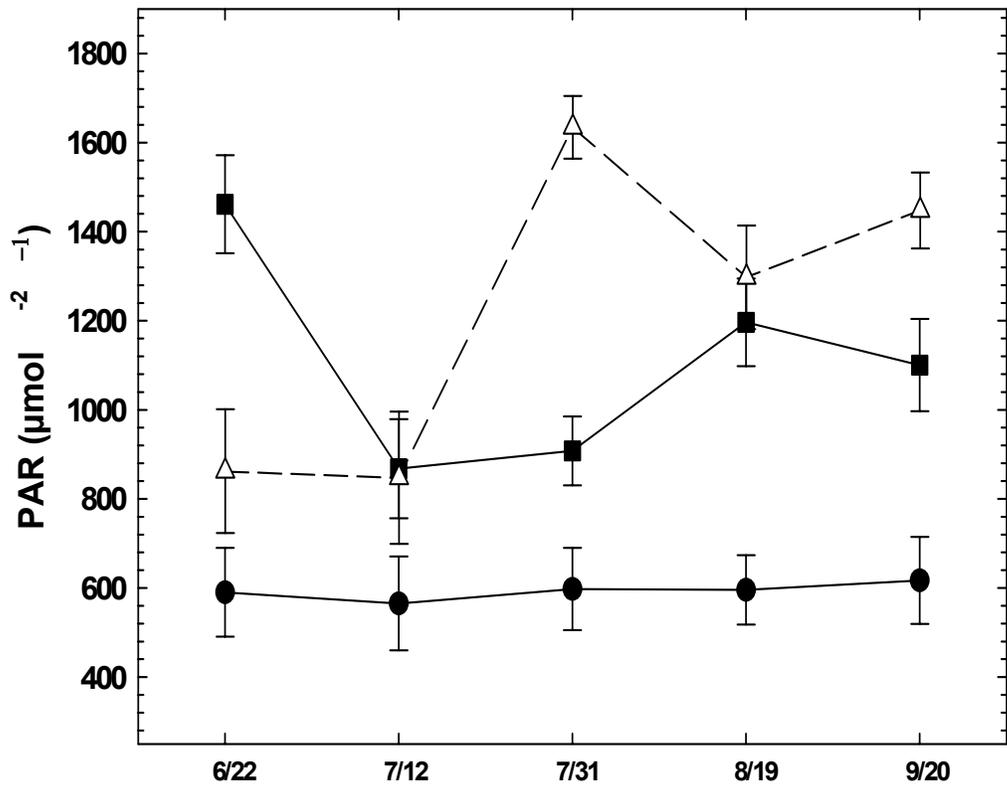


Figure 2. Mean photosynthetically active radiation received throughout 2002 growing season at FS (closed circle), TS (closed square), and AS (open triangle). Vertical bars represent standard errors.

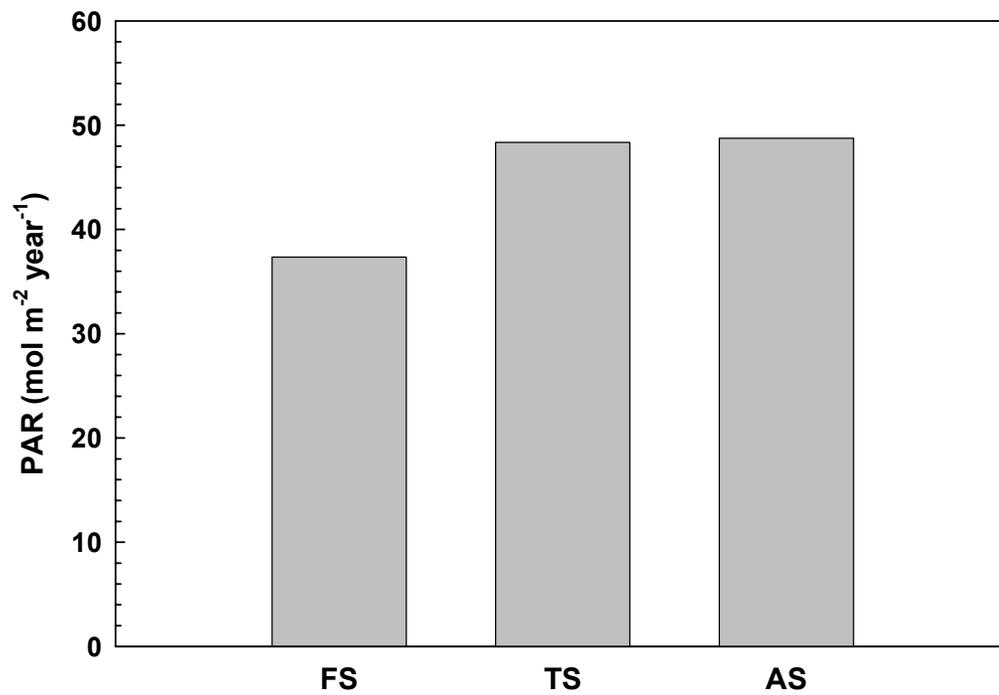


Figure 3. Integrated season *PAR* for each site FS (2965 m), TS (3198 m), AS (3256 m).

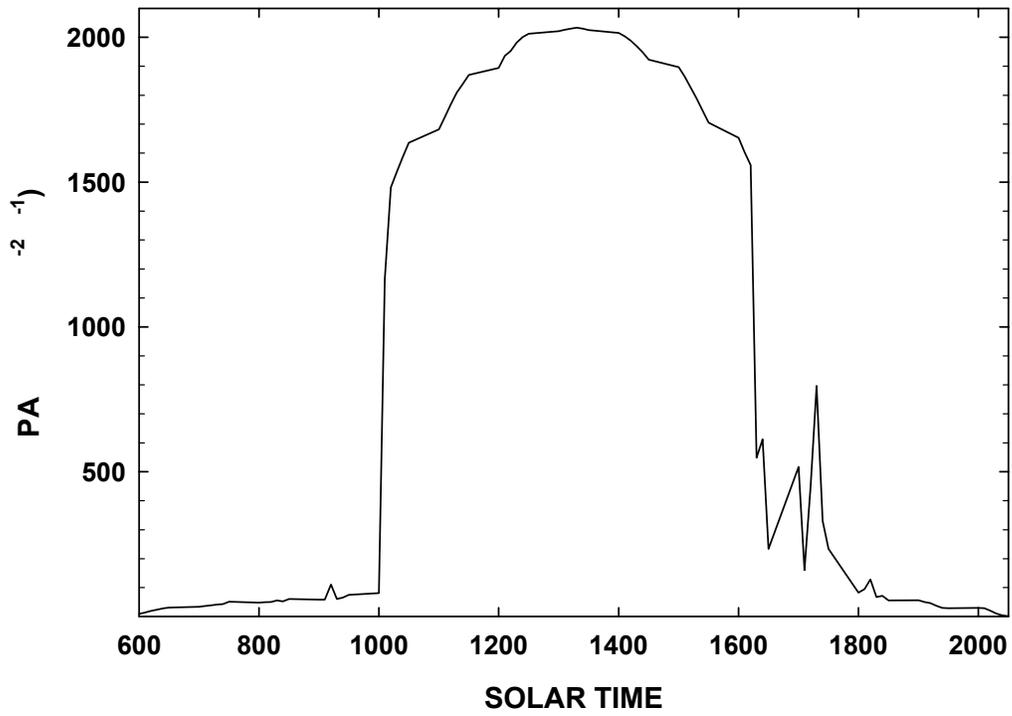


Figure 4. Representative PAR levels at the Alpine Site (AS) measured on a typically clear day during gas exchange measurement periods.

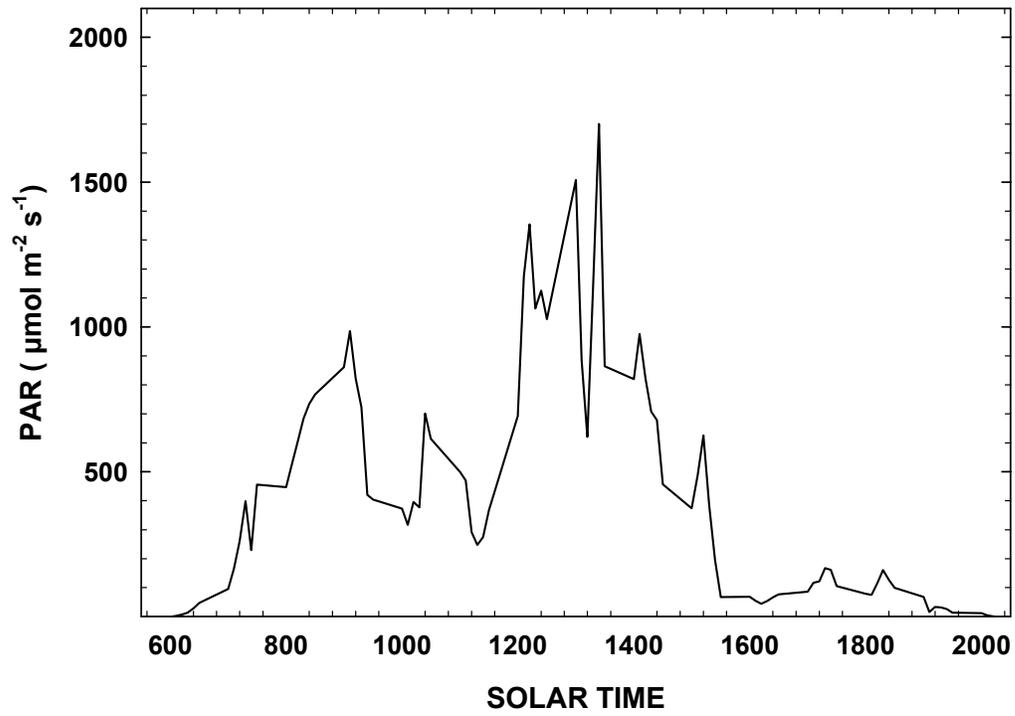


Figure 5. Representative PAR levels at the Alpine Site (AS) measured on a typically cloudy day during gas exchange measurement periods.

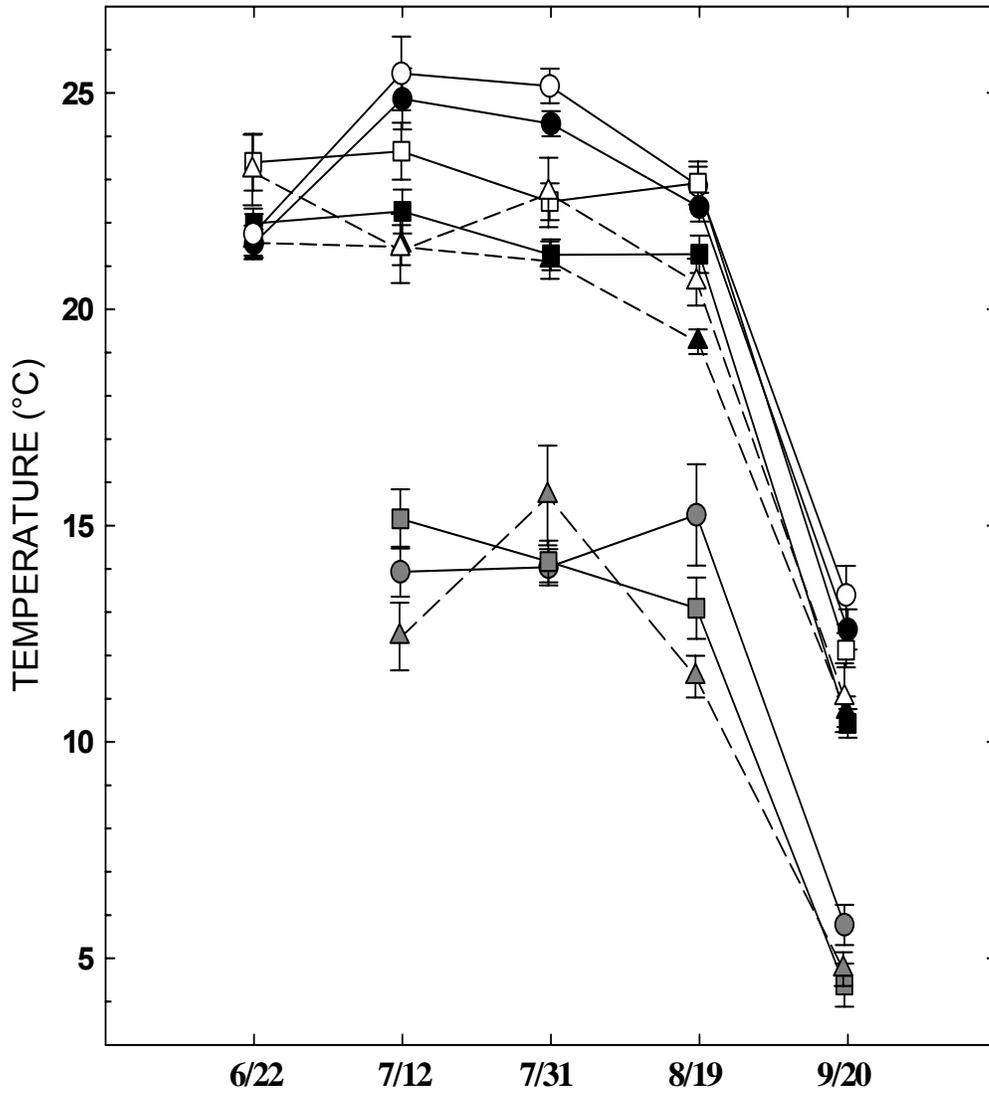


Figure 6. Mean daily T_{air} (black symbols), T_{leaf} (open symbols), and T_{soil} (gray symbols) for the three study sites FS (circles), TS (squares), and AS (triangles). Vertical bars represent standard errors.

temperatures were highest at AS, followed by FS and TS respectively (Figure 7). Representative late season diurnal soil temperatures were highest at the FS, followed by TS and AS respectively (Figure 8). The greatest intersite soil temperature differences typically occurred during the early morning and the late afternoon.

Based on T_{air} , T_{leaf} , RH, and saturation vapor pressure values (List 1971), the mean leaf to air vapor pressure deficit was calculated for *A. lasiocarpa* and *P. engelmannii* and combined through the season as described above. During the warmest parts of the summer (7/12 – 7/31), FS trees showed the highest *LAVD*. TS and AS *LAVD* was steady through the season, with AS trees typically having lower *LAVD* than TS, except for the 7/31 measurement (Figure 9).

Photosynthetic carbon gain (*A*) and estimated seasonal photosynthetic carbon gain (A_{int}) throughout the 2002 growing season was highest at the TS, followed by AS and FS for both *P. engelmannii* and *A. lasiocarpa* (Figure 10). All sites and both species showed increasing carbon gain throughout the summer. FS and TS *A. lasiocarpa* trees showed higher A_{int} than *P. engelmannii* (31 and 24% greater for FS and TS respectively), whereas AS *P. engelmannii* showed higher (4%) A_{int} than *A. lasiocarpa* (Figure 10). Mean A_{int} for *A. lasiocarpa* and *P. engelmannii* combined were as follows for each site: FS 5.1 mol m⁻² year⁻¹, TS 12.5 mol m⁻² year⁻¹, and AS 10.1 mol m⁻² year⁻¹. Individually, total annual CO₂ uptake in *A. lasiocarpa* was 5.7, 13.9 and 9.8 mol m⁻² year⁻¹ at FS, TS and AS, respectively, while *P. engelmannii* had somewhat lower values at FS and TS, but a greater value at AS (4.4, 11.1, and 10.3 mol m⁻² year⁻¹, respectively) (Figures 10 and 11).

Water status, measured via xylem water potential (ψ), was lowest in the beginning of the season, followed by generally constant, low values for all sites and both species

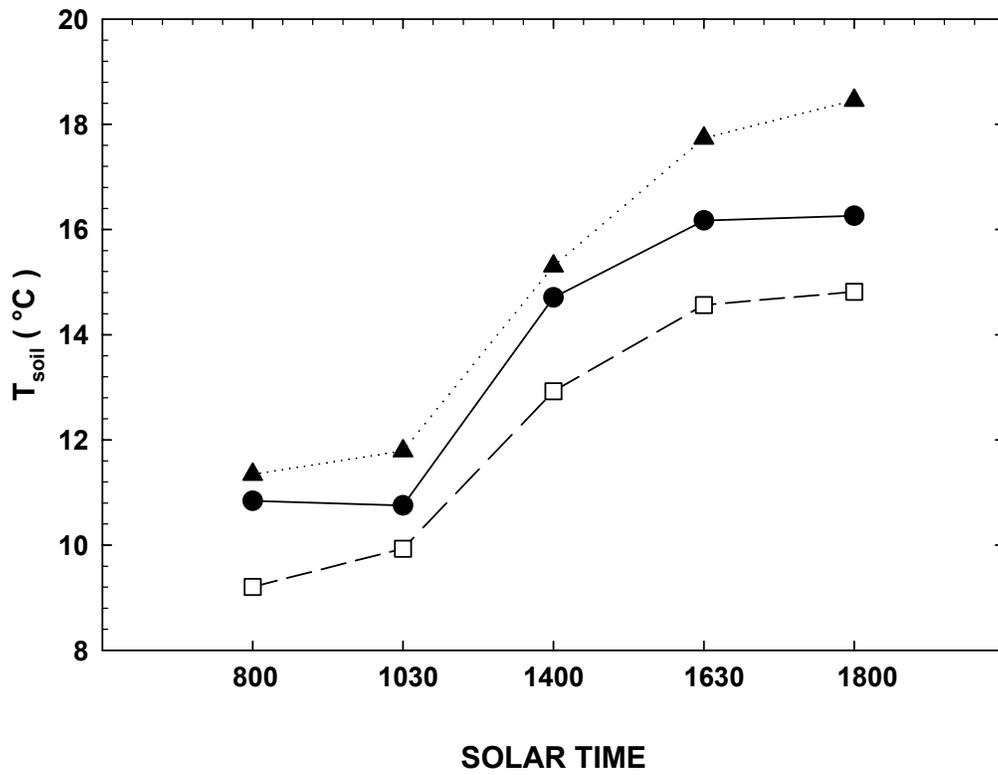


Figure 7. Diurnal soil temperature for representative early season day (7/12/2002) at the FS (closed circles), TS (open squares), and AS (closed triangles).

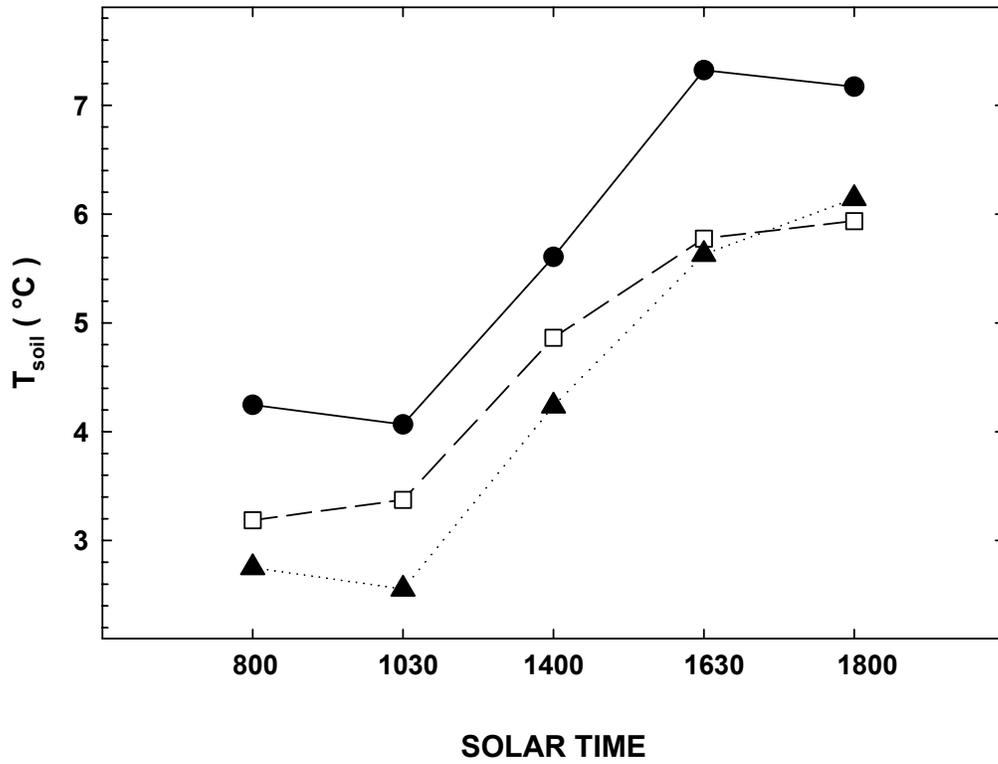


Figure 8. Diurnal soil temperature for representative late season day (7/12/2002) at the FS (closed circles), TS (open squares), and AS (closed triangles).

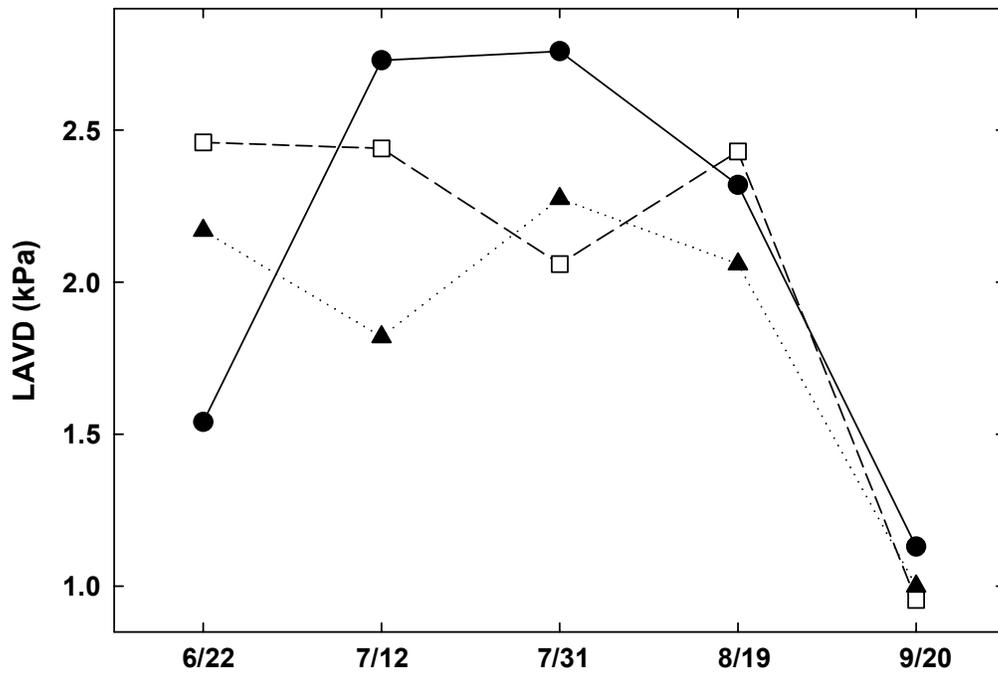


Figure 9. Mean leaf to air vapor pressure deficit (*LAVD*) for spruce and fir at the FS (closed circles), TS (open squares), and AS (closed triangles).

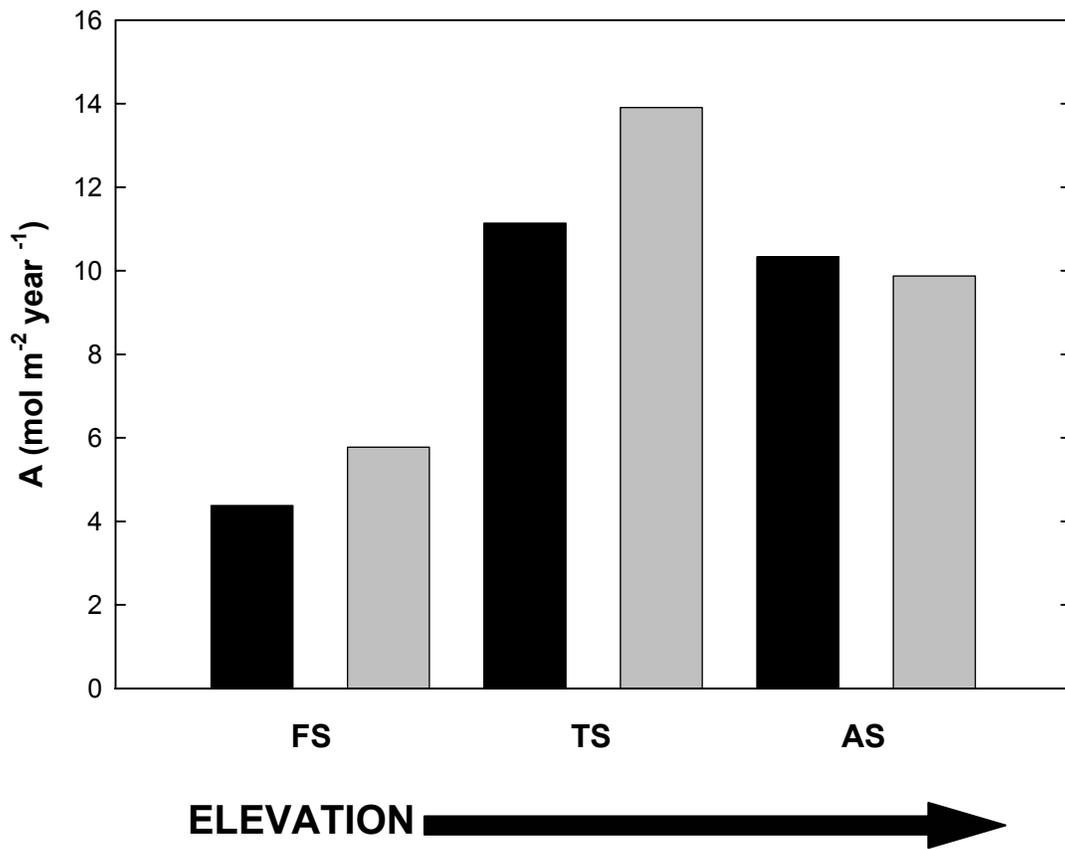


Figure 10. Integrated carbon gain for 2002 growing season for *A. lasiocarpa* (black bars) and *P. engelmannii* (gray bars) in response to increasing elevation across the alpine treeline ecotone.

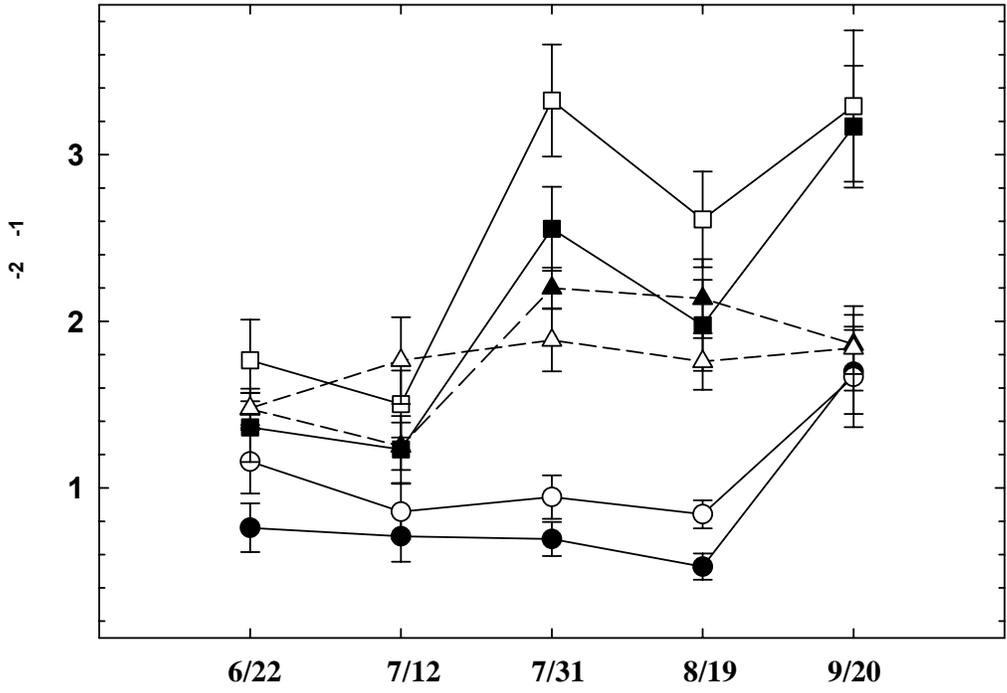


Figure 11. Mean daily carbon gain for *A. lasiocarpa* (open symbols) and *P. engelmannii* (closed symbols) at three different elevations: FS (circles), TS (squares), and AS (triangles). Vertical bars represent standard errors.

Early measurements (6/10/2002) showed the lowest ψ values of the season (-3.4MPa), reflecting low winter precipitation. During the period when photosynthesis measurements were conducted, ψ typically ranged between -1.0 and -2.0MPa. Both *A. lasiocarpa* and *P. engelmannii* appeared to be equally affected by the low water availability, and no distinct interspecific pattern emerged (Figure 12).

Stomatal conductance of water vapor (g_s) at FS followed a similar decreasing trend to FS *A* throughout the season with a sharp late season increase for both *A. lasiocarpa* and *P. engelmannii*. Mean transpiration (E) at FS also decreased through the season, with a slight increase during the September measurement in both species (Figure 13). Mean water use efficiency (WUE) gradually increased through the growing season at the FS. *Abies lasiocarpa* typically had higher values for each of the above physiological parameters than *Picea engelmannii* at the FS throughout the summer (Figure 13).

Stomatal conductance (g_s) at TS fluctuated throughout the season, exhibiting higher mean values during the September measurement for both *A. lasiocarpa* and *P. engelmannii* (Figure 13). Mean E at TS decreased throughout the season, while WUE increased. TS C_i increased from 6/22 – 7/12, then decreased to 8/17, followed by an increase to the end of the season. *A. lasiocarpa* exhibited higher values through the season for A , g_s , and E , while *P. engelmannii* showed higher values for WUE , and C_i (Figure 13).

Mean A at AS showed only a slight increase through the summer, with *A. lasiocarpa* having the greatest increase from 7/12 – 7/31 (Figure 13). Mean g_s , E , and C_i

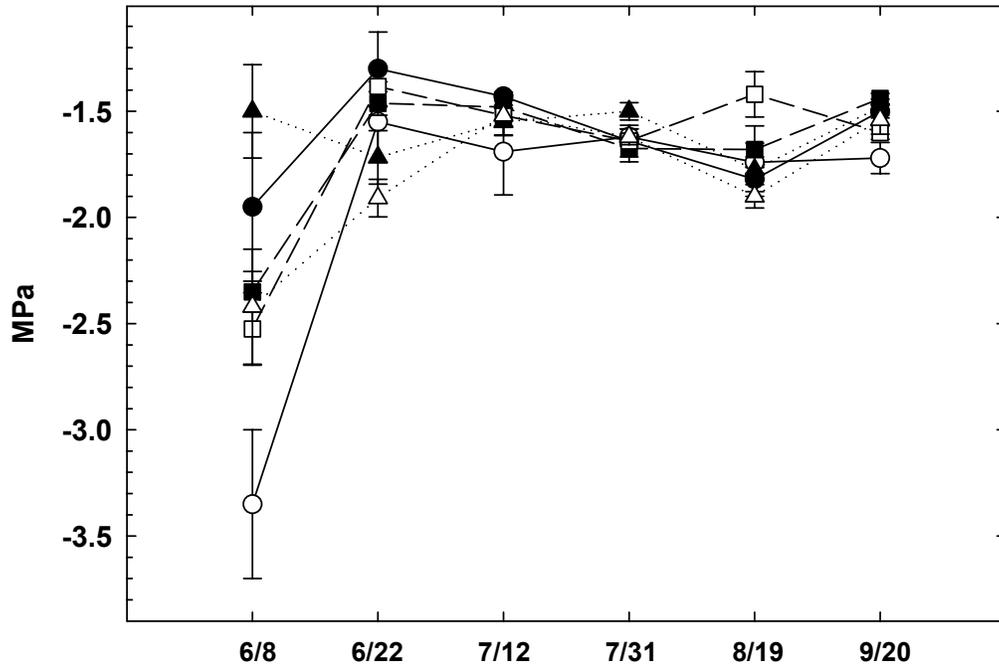


Figure 12. Mean daily xylem water potentials (ψ) for *A. lasiocarpa* (open symbols) and *P. engelmannii* (closed symbols) for the three study sites FS (circles), TS (squares), and AS (triangles) through the 2002 growing season. Vertical bars represent standard errors.

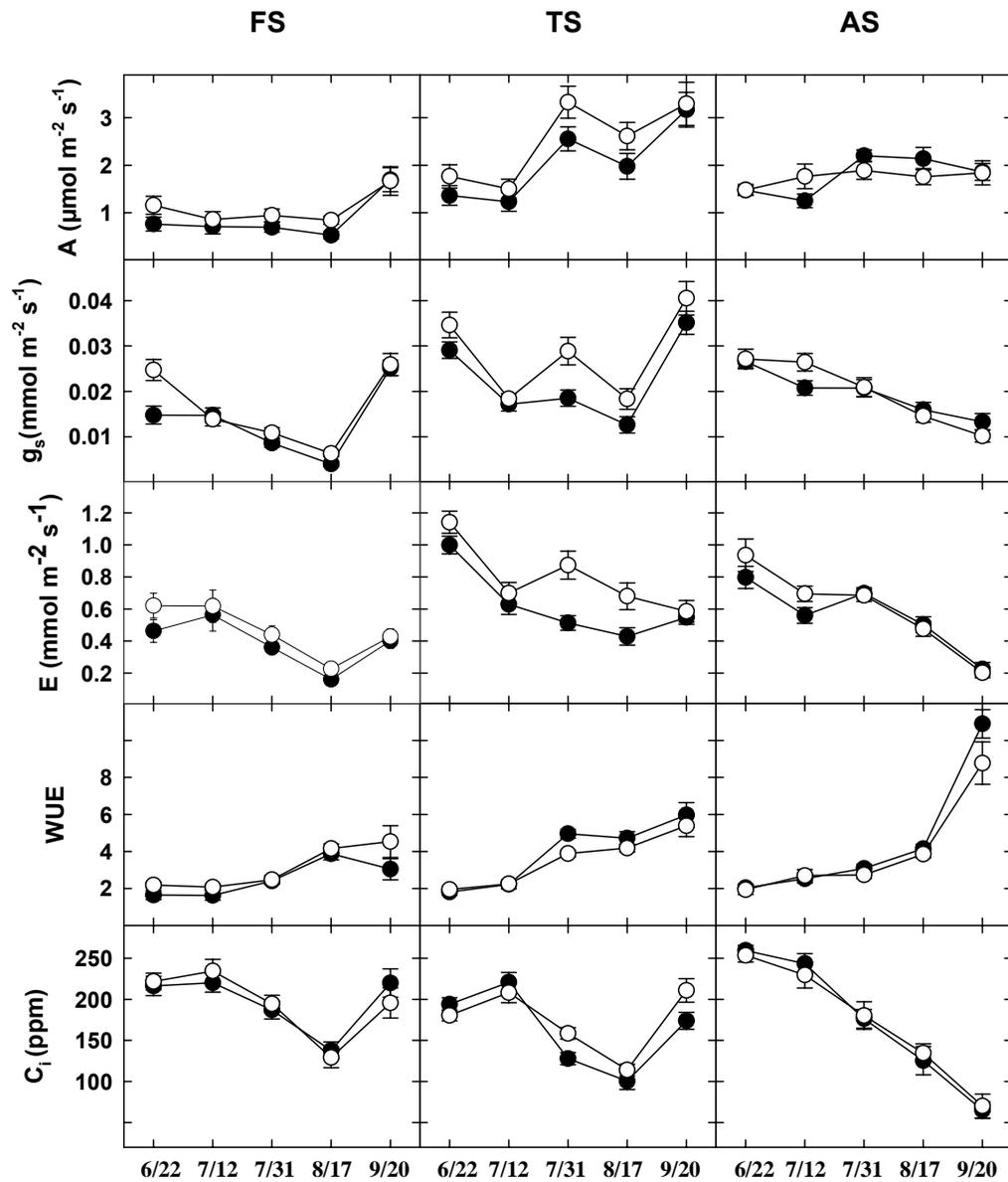


Figure 13. Season mean physiological measurements for *A. lasiocarpa* (open symbols) and *P. engelmannii* (closed symbols), including mean photosynthesis (A), stomatal conductance (g_s), transpiration (E), water use efficiency (WUE), and intracellular concentration of CO_2 (C_i) within the mesophyll. Vertical bars represent standard errors.

decreased throughout the growing season for both *A. lasiocarpa* and *P. engelmannii*, while *WUE* increased dramatically from the beginning to the end of the growing season for both species that were nearly four times higher at the end of the season than the beginning (Figure 13).

Daily trends

Two study periods, 7/12 – 7/17 and 9/20 – 9/22, showed the greatest differences in *A* across the elevational gradient. The July measurements showed similar *A* values for the TS and AS throughout the day, especially during the morning sample periods. The remaining physiological measurements (g_s , *E*, *WUE*, and C_i) were similar for both species throughout the day for the TS and AS. The September measurements showed much higher *A* values for the TS than the AS, predominantly during the morning sample period. g_s , *E*, and C_i during the September measurements showed the greatest differences between the TS and AS, especially during the first three sample periods of the day (Figure 14). The greatest differences in photosynthesis occurred during the morning measurements, when differences in T_{leaf} and T_{soil} were greatest and exposure to solar radiation was similar to mid-day maximums at the TS and AS. Mean daily photosynthetic carbon gain showed a general increasing trend with increasing mean daily *PAR* (Figure 15).

When the previous night's T_{min} was above 0°C, A_{max} showed an increasing trend ($r^2 = 0.731$) with highest A_{max} associated with highest T_{min} . Most nights with T_{min} above 0°C occurred during the 7/12 – 8/19 period. Nights where T_{min} was below 0°C occurred



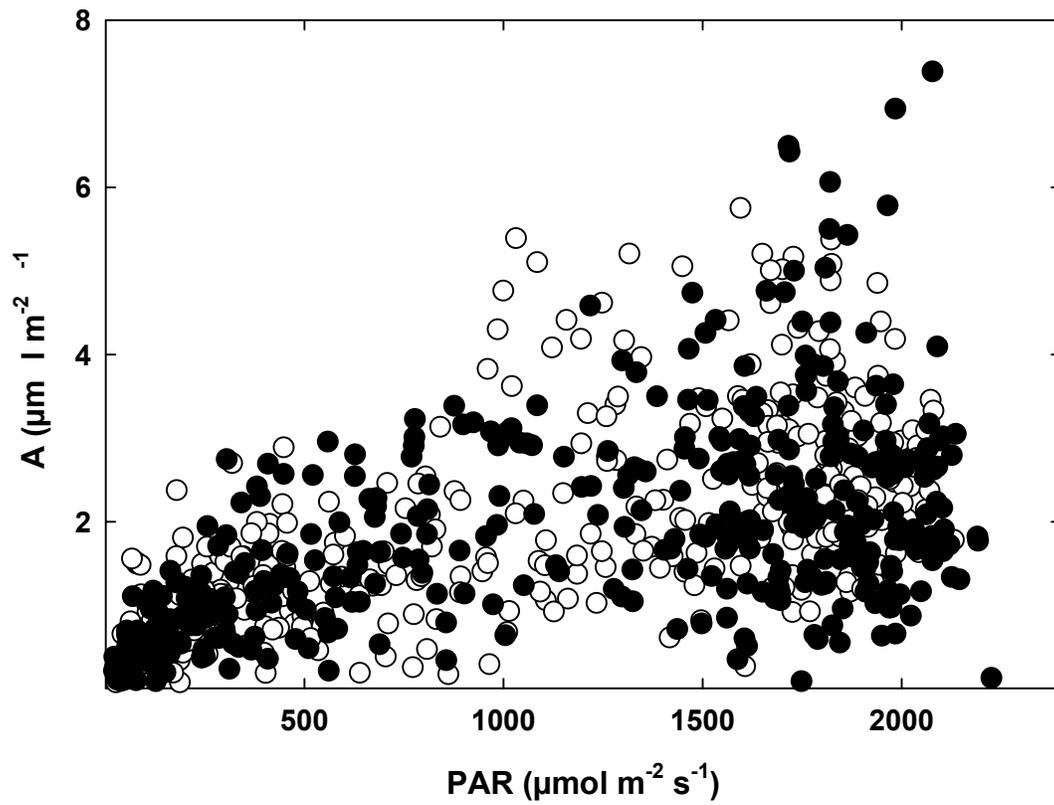


Figure 15. Mean daily photosynthesis (A_{\max}) and mean daily PAR (PAR_{\max}) for *A. lasiocarpa* (open symbols) and *P. engelmannii* (closed symbols) at all study sites throughout the 2002 growing season.

during the 9/20 – 9/22 measurements and showed a positive correlation between low nighttime temperature and increasing A_{\max} the following day (Figure 16). Xylem water potential (ψ) remained below 1.3MPa during the entire measurement period and there was no significant correlation between A and ψ for either *A. lasiocarpa* or *P. Engelmannii* at any of the three sites across the treeline ecotone (Figure 17).

A versus C_i and g

For both *A. lasiocarpa* and *P. engelmannii* at the FS, TS, and AS the C_i decreased throughout the season independently of A , with the most dominant trend occurring at AS (Figures 18, 19, and 20). At AS, relatively stable A values occurred throughout the entire summer, while C_i decreased through the summer until the final measurement period in September when C_i values returned to early summer levels at TS and FS, respectively (Figure 20). Stomatal conductance (g_s) showed the strongest decrease at the AS, while FS and TS g_s followed similar patterns to the A trends through the season. The linear relationship of A and g_s was evident throughout the growing season at all sites, e.g. at AS (Figure 20). Table I lists the r^2 and slope values for linear regressions at all sites through the season for the data represented. The r^2 values for the A versus g_s plots were typically higher throughout the season and across all sites than those for the $A:C_i$ regressions (Table II). Combining gas-exchange data for all three sites (FS, TS, and AS), the $A:C_i$ ratio increased through the growing season. The AS had the steepest slope, followed by the TS and FS respectively. Linear regressions for the FS, TS, and AS data were calculated as follows, (FS) $y = 0.00004x - 3.748$, $r^2 = 0.724$; (TS) $y = 0.0002x - 7.122$, $r^2 = 0.642$; (AS) $y = 0.0003x - 10.461$, $r^2 = 0.944$ (Figure 21).

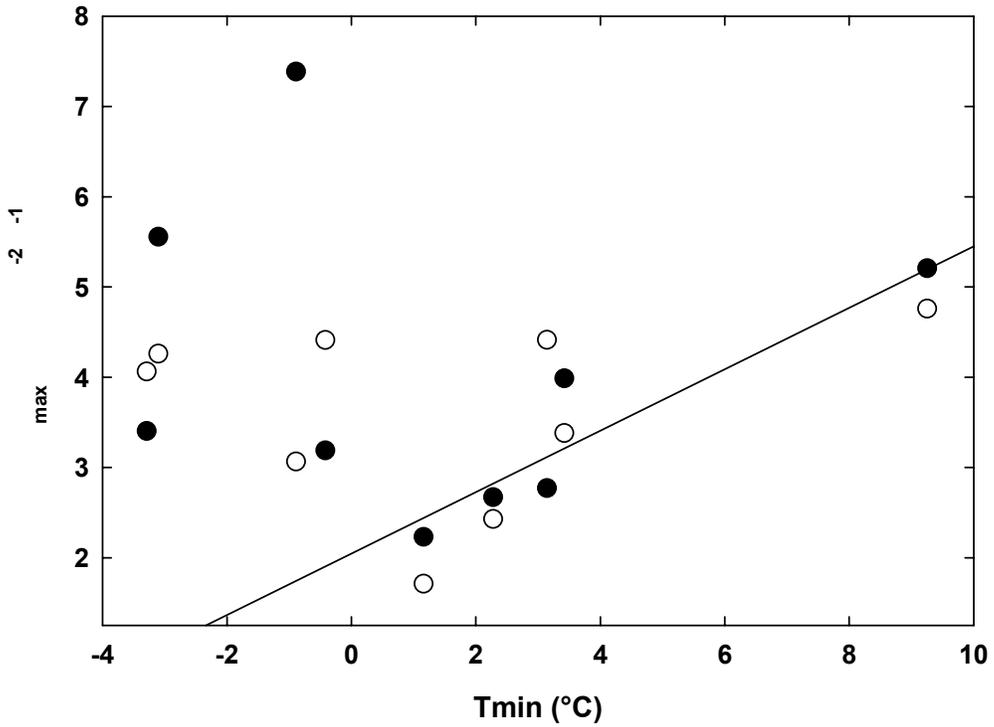


Figure 16. Maximum daily photosynthesis (A_{\max}) and previous night's minimum temperature (T_{\min}) in *A. lasiocarpa* (open symbols) and *P. engelmannii* at study sites FS (circles), TS (squares), and AS (triangles) through the 2002 growing season. Linear regression for temperatures above 0°C, equation: $y = 0.3405x + 2.0456$, $r^2 = 0.7308$.

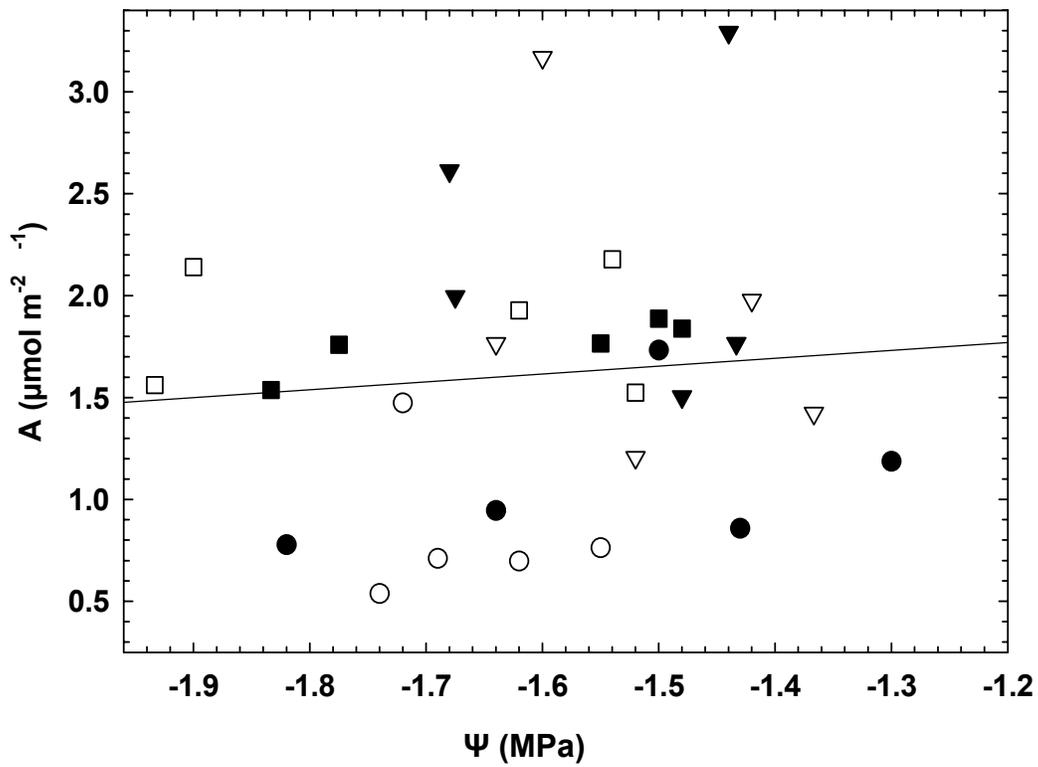


Figure 17. Maximum daily photosynthesis (A_{max}) and xylem water potentials (ψ) for *A. lasiocarpa* (open symbols) and *P. engelmannii* at study sites FS (circles), TS (squares), and AS (triangles) through the 2002 growing season. Linear regression for all data points, equation: $y = 0.3864x + 2.2337$, $r^2 = 0.0082$.

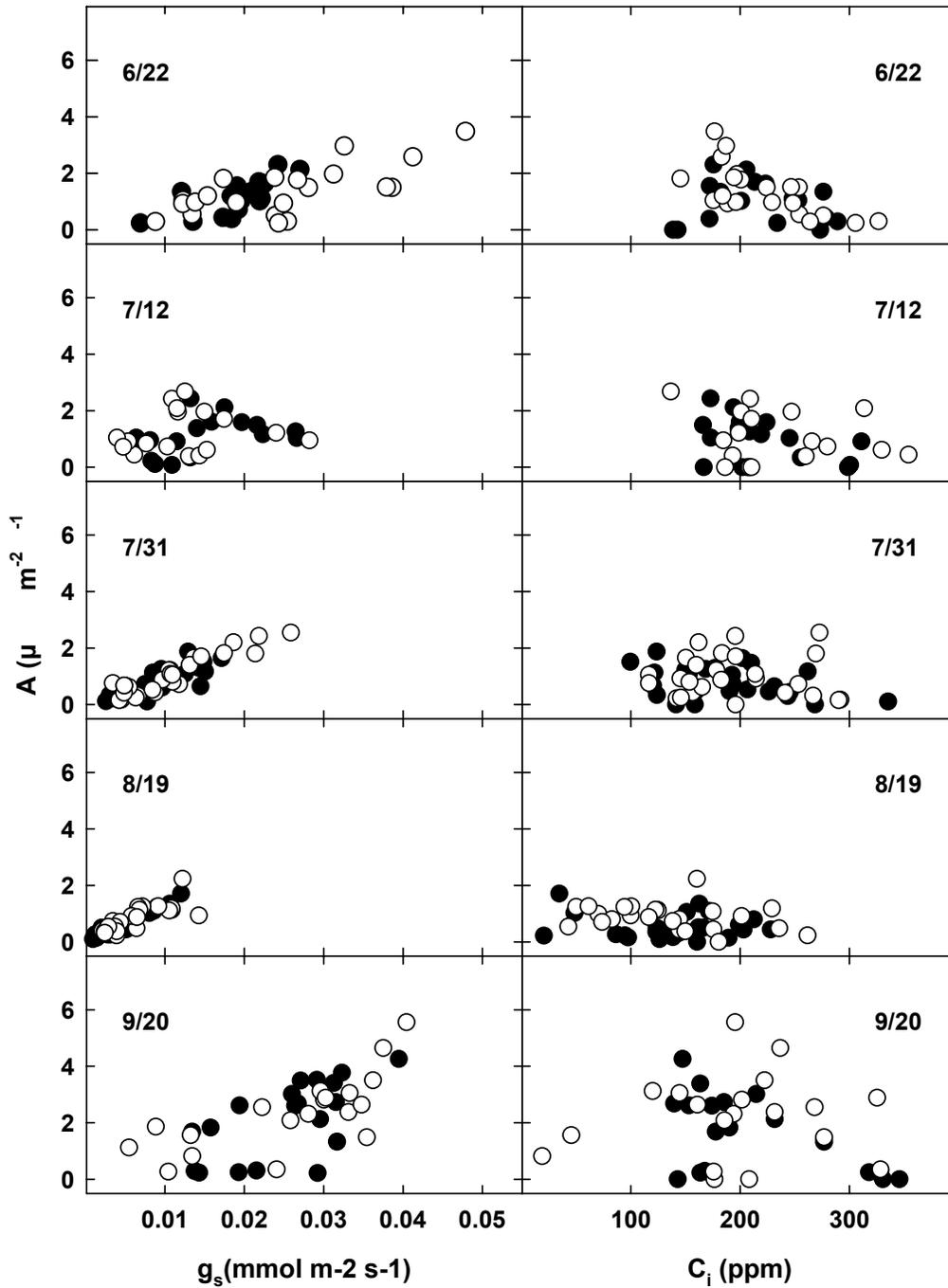


Figure 18. Daily photosynthetic measureasurmMopen

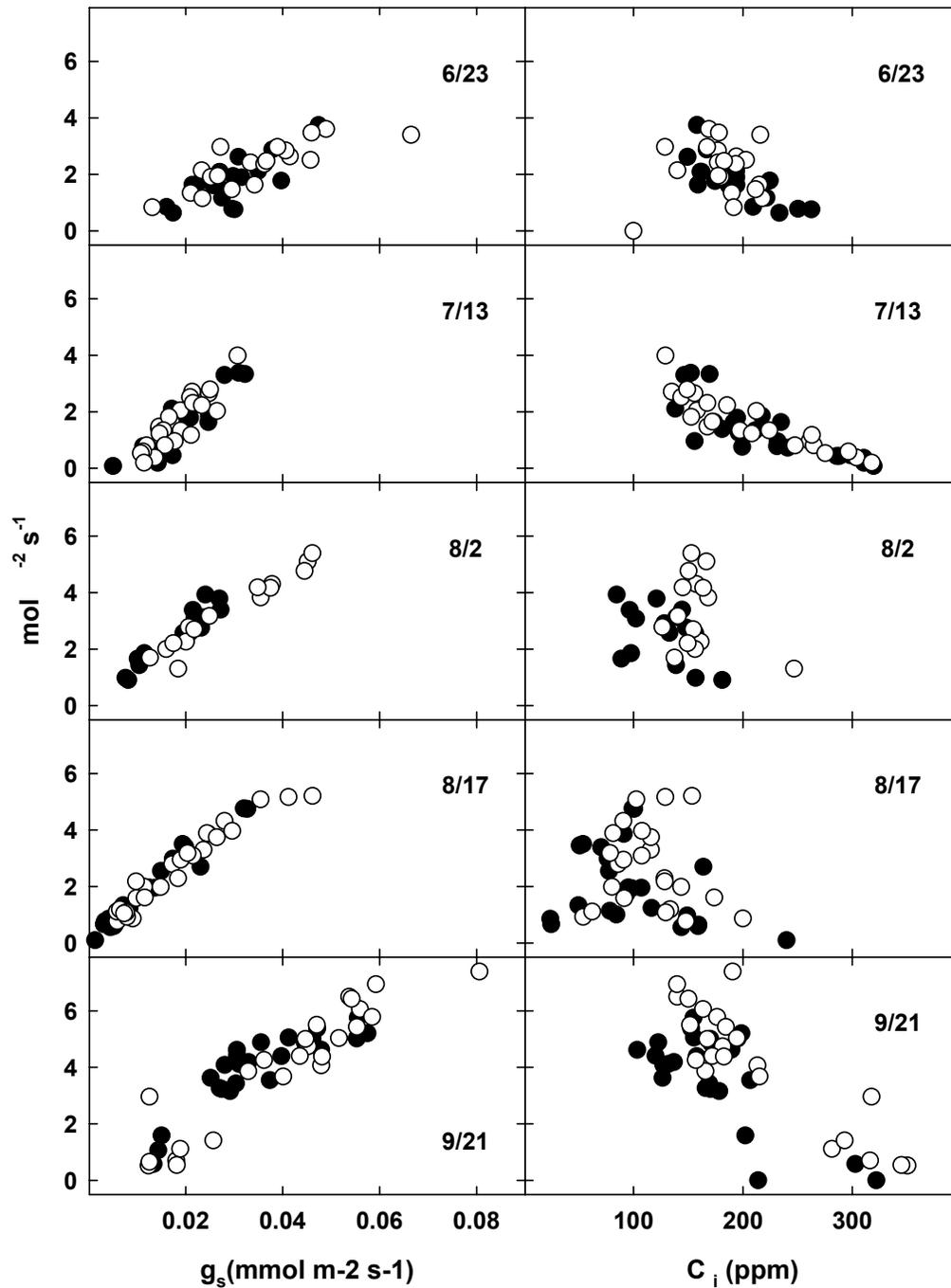


Figure 19. Daily photosynthetic measurements and stomatal conductance (g_s) and intracellular CO_2 concentration (C_i) for *A. lasiocarpa* (open symbols) and *P. engelmannii* (closed symbols) for five study periods (6/26, 7/17, 7/30, 8/18, and 9/23) at the TS.

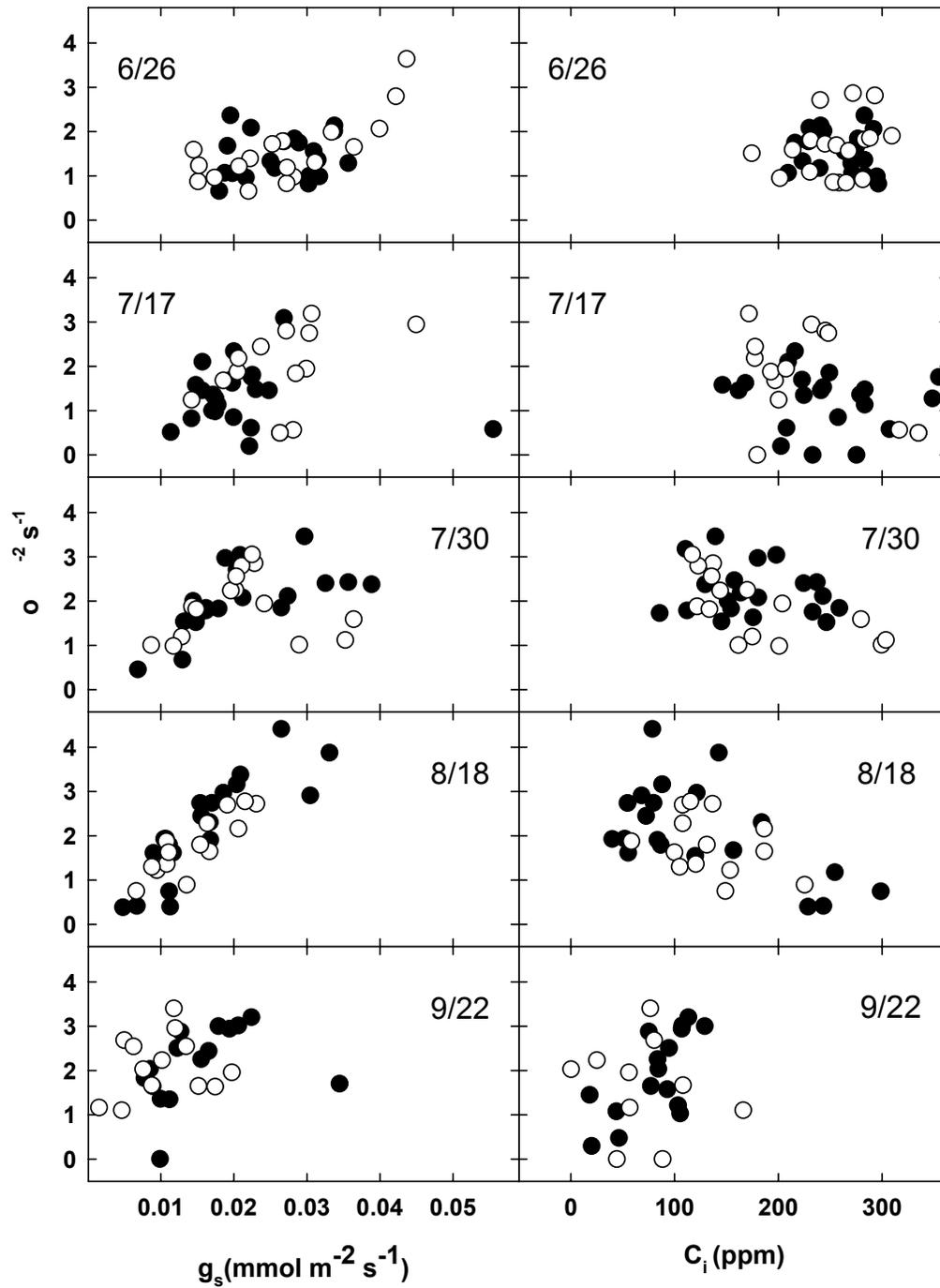


Figure 20. Daily photosynthetic measurements and stomatal conductance (g_s) and intracellular CO_2 concentration (C_i) for *A. lasiocarpa* (open symbols) and *P. engelmannii* (closed symbols) for five study periods (6/26, 7/17, 7/30, 8/18, and 9/23) at the AS.

A / g_s

23-Jun

17-Jul

30-Jul

18-Aug

22-Sep

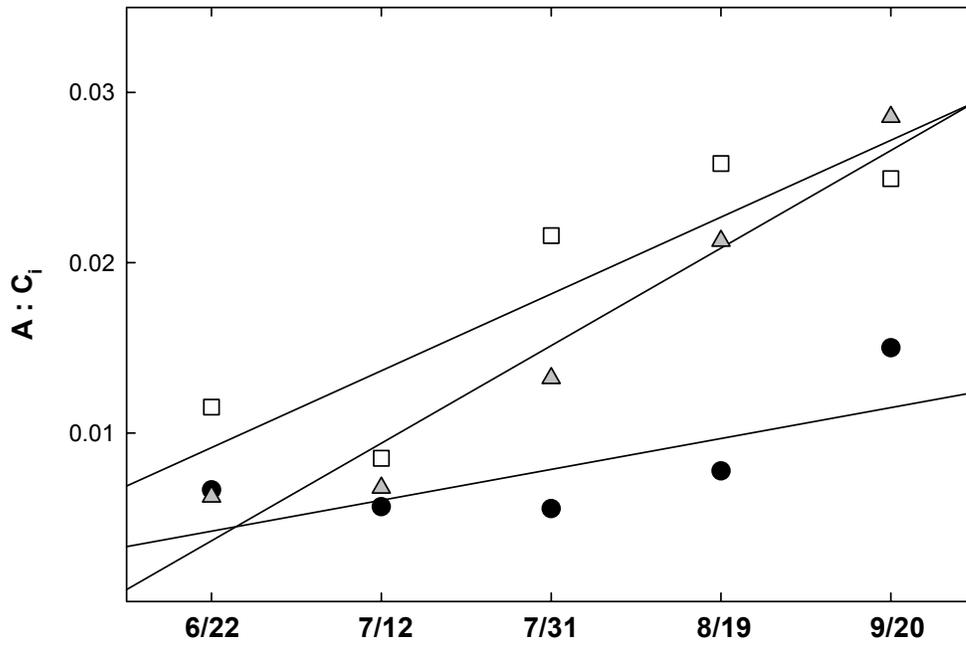


Figure 21. Mean daily photosynthesis (A) to intracellular concentration of CO₂ (C_i) ratio (A:C_i) for FS (closed circle), TS (open square), and AS (grey triangle). Solid lines represent best fit linear regressions.

Discussion

Environmental stresses, particularly those of the abiotic category, appear to be the mechanistic basis for treeline stability and may be closely associated with changes in global atmospheric conditions. How abiotic environmental factors differ across an elevational gradient can offer insight into how future global change (e.g. warming) may impact different species, yielding solutions to foreseeable problems resulting from the predicted changes in distribution patterns of lower elevation species. Species found currently at their upper elevational limit (treeline ecotone) may act as harbingers to changes that will eventually occur in similar species much lower in elevation (subalpine forest). More specifically, an understanding of the stability of the alpine timberline may be important for predicting future changes in global biodiversity because alpine areas could be threatened by the encroachment of the subalpine forest below, as suggested by most global change scenarios (Moir et al. 1999, Jobbagy and Jackson 2000, Paulsen et al. 2000, Rupp et al. 2001, Grace et al. 2002). Warmer air temperatures coupled with increasing atmospheric CO₂ concentrations could provide increasingly favorable conditions for the advance of subalpine forest into the treeline ecotone, rendering current alpine regions uninhabitable for many niche-specific species (Messerli and Ives 1997, Luckman and Kavanagh 2000).

The 2002 growing season in the Snowy Mountains of Southeastern Wyoming was marked by, the seventh most severe drought in over 100 years (WY state mean for April – September 210mm, where 2002 reported ~150mm) (NOAA Drought Information Center). The effects of this drought were reflected in the low xylem water potentials (ψ) in adult trees of *A. lasiocarpa* and *P. engelmannii* throughout summer, particularly during

early summer. Considering values reported for years with more typical precipitation (see Smith 1985 for review; Carter and Smith 1988), a rather severe limitation to photosynthetic carbon gain due to low water availability was apparent for the summer of 2002. Carter and Smith (1988) reported mean maximum photosynthesis values for *P. engelmannii* of 1.1 ± 0.4 , 1.6 ± 0.5 , and 4.2 ± 0.9 respectively, and for *A. lasiocarpa* 1.5 ± 0.6 , 2.1 ± 0.5 , and 4.0 ± 1.4 , respectively, for measurements taken within an understory forest, forest gap, and a disturbed south-facing site that had been “clear-cut” 16 years prior. Trees sampled during this study at a similar time period had approximately 50% lower photosynthesis compared to values for the saplings in Carter and Smith (1988). The effects of the 2002 drought can also be seen when comparing values for the same tree species during a year with above nearly average rainfall (Carter et al. 1988), where mature trees of *A. lasiocarpa* and *P. engelmannii* at similar elevations had g_s values up to three times those measured during the summer of 2002. This unique situation enabled a comparison of the gas exchange responses of *A. lasiocarpa* and *P. engelmannii* to drought stress under an otherwise typical environmental regime of sunlight and temperature (Smith 1985; Carter et al. 1988).

As documented above, the primary factor generating the relatively low photosynthesis for both species at all three sites was most likely the influence of low water status generated by a low annual snowpack recorded for the 2001/2 winter. In contrast to virtually all studies of seasonal photosynthesis in subalpine conifer trees, the lowest values of A occurred at the beginning of summer, and corresponded to the lowest water potentials measured for the entire summer. Also, A values for both *P. engelmannii* and *A. lasiocarpa* recovered only to the early summer values characteristic of normal

precipitation years by the end of August. Because ψ remained low throughout the entire season, neither species were able to approach the maximum photosynthetic capability reported for years with closer to normal precipitation. Moreover, no significant relationship between maximum photosynthetic values and threshold ψ values were observed (Figures 6 & 12). Thus, a lack of water availability appeared to be the major limiting abiotic factor during the summer of 2002 based on comparisons of identical values for the same species on previous years with more normal snowpack.

Despite the general depression in A due to low winter snowpack, differences in photosynthetic values did vary between the three sites across the treeline ecotone. FS trees had the lowest A values throughout summer, which also corresponded to the lowest PAR and PAR_{int} values. A values remained fairly stable throughout summer, except for somewhat greater values measured during the final sample period in September that was preceded by a significant precipitation event. Both TS and AS measurement trees received similar amounts of incident PAR throughout the season and approximately 1.3 times more than the trees measured at FS. Thus, PAR appeared to be a potentially significant limitation to photosynthesis at FS compared to TS and AS, despite the strong overall limitation induced by drought at all sites. Sunlight penetration into the FS canopy is also dependent on the intensity and quality of light received (Smith et al. 1989). Previous studies in the Snowy Mountains have shown that approximately 40% of days during the growing season were “cloudy,” thus decreasing the amount of direct sunlight and increasing the amount of diffuse sunlight (Young and Smith 1983, Johnson et al. 2003). Similar results were found in this study, where cloudy days yielded ~48% less PAR than sunny days (Figures 4 and 5). Therefore, cloud cover further compounds the

light limitations experienced by trees at the FS. Sky exposure therefore could be limiting in different ways depending on location in the alpine. Trees at FS received less *PAR* due to self shading, a distributional pattern that inherently decreases sky exposure. AS trees, however, are grouped into smaller islands with shorter stature, as well as being further apart from neighboring tree islands than at TS. This situation of increased sky exposure does not limit *PAR* received, but does increase night time sky exposure, leading to increased long wave radiation loss at night. Increased sky exposure is known to negatively affect alpine plants, especially in respect to low temperature photoinhibition (Germino and Smith 1999). Trees at the TS have the contiguous forest to block a significant portion of early morning sunlight, which can be the most damaging due to cold needle temperatures. Trees at FS and TS are able to increase needle temperature during the morning hours without suffering from intense morning sunlight, but the TS tree islands allow for full exposure to afternoon sun that FS trees are partially shaded from.

Mean photosynthesis generally increased in correspondence with increasing incident *PAR* levels at all sites (Figure 15). However, FS had the highest correlation between PAR_{\max} and A_{\max} ($r^2 = 0.162$), followed by AS and TS ($r^2 = 0.144$ and 0.091 , respectively). Therefore, A_{\max} at FS appeared to be the most affected by increasing PAR_{\max} , and the same trend occurred for instantaneous *A* and *PAR* (Figure 15). While receiving extremely similar *PAR* levels through the season on an integrated scale, TS and AS still showed differences in daily mean photosynthesis. The high levels of incident sunlight at these two sites and the low correlation between A_{\max} and PAR_{\max} suggests that

some factor other than light and water may have been responsible for the observed differences in A .

Differences in daily photosynthetic carbon gain at the two highest sites (TS and AS) appeared to be, at least, partially the result of significant early morning reductions in photosynthesis, possibly due to photoinhibitory effects (Figure 14). Trees of both species at TS and AS received similar amounts of total PAR for the season, but due to morning shading by other tree islands and the contiguous forest located approximately 30 m to the east, trees at TS received less PAR during the early morning hours. In addition, T_{leaf} was typically greater at FS, followed by trees at TS and then AS (Figure 4). Thus, the early morning depression in A may have been due to the combination of lower nighttime leaf temperatures, combined with higher incident sunlight levels in the morning (low-temperature photoinhibition, Germino and Smith 1999).

Variations in seasonal and daily soil temperatures probably had little effect on carbon gain at each site, even though soil temperatures are inherently coupled to air temperature to approximately 30cm in depth; root mass in these two species is typically limited to the top 20cm of soil. As noted above, morning A measurements typically showed some of the greatest differences between sites. Soil temperatures also show large differences in the mornings, particularly between the TS and AS (Figures 7 and 8). Early in the season (7/12) TS and AS trees showed similar A values, and T_{soil} at the AS was ~2.5 degrees warmer than the TS (Figure 7). Later in the season (9/20), however, when TS trees had much higher A , T_{soil} at AS was lowest through most of the day. Conversely, carbon gain at the AS increased only slightly through the season, while T_{soil} dropped

nearly 10 degrees during the course of the growing season. TS trees also showed the greatest carbon gain during the end of the season, when soil temperatures were coldest.

Transpiration and water use efficiency

Both species at all three sites had decreasing E throughout summer (Figure 13), although AS plants had the greatest decline, followed by TS and FS trees. E was least at FS, except for the 9/20 sampling period, and these lower E values were most likely due to the lower incident PAR values. These air and leaf temperature data support the idea that E and PAR are often related. Moreover, needle warming can be directly traced to high altitude shoot morphology, where *A. lasiocarpa* and *P. engelmannii* typically have higher needle aggregation (Ninnemets et al 2001), enabling these species to uncouple their photosynthetic organs from the low air temperatures, without suffering declines in photosynthesis due to inadequate light interception (Smith and Carter 1988).

Higher PAR and T_{air} to T_{leaf} differences could account, at least partially, for the higher E values measured at TS and AS. The decreasing E trend throughout the summer for all sites can be attributed to the decreasing T_{air} seasonal trend. FS T_{air} increased from the 6/22 – 7/12 sample period, however this increase was also marked by an increase in E , whereas trees at both TS and AS both showed decreasing T_{air} and E throughout the season. This increase of T_{air} also resulted in increasing leaf to air vapor pressure deficit ($LAVD$) at FS (Figure 9). Changes in E are driven by vapor pressure deficits from the leaf to the air, where internal leaf relative humidity is assumed to be 100%. Due to the temperature dependent response of water vapor pressure in air, at higher temperatures, ambient air generally has a higher vapor saturation point than cooler air (List 1971). As

leaves or needles become increasingly warmer, ambient air is able to become more saturated; therefore transpiration generally increases to the expense of the tree in terms of water loss, thus causing stomatal closure. Increased $LAVD$, in comparison to TS and AS, during the middle of the growing season most likely compounded the lower light availability limitations to further decrease photosynthetic capacity.

During the extreme drought of summer, 2002, WUE gradually increased for both species at all three sites, and especially at AS near the end of the summer growth period. The consistent ψ values recorded for both species indicate significant water stress, although these intermittent measurements of ψ may not reveal possible short-term responses to the sporadic precipitation events that occurred throughout summer. Regardless, increases in WUE were due to the relatively constant A , but decreasing g_s . For example, the increase in photosynthesis on 9/20 at FS and TS was greater than the previous sample period (8/19/02). Possibly, the colder T_{air} , T_{leaf} , and T_{soil} occurring at AS around mid-September could have limited the potential increases in A in response to continued rainfall. Therefore, AS trees had higher WUE , but at some cost to photosynthetic carbon gain. Thus, although WUE for both species at AS had the greatest increase from the 8/19 to 9/20 sample periods, photosynthesis did not respond to summer rainfall as well as the two lower, less exposed sites.

A, g_s , and C_i

The ability of trees to regulate gas exchange through regulation of stomatal aperture inherently affects the amount of CO_2 available to mesophyll cells. Increasing stomatal conductance and therefore reduced resistance to gas exchange at the stomatal

pore, allows for CO₂ to diffuse from higher concentrations (ambient air) to lower concentrations (intercellular air spaces within the leaf or needle). Mesophyll cell health and activity will determine the basic demand for CO₂ in the cells by reducing the intercellular CO₂ concentration, thereby creating an increasing gradient between internal and external air. If mesophyll cells continue to incorporate CO₂ into photosynthesis, then C_i will decrease. Stomata are generally more responsive to light than other abiotic influences, and respond to increasing *PAR* levels by increasing aperture to compensate for increased leaf heating, leading to increased *E*, and increased mesophyll demand for CO₂, as photosynthesis generally increases with increasing *PAR*. Therefore, mesophyll demand for CO₂ and stomatal aperture are not necessarily directly linked. The goal for plants and trees then is to optimize the ratio of *A* to *E*, essentially keeping the ratio relatively constant. Fluctuations in this ratio will lead to either high water loss or low photosynthetic carbon gain (Cowan and Farquhar 1971).

Internal CO₂ concentration (C_i) in *A. lasiocarpa* and *P. engelmannii* varied throughout the growing season, a similar pattern at all three sites, showing a decreasing trend through the season (Figure 13). Observations reveal that FS and TS trees had similar trends in CO₂ sink demands (mesophyll cells), based on nearly identical C_i trends through the season, despite their environmental altitudinal differences (including T_{air} , T_{leaf} , T_{soil} , and *PAR*). Albeit the trends were similar, the TS reported lower C_i values throughout the season, due to higher ratio of g_{st} to mesophyll conductance. Past research has shown that C₃ plants grown in low light conditions generally require a higher C_i to offset a lower mesophyll conductance, and those grown in warmer temperatures also require higher C_i (Bauer et al. 1983). As described above, FS trees of both species

showed consistently warmer temperatures and lower PAR throughout the growing season, suggesting a demand for higher C_i . The AS plants had similar T_{air} and T_{leaf} during the June measurement, but from that point on, AS values for T_{air} and T_{leaf} values were lower (Figure 5). The linear decrease in C_i of AS trees through the season suggests that trees at this site were influenced more by stronger decreases in T_{air} , T_{leaf} , and seasonally decreasing PAR . While AS was equally warm (T_{air}) with correspondingly higher T_{leaf} values (6/22), C_i values were as high as the FS and TS, but through the rest of the season (7/12 – 9/22), the T_{air} at AS was considerably lower than the two lower elevation sites, supporting a lower C_i requirement for potential A given the environmental parameters. AS *P. engelmannii* showed a slight increase in A , while *A. lasiocarpa* showed a slight decrease in A for the 9/20 sample period.

However, seasonal decreases in C_i at all sites, did not appear to be directly related to changes in A , as mean A values changed only slightly through most of the season at FS and AS. Instead, increases in stomatal conductance (g_s) appeared to be more tightly correlated with increasing A , especially at TS (Figure 12, Table I, and Table II). Decreasing g_s throughout the season at AS was coupled by decreasing C_i and E , as well as experiencing the lowest T_{air} , suggesting that AS trees of *P. engelmannii* and *A. lasiocarpa* were more tightly coupled physiologically to the environment than either TS or FS trees. Therefore, at the highest elevation trees may be more affected photosynthetically due to stomatal limitations than other non-stomatal limitations. September measurements of C_i and g_s (9/20-22) at all sites appeared to be different from those taken throughout the rest of the season. This was most likely due to the significant

precipitation event that preceded those measurements, again illustrating the severe effects of the drought.

Liukang and Baldocchi (2003) showed that *Quercus douglasii* had similar physiological responses to under extreme drought conditions as *A. lasiocarpa* and *P. engelmannii* did in this study. *WUE* in the drought stressed *Q. douglasii* increased while g_s decreased through the growing season, the same trend as seen in these two conifer species. Findings from the Liukang and Baldocchi study and Cowan and Farquhar's (1977) optimal water use theory suggests that under the most stressful conditions (such as the AS) g_s will continually decrease through the season provided no alleviation from drought stress. In the present study, while A at AS was held relatively constant through the season, g_s appeared to be sensitive to water loss, resulting in the observed decrease in g_s and C_i throughout the growing season without. Optimizing *WUE* by regulating E via g_s may be a key for maintaining sufficient carbon assimilation over the season. Despite decreasing T_{air} through the season, the high evaporative demand of the dry, windy environment at AS was most likely to have caused stomatal responses to override non-stomatal mesophyll cell demands for CO_2 (Figure 9). Trees at the less exposed TS, with higher water availability (rather than water sequestered as snow at the AS), were less limited by stomatal closure (Figure 7) i.e. g_s values were similar for both the TS and AS, while TS trees had higher A values. Correspondingly, TS trees had consistently lower C_i values than AS trees through the first four measurement periods of the summer. Thus, an apparently greater mesophyll demand (sink) for CO_2 , led to the higher A recorded for trees at TS. As seen in Table I and Table II, the A of AS trees was most tightly correlated to C_i , whereas A of TS trees was most tightly correlated to g_s . Trees at AS showed the

strongest decreases in C_i throughout the growth season while maintaining a relatively constant A , most likely due to the seasonal decreases measured for g_s . Lower C_i can be interpreted as a decrease in CO_2 availability for carboxylation in the chloroplasts of mesophyll cells (Pons and Welschen 2003). A second possibility for the higher C_i measured in AS trees, even though TS and AS had similar g_s , would be a lower mesophyll cell demand for CO_2 , implicating greater sink limitations due to greater stress in AS trees.

Results from this study therefore suggest that these two species experienced carbon uptake limitations at their furthest extent at the alpine treeline. Contrary to Körner's (2002) findings in the Swiss alpine, there appears to be CO_2 source limitations, rather than storage limitations alone due to cold soil temperatures. Carbon assimilation varied in this system with increasing altitude, and an optimal niche most likely exists for these two species somewhere along the elevational gradient, rather than deteriorating habitat quality with increasing elevation, as inferred from Körner's study.

Interspecific differences between A. lasiocarpa and P. engelmannii

Based on photosynthetic carbon gain observations alone, it was quite evident that physiological differences between *A. lasiocarpa* and *P. engelmannii* existed during this study. Figure 2 shows the interspecific and intraspecific variation observed between the sites spanning the treeline ecotone. At both FS and TS, *A. lasiocarpa* had significantly greater photosynthetic carbon gain than *P. engelmannii*. Both of these species display a unique ability to change needle and shoot morphology depending on microsite environmental characteristics. The larger tr

experienced substantially longer periods of shade during the early morning and late evening hours. During mid-morning at FS (intact subalpine forest), shoot measurements were more likely to experience self shading and shading by neighbor trees (intermittent sun-flecks or sunpatches), than at either TS or AS. Moreover, greater shade tolerance in *A. lasiocarpa* may have contributed higher carbon gain measured for this species in the lower light environment of FS (Carter and Smith 1988). *A. lasiocarpa* at the TS also had higher A , g_s , and E throughout the season, while maintaining similar WUE to *P. engelmannii*, suggesting a greater ability to respond to the TS environment. Somewhat confounding to this idea is the general trend in this area for higher spruce dominance with increasing elevation. However, these physiological trends reverse at AS, where *P. engelmannii* showed slightly higher carbon gain than *A. lasiocarpa*. The TS, therefore, may determine the successful elevational limit for *A. lasiocarpa*, where *P. engelmannii* reproductively succeeds. The differential success of these two species has also been attributed to seedling establishment and survival at high altitude, with *P. engelmannii* generally more successful in the alpine timberline areas (Germino et al. 2003). The greater abundance of *P. engelmannii* at higher altitudes is likely due to internal physiological adaptations, as well as morphological plasticity in shoot and needle structure. Seedling studies have yielded evidence that initial emergence and survival at the seedling stage may be one of the most important life stages when considering the position of alpine treeline. There still remains a void in the literature where emergent seedlings, saplings, and mature trees are compared both physiologically and ecologically.

Conclusions

1) Trees at all sites appeared to be limited photosynthetically, regardless of altitude, though in varying degrees and in apparent response to different environmental factors.

Despite low photosynthesis at all three sites in response to a severe drought, photosynthetic carbon gain appeared limited at all three sites across the treeline ecotone due to suboptimal light and temperature regimes. The lowest elevation site in the intact subalpine forest (FS), as well as the highest elevation site (AS) had lower photosynthetic carbon gain compared to the mid-elevation (TS) site. These findings suggest that trees growing in areas of increased environmental exposure are limited in their capability for assimilating photosynthetic carbon based on microsite differences and not elevation alone, even during a severe year of drought.

2) Microsite differences in sun and sky exposure at each site across the treeline ecotone limited carbon uptake differently at each site

Environmental abiotic factors (sunlight and temperature) were associated with the variance in photosynthetic carbon gain across the treeline ecotone in *A. lasiocarpa* and *P. engelmannii* in the Snowy Mountains of Southeastern Wyoming. Contrary to ideas stemming from non-structural carbon studies in the Swiss Alps (e.g. Korner 1998), all three sites were associated with substantial restrictions in photosynthetic carbon gain, both due to drought and other environmental stresses. Sky exposure (e.g. sunlight and cold nighttime skies) that was too little (FS), or possibly too much (AS), appeared responsible for the measured depressions in photosynthesis in comparison to past studies

of the same species during years with normal precipitation. Photosynthesis was reduced at the open tundra site (AS) and at the lowest elevation forest site (FS), in comparison to the highest carbon gain observed of at TS, located near the mid-portion of the treeline ecotone. These differences also corresponded to the more exposed sky conditions of AS, the least sky exposed (FS), and the intermediate TS.

3) Environmental stresses appeared to be most influential on stomatal function, rather than non-stomatal processes.

Relatively constant A values at AS indicated that g_s may be more inhibited at the highest elevation site due to colder air and soil temperatures sooner in summer (nighttime sky exposure), as evident in the corresponding decreases in temperatures, g_s , and C_i values through the season. Stomatal conductance was most tightly correlated to the greater A values at TS, suggesting that this middle ecotone intermediate sky exposure regime provided the most optimal microsite for photosynthesis in the study. Therefore, with greater exposure further into the treeline (Figure 1), along with increasing elevation, in this Rocky Mountain alpine system, conifers did not appear to be more limited in photosynthesis, a conclusion contrary to the findings of two studies with deciduous trees, one tropical and one temperate, (Cavieres et al. 2000; Richardson and Berlyn 2002). It is still necessary to test previous findings that carbon processing and storage are more limited in alpine treeline conifers compared to trees growing in a subalpine forest stand (Körner 1998, 1999). However, the results presented here show that both temperature and sunlight regimes (microsite differences) appeared to limit photosynthetic carbon

gain, even under extreme conditions of drought, rather than a direct correlation to reductions in photosynthesis due to increasing altitude.

4) Although drought effects appeared to be the primary cause of reduced photosynthetic carbon gain at all three sites across the treeline ecotone, limitations due to suboptimal sunlight and temperature regimes were also apparent.

Even though carbon gain appeared limited at all three treeline sites due to a drought-induced restriction of photosynthesis during this extremely dry year (2002), other environmental factors (temperature and sunlight regimes) also appeared associated with reductions in potential carbon gain. The current study also revealed that trees at each site may have been limited by different microenvironmental stress factors at different times of the summer growth period, and that were not associated with differences in altitude alone. Current climate change predictions suggest increased climate warming, ultimately leading to warmer temperatures, increased cloud cover and rain (Brown and McLachlan 2002). The effects of these predictions would alter both sunlight and temperature regimes that were associated here with reductions in photosynthetic carbon gain, leading ultimately to a potential encroachment of subalpine forest into the alpine zone and possible loss of alpine biodiversity.

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Wardle, P. 1968. Engelmann spruce at its upper limits on the Front Range, Colorado. *Ecology* 49:483-495.

Young, D.R. and W.K. Smith. 1983. Effect of cloudcover on photosynthesis and transpiration in the subalpine understory species *Arnica latifolia*. *Ecology* 64:681-687.

Craig R. Brodersen - Curriculum Vitae

PERSONAL INFORMATION

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D.O.B.: 6/15/1979

ACADEMIC INFORMATION

Education

2002 - Wake Forest University, Winston-Salem, NC, B.S. (Biology)

G.P.A : 3.29

Present-2002 Wake Forest University, Winston-Salem, NC, M.S.(Biology, In Progress)

MS G.P.A.: 3.65

Course Work Summary

Undergraduate Science Courses

Calculus

Intro Chemistry I, II

Organic Chemistry

Physics and Chemistry of the Environment

Intro Biology I, II

Animal Behavior

Aquatic Ecology

Biophysical Ecology

Cellular and Molecular Biology

Evolution

Physiological Plant Ecology

Tropical Ecology

Graduate Courses

Genetics

Foundations of Ecology

Plant Ecology

Community Ecology

Microscopy in the Biological Sciences

Evolution of Land Plants

Plant Physiology

Scholarships

2000 Sullivan Scholarship
2002 Sullivan Scholarship
2003 Vecellio Scholarship

RESEARCH EXPERIENCE

1999 – 2002 – Research Assistant in the laboratory of Dr. William K. Smith at Wake Forest University.

2000 Summer – Research Assistant for Dr. William K. Smith and Judson Hill – Physiological Ecology of *Artemesia tridentata*, (Shirley Basin, WY) and independent study of *Chlamydomonas nivalis* (Snowy Mountains, WY).

2002 – Leaf form and structure study in the Monte Verde Cloud Forest and surrounding Costa Rican tropical forests (Project funded by 2002 Sullivan Scholarship Award).

2002 – 03:M.S. research in the mountains of Southeastern Wyoming – Physiological Ecology of *Abies lasiocarpa* and *Picea engelmannii* – biotic and abiotic limitations to carbon gain and treeline advancement.

Publications, Posters, Presentations, and Meetings

Smith, W.K., Brodersen, C.R., Hancock, T.E., and Johnson, D.M. Integrated surface temperature measurement using heat-sensitive paint and colour image analysis. *Functional Ecology*. In Press.

2002 – ASB (Association of Southeastern Biologists) Poster Presentation, Boone, NC. – *Photosynthetic acclimation to changing light regimes in understory evergreen species of a mixed deciduous forest*.

2003 – ESA (Ecological Society of America) Abstract submitted for presentation, Savannah, GA (August 2003) - *Carbon uptake limitations in Abies lasiocarpa and Picea engelmannii across an alpine treeline ecotone*.

2003 – International Workshop on “Ecophysiology of Ecotones” Poster Presentation, Fujiyoshida, Japan . *Abiotic factors limiting photosynthetic carbon gain in Abies lasiocarpa and Picea engelmannii within and below an alpine treeline ecotone*.