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Autumn stomatal closure in six conifer species of the Central Rocky Mountains

W.K. Smith, D.R. Young, G.A. Carter, J.L. Hadley, and G.M. McNaughton
Department of Botany, University of Wyoming, Laramie, WY 82071, USA

Summary. Environmental and water relations parameters during fall were monitored for six conifer tree species common to the central Rocky Mountains growing naturally at the same location (*Pinus contorta, Pinus ponderosa, Pinus flexilus, Pseudotsuga menziesii, Abies lasiocarpa, Picea engelmannii*). Subsequent to what appeared to be the beginning of seasonal stomatal closure, leaf conductance to water vapor declined sharply following the onset of freezing air temperatures at night. A coincident rapid decline in morning xylem pressure potentials (ψ_p) also occurred which resulted in values that were considerably below afternoon ψ_p. Continuing decreases in maximum leaf conductance during the day were highly correlated with corresponding decreases in minimum nocturnal air temperatures of the preceding night. By mid-December, morning ψ_p returned to values very near afternoon ψ_p and were only slightly lower than before the onset of subfreezing nights. A preliminary model is proposed which interprets the qualitative interaction between air and soil temperatures, soil and plant water potentials, and leaf conductance during seasonal stomatal closure in fall.

Atmospheric factors which have been associated with stomatal behavior in conifers include air temperature, solar irradiance, and the leaf-to-air water vapor deficit (see Waring and Running 1976; Jarvis 1980; Kaufmann 1982a, b; Meinzer 1982a, b; Schulze and Hall 1982 for recent reviews). Recent attention has focused on the effects of cold air temperatures at night on stomatal closure the following day during spring and fall (Kaufmann 1976; 1982b; Fahey 1979). Substantial decreases in CO_2 assimilation rates following freezing nights have also been reported (Tranquillini 1957; Pisek and Kemnitzer 1968). In addition to the primary affects of solar irradiance and the vapor deficit, Kaufmann (1982b) proposed an empirical model for computing the influence of environmental factors on leaf conductance which included a term that reduced estimated leaf conductance in response to nighttime minimum temperatures that were below freezing. Numerous studies have also associated the influence of soil factors such as temperature and moisture on water status and leaf conductance in conifers during the growth season (e.g. Waring and Running 1976; Jarvis 1980; Running and Reid 1980; Schulze and Hall 1982).

The purpose of the present investigation was to evaluate environmental influences on seasonal stomatal closure in six species of central Rocky Mountain conifers. Specifically, changes in leaf conductance to water vapor and xylem pressure potentials were correlated with changes in air and soil temperatures, soil water potentials, and the leaf-to-air water vapor deficits that coincided with the onset of stomatal closure in fall. The influences of the above environmental and plant parameters were interpreted according to their interactive effects on leaf conductance. All six conifer species occurred naturally at the same study site, without any apparent differences in topography or edaphic factors.

Methods

The study site was located at an elevation of 2872 m in the Medicine Bow Mountains of southeastern Wyoming, U.S.A. (41°21′N, 106°10′W). All of the six common conifer species of the central Rocky Mountains were found at the study site, growing within a radius of about 30 m from one another. The species were *Pinus contorta* Dougl. ex Loud. ssp. *latifolia* (Engelm.) Critchfield (lodgepole pine), *Pinus ponderosa* Dougl. (ponderosa pine), *Pinus flexilis* James (limber pine), *Pseudotsuga menziesii* ssp. *glauca* Franco (Douglas fir), *Abies lasiocarpa* Nutt. (subalpine fir), and *Picea engelmannii* Parry (Engelmann spruce). Three mature individuals of each species were selected for sampling according to size (>5 m tall) and genral appearance. All plant measurements were taken on clear, seasonably mild days following at least one day of similarly seasonable conditions. Thus, if significant stomatal opening were possible at this time of year, it would be expected to occur on these days.

Air temperature and relative humidity were recorded continuously during the study period (Sept 9–Dec. 2, 1982) using a hygrothermograph (Weather Measure model H311) located in a small clearing near the center of the research site (3 m height). Although the hygrothermograph was considerably lower than canopy heights (3–6 m), air temperature readings were similar to measuremtns taken at actual shoot locations using the leaf porometer described below ($\pm 2.2°$ C, $n=66$). The hygrothermograph was calibrated weekly using a sling psychrometer. Subsurface soil water potentials and temperatures were measured at approximately 5, 10, 20, 40 cm depths at four locations using soil thermocouple psychrometers (Wescor model PT 51-05 probes and model HR-33T dewpoint microvoltmeter). Surface soil

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Offprint requests to: W.K. Smith

temperatures were measured using an infrared field thermometer (Barnes Engineering model 14-220-4). Xylem pressure potentials were measured during early morning (before 0800) and midafternoon (1300–1430) using a Scholander-type pressure chamber (PMS model 1000) for excised 10–20 cm branch tips at midcanopy height (5–8 m) that were located close to branches for which leaf conductances were measured. Determination of "end points" for xylem water exudation from the cut ends of branches were made using the precautions outlined in Kaufmann (1968). Leaf conductances to water vapor were computed based on measurements using a ventilated transient porometer with a Vaisala humidity sensor (Kaufmann and Eckard 1977) and employing the calibration procedures described by Kaufmann (1979). The porometer was calibrated for the sorption characteristics of the chamber at various humidities and temperatures. All measurements were taken at near ambient humidity and temperature levels (±7% rh and ±3.3° C) and at photon flux densities of greater than 1450 mmoles m^{-2} s^{-1}. One or two year-old needles (8–12) on sunlit branch tips were excised from branches at mid-canopy heights (5–8 m), the cut ends sealed with petroleum jelly, and forced about 1 mm into an oil-base putty for insertion into the porometer. The entire procedure for needle removal and placement into the porometer required less than 30 sec. Measurements of leaf conductance for excised versus attached needles were compared on three dates (Sept. 28, Oct. 14, and Nov. 26) and showed no significant differences at the 95% confidence level. Although leaf conductance values were corrected for known pressure and temperature effects on diffusion and expressed in units of mm s^{-1} multiplying by 40 will convert to the units recommended by Cowan (1977), or mmoles m^{-2} s^{-1}, with a ±4% error due to temperature variations (see Nobel (1983) for a detailed comparison of these computation methods). Local zone times are expressed as True Solar Time according to List (1957).

Needle surface areas within the porometer chamber were determined by computing area dry-weight relationships for each of the six species. Needle areas for 30–40 needles of each species were determined geometrically and correlated with dry weights after drying for 48 hr at 80° C. The surface area to dry weight ratios (cm^2/g) for each of six species were as follows: *P. contorta* (72.4±4), *P. ponderosa* (69.0±3), *P. flexilus* (91.9±6), *P. menziesii* (105.2±5), *A. lasiocarpa* (114.8±6), and *P. engelmannii* (75.8±5).

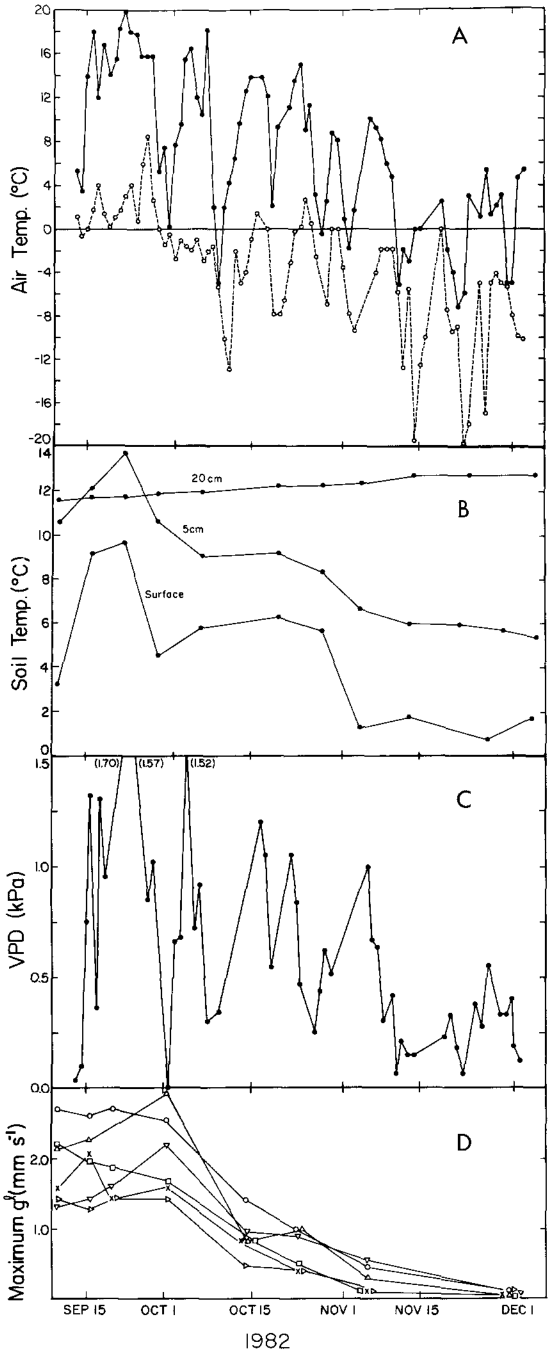

Fig. 1. A Absolute maximum and minimum air temperatures at the study site along with **B** soil temperatures, and **C** the saturated vapor pressure deficits at the time **D** maximum leaf conductance occurred during a sampled day for *P. contorta* (o), *P. ponderosa* (Δ), *P. flexilus* (□), *A. lasiocarpa* (X), *P. menziesii* (▷), and *P. engelmannii* (▽) during stomatal closure in fall, 1982

Results

During the study period numerous light rains and snowfalls resulted in consistantly high soil water potentials that were greater than −0.4 MPa at all depths sampled (5, 10, 20, 40 cm). Morning soil temperatures at 5 cm varied from near 14° C to less than 6° C while 20 cm temperatures ranged from 11.5 to 13.3° C (Fig. 1 B). Surface soil temperatures varied from about 10° C to 1° C.

There was a steady decline in maximum daytime and minimum nighttime air temperatures with highs of near 20° C and lows of slightly above freezing in September (Fig. 1 A). These values had decreased to about 3 to 4° C and below −10° C, respectively, by late November. Vapor pressure deficits of the air (VPD) measured at the maximum daytime temperature was over 1.5 kPa in September, but less than 0.5 kPa by late November (Fig. 1 C). Also, maximum VPD were strongly correlated with maximum air temperatures ($r^2 = 0.94$) throughout the study period indicating little water vapor input from the ground or vegetation sources and/or good wind mixing.

Maximum leaf conductances measured during a day were relatively high for all six species (1.2–2.9 mm s^{-1}) until early October, followed by a general decrease in all species to near 0.5 mm s^{-1} or less by mid-November (Fig. 1 D). By the end of Novmeber, maximum leaf conductances were

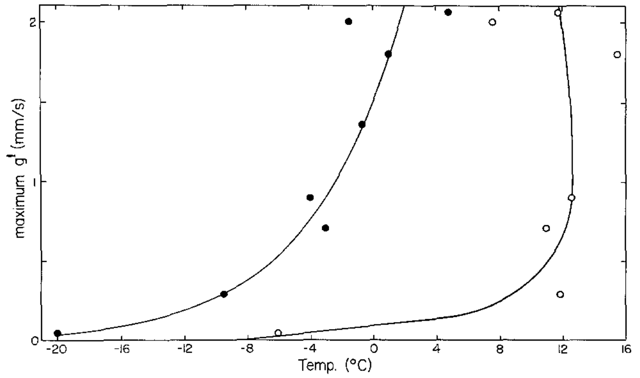

Fig. 2. Maximum daytime leaf conductances (g^1) plotted versus the previous nights minimum air temperatures (●) and the maximum air temperatures for the same day of the g^1 measurements (o)

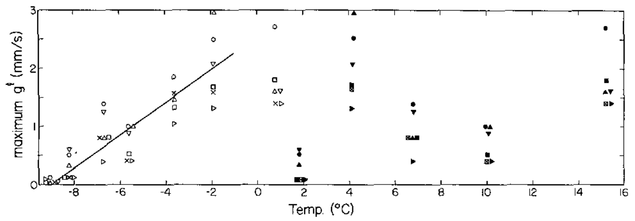

Fig. 3. Maximum daytime leaf conductance (g^1) plotted versus the absolute mean minimum air temperature for the three previous nights (closed symbols) and the mean maximum air temperature for the two previous days and same day of the (g^1) measurements (open symbols) (see Fig. 3 caption for symbol key). A regression line for the g^1 and minimum night temperature data was statistically significant at $\alpha = 0.05$ (ANOV) and generated a slope of 0.267 mm s^{-1} °C^{-1} over the temperature interval of -1.0 to $-9.0°$ C

very near zero for all six species and remained near zero on three subsequent measurement days in December. In general, *Pinus contorta* had consistently greater leaf conductances followed in order by *P. ponderosa*, *P. flexilus*, *Picea engelmannii*, *A. lasiocarpa*, and *P. menziesii*. Comparing the maximum leaf conductance measured during the day (computed as the mean of all six species) to the minimum air temperature of the previous night showed a strong and significant curvilinear relationship ($r^2 = 0.92$, $= 0.05$, Fig. 2). A similar comparison with maximum daytime temperatures for the corresponding days of the leaf conductance measurements (seasonable days) resulted in a statistically nonsignificant relationship as well as a low correlation coefficient ($r^2 = 0.21$).

Comparing mean maximum leaf conductance for each species on a given day with the mean nighttime minimum temperature for the three previous nights resulted in a stronger linear correlation ($r^2 = 0.90$, Fig. 3) than for only a single previous nights minimum temperature. The regression equation for these data predicted a decrease in maximum leaf conductance of about 0.25 mm $s^{-1°}$ C^{-1} when nighttime temperatures dropped below about $-2°$ C. A similar comparison of maximum leaf conductance with the 3-day mean maximum air temperatures during the day showed little correlation (Fig. 3).

Xylem pressure potentials (ψ_p) measured during early morning fell sharply between the Sept. 21 and Oct. 2 measurement dates for all species except *P. contorta* (Fig. 4A). The greatest decline in morning ψ_p occurred in *P. engelmannii* followed by *A. lasiocarpa* and *P. menziesii*. This sharp decline was followed by a gradual increase in morning ψ_p until, by the end of November, all six species had early morning ψ_p values that ranged from about 0.1 to 0.6 MPa less than September values. In contrast, ψ_p during the afternoon increased gradually, although with some variability, throughout the study period (Fig. 4B). Relatively large increases in afternoon ψ_p (0.8–0.9 MPa) occurred for *A. lasiocarpa*, *P. menzienii*, and *P. ponderosa* between Sept. 21 and Oct. 14.

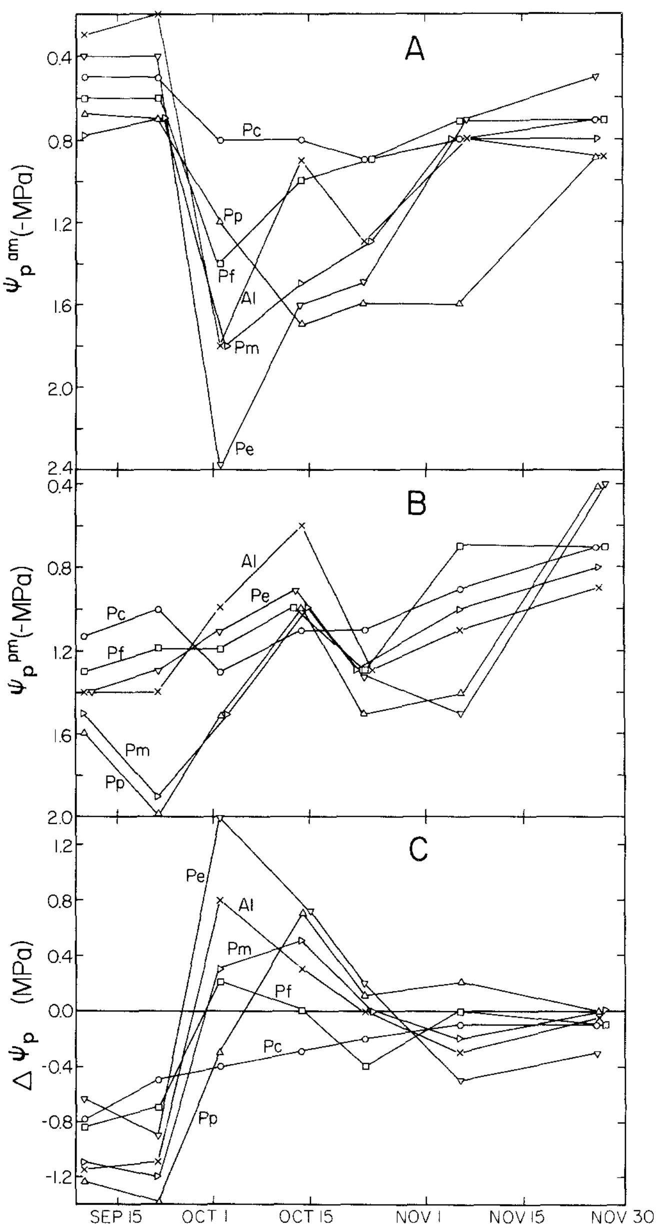

Fig. 4 A–C. Mean xylem pressure potentials measured in **A** the early morning (0700–0800, ψ_p^{am}), **B** afternoon (1200–1330, ψ_p^{pm}), and **C** the difference between afternoon and morning ψ_p the six conifer species (see Fig. 3 caption for symbol key). Positive values indicate a more negative ψ_p^{am} than ψ_p^{pm}

Subtracting the mean afternoon ψ_p from early morning ψ_p ($\Delta\psi_p$) showed that sometime between the Sept. 21 and

Oct. 2 measurement dates morning ψ_p values fell considerably below afternoon values for all species except *P. contorta* (Fig. 4C). On Oct. 2 $\Delta\psi_p$ was greatest for *P. engelmannii* (1.3 MPA) followed by *A. lasiocarpa* (0.8 MPa) and *P. menzienii (0.35 MPa). P. contorta* had a gradual increase in $\Delta\psi_p$ until the end of the study period when $\Delta\psi_p$ for all species was within −0.3 MPa of zero, indicating little differences between afternoon and morning ψ_p (Fig. 4C).

Discussion

Although all six conifer species had different values of maximum leaf conductances in early fall, similar patterns of decreasing conductances were evident throughout October and Novemeber (Fig. 1). A strong curvilinear relationship developed between the minimum air temperature at night and the maximum daytime conductance for the following day immediately following the onset of subfreezing nights (Figs. 1 and 2). Averaging the minimum air temperatures that occurred over the three previous nights resulted in a significent linear relationship between minimum nighttime air temperatures and leaf conductances (Fig. 3). Also, there were no apparent correlations between maximum leaf conductance and maximum daytime temepratures (Fig. 2 and 3) or minimum vapor pressure deficits. Early morning water status also responded dramatically to the onset of freezing nights with a major decrease in morning ψ_p (Fig. 4). For the remainder of the study period, morning ψ_p progressively increased to levels near afternoon ψ_p.

Kaufmann (1982a, b) proposed a phenomenological model of conifer leaf conductance which incorporated solar irradiance and the vapor deficit between the leaf and air as primary environmental factors. Temperature and water stress were considered secondary, but seasonally important factors. More specifically, Kaufmann (1982b) reported significant reductions in leaf conductance during late summer following nighttime minimum air temperature below about 4° C. Kaufmann (1976) and Fahey (1979) reported a similar relationship between conifer leaf conductance and nighttime air temperatures in early spring. Also, Walker and Zelitch (1963) and Drew and Bazzaz (1979) found that cold nights lead to decreased leaf conductance in broadleaf species.

To our knowledge, no investigators have attempted to develop an interactive model of environmental constraints on stomatal opening during the seasonal transition periods of Spring and Fall. These transition periods may be especially important to high elevation species where a large portion of the total growth season may overlap these periods. According to the results presented here, decreases in leaf conductance as well as major decreases in morning ψ_p (above afternoon ψ_p) for all six species occurred to varying degrees after the onset of freezing nights in early Fall. Afternoon ψ_p was considerably more variable among the species, but increased gradually over the study period. Also, morning ψ_p gradually increased to levels that were only slightly lower than before the onset of freezing nights. The onset of subfreezing nocturnal air temperatures and the coincident changes in ψ_p would be expected to potentially influence stomatal behavior. Based on the above data and the findings of other investigators, we have proposed an interactive system for environmental influences on seasonal stomatal closure which is illustrated schematically in Fig. 5.

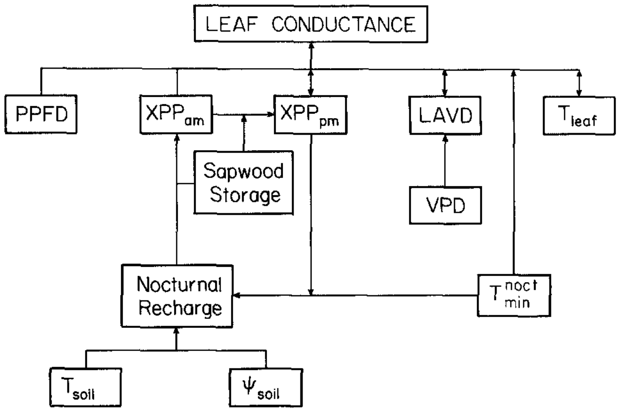

Fig. 5. Primary interactions between plant and environmental factors that have been identified in the literature (see text) and may have strong influences on leaf conductance during stomatal closure in Fall. Environmental factors: photon flux density, PPFD; vapor deficit of the air (VPD) and from the leaf-to-air (LAVD); leaf temperature minimum air temperature at night (T_{min}^{noct}); soil temperature (T_{soil}) and water potential (ψ_{soil}). Plant parameters: xylem pressure potential in the morning (ψ_p^{am}) and afternoon (ψ_p^{pm}); sapwood water storage; leaf temperature; nocturnal recharge mechanisms for water uptake

According to this interpretation, leaf conductance is influenced by the now well known effects of solar irradiance; soil and plant water status; leaf-to-air vapor deficit (LAVD); and effects due to air, leaf, and soil temperature variations, all of which have been previously reported for numerous species besides conifers (See Schulze and Hall 1982 review). However, we have now included an interactive interpretation of the observed changes in leaf conductance for the seasonal transition period in early Fall. As freezing nights begin to occur, there appears to be a documented, direct effect on stomatal opening the following day (Walker and Zelitch 1963, Kaufmann 1976, Fahey 1979, Drew and Bazzaz 1979), but also a possible indirect influence via decreases in morning ψ_p (Fig. 5). This decrease in morning ψ_p may be due to an inhibition of sapwood water movement during the night which may be linked to the cold temperature of the above ground tissue. Zimmerman (1964) found that stem temperatures below about −2° C stopped the ascent of sap in conifers. As indicated in Fig. 5, a similar reduction in soil water uptake by the roots may also occur when soil temperatures are low (Kaufmann 1975, Dalton and Gardner 1978, Running and Reid 1980, Teskey et al. 1983). Other recent work has found a strong correlation between maximum daily leaf conductance and soil temperatures for *A. lasiocarpa* and *P. engelmannii* growing at high elevations (Carter et al. 1984). Leaf conductance during the summer increased dramatically to maximum values during mid-August at the same time warming soil temperatures at 25 cm approached 7° C. A similar value of near 7° C was found to be near a limiting threshold for root resistance to water uptake in *P. engelmannii* (Kaufmann 1975). Running and Reid (1980) also observed an approximate 7° C threshold for increased root conductance to water uptake in *P. contorta* seedlings. Recently, Teskey et al. (1983) reported that cold root temperatures resulted in stomatal closure that was independent of leaf water potential in *Abies amabilis.*

Referring again to Fig. 5, the indirect effects of soil temperature and soil water potential on nocturnal water recharge and, thus, morning ψ_p may be mediated somewhat by the capacity for water storage in the sapwood and the leaf conductance and transpiration rate of the preceeding day. Running (1980) estimated that sapwood water storage in *P. contorta* could support about 0.6 hr of maximum transpiration and 4.7 hr of minimum transpiration. Leaf conductance is a primary determinant of the afternoon ψ_p, but may also influence the following morning ψ_p, depending on the capacity for nocturnal water uptake. Thus, leaf conductance may have a primary influence of afternoon ψ_p, while air and soil temperatures may have a more direct influence on morning ψ_p. Differences among species in sapwood water storage capabilities could also exert an important influence on maximum leaf conductance values and ψ_p, especially afternoon ψ_p (Waring and Running 1978; Running 1980).

Applying the interactions in Fig. 5 to the data presented in Figs. 2–4 provides a possible interpretation of the primary environmental factors that may be influencing seasonal stomatal closure during Fall, and, possibly, seasonal stomatal opening in Spring. With the onset of near freezing nighttime air temperatures, water movement in the xylem may have been restricted in above-ground tissue which led to the concurrent decreases in morning ψ_p. However, the ensuing decreases in leaf conductance in response to the cold nighttime air temperatures and the lower morning ψ_p, gradually led to a return of higher morning ψ_p and, thus, more similar morning and afternoon ψ_p (Fig. 5). The gradual increase in afternoon ψ_p would be anticipated as a result of the decreasing leaf conductance values during the day.

The contribution of cold soil temperatures to the sharp decrease in leaf conductance and ψ_p during the first part of October (Fig. 1 and 4) may have been secondary to cold air temperatures. At 5 and 20 cm depths, freezing soil temperatures did not occur during the study period, and temperatures of near 7° C did not occur until after Nov. 4 (Fig. 1 B).

Although the influence of cold soil temperatures and low soil water potential may have not been of primary importance, due to the relatively warm and wet soil at this lower elevation site, these factors may be of greater importance at higher elevations and more normal precipiation summers than occurred in 1982. At higher elevations in the forest, cooler soil temperatures may be more of a limiting factor and soil water potential less due to increased snowpack. In contrast, stomatal behavior for species growing in windy, exposed areas such as found in timberline zones may experience considerably greater soil moisture stress due to a lack of surface snow accumulation, while soil temperatures would be warmer due to greater insolation.

Soil temperatures at root depths could be expected to lag behind air temperature variations in both the warming period in spring and the cooling trend of fall. Thus, influences of less than optimal soil temperatures on stomatal conductance may be prolonged in spring, but minimal in fall when cold air temperatures are the primary cause of permanent stomatal closure. More infomration is needed which correlates any apparent threshold or graded changes in leaf conductance in response to seasonal air and soil temperature patterns.

Again, because trees living at particularly high elevations may experience a large part of their growth season in the transitional states of breaking and entering winter dormancy, the seasonal model depicted in Fig. 5 may actually describe the stomatal behavior and water relations of a large portion of their growth period. Moreover, specific differences in their stomatal responses to environmental conditions in spring and fall could lead to such important differences among species as total seasonal carbon gain during an already abbreviated growth season.

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