Summer Water Relations of <u>Abies</u>
<u>lasiocarpa</u>, <u>Picea</u> <u>engelmannii</u>, and <u>Pinus</u>
<u>contorta</u> at Higher and Lower Elevation
Sites in Southeastern Wyoming

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# TABLE OF CONTENTS

Acknowledgements

# INTRODUCTION

Recent studies on conifers of the western United States have examined the effects of several environmental factors on plant water stress and leaf conductance to water vapor loss. It has been demonstrated that with high soil moisture and overnight temperatures above 4 C, stomatal conductance for Engelmann spruce (Picea engelmannii Parry ex Engelm.), subalpine fir (Abies lasiocarpa [Hook.] Nutt.) and lodgepole pine (Pinus contorta Engelm.) is a function of photosynthetically active radiation (Kaufmann, 1982a), leaf-to-air absolute humidity difference (Kaufmann, 1982a), and saturation vapor deficit of the air (Running, 1980a). Running (1980a) also found that at leaf water potentials below -1.8 to -2.0 MPa, stomatal conductance was reduced in lodgepole pine. Moreover, Kaufmann (1982b), Fahey (1979), and Smith et al. (unpublished data) observed significantly reduced conductances following near-freezing or subfreezing nights.

In southeastern Wyoming, Engelmann spruce-subalpine fir forests range from approximately 2900 m elevation to timberline at about 3350 m. With increasing elevation, solar irradiance, mean leaf-to-air temperature differences, and diffusivity of water vapor increase, while mean air temperature decreases (Smith and Geller, 1979). With these factors in mind, the purpose of the present study was to determine changes with elevation in stomatal conductance to water vapor loss of Engelmann spruce and subalpine fir, with comparisons to lodgepole pine. The study was conducted to facilitate the application of a physiologically-based hydrologic model to spruce-fir forests in Wyoming.

METHODS

The lower elevation study site (2860 m) was a mature mixed stand of lodgepole pine, Engelmann spruce, and subalpine fir. Two trees each of the three species were chosen for conductance measurements. Selected trees were located on a somewhat level portion of a slightly southeasterly-facing slope. The higher elevation site (3200 m) was an older stand of Engelmann spruce and subalpine fir and was located on nearly level ground.

Continuous records of air temperature ($T_{air}$) and relative humidity were obtained by placing a hygrothermograph in a protective weather shelter approximately 5 m above ground level at each site. Saturation vapor deficit of the air (SVD) was calculated from these data. Soil temperature ($T_{soil}$) and water potential ($\psi_{soil}$) were measured during midday using soil thermocouple psychrometers (Wescor model PT-10) buried at 10 and 40 cm. Xylem pressure potentials (XPP) were determined with a Scholander-type pressure chamber.

Conductances were determined approximately biweekly (more frequently early in the summer) on clear days when possible at each site from late May through mid-August. Measurements were obtained from approximately 0800 to 1900 (solar time) at 3-hr intervals when weather conditions permitted using a field-calibrated ventilated diffusion porometer. Branch tips approximately 5 to 10 cm in length were cut from the mid-canopy region of a given tree with clippers on an extension pole. The branch tip (or 10 needle fascicles in the case of lodgepole pine) was quickly shortened to fit the porometer chamber, cut surfaces were coated with petroleum jelly, and then sealed into the

chamber. After determining time necessary for calibration
humidity change to occur inside the chamber, the chamber was
ventilated and ready for the next determination. During each
measurement period, two branch tips from both the shaded and
sunlit portions of the canopy of a given tree were used in
conductance measurements so that an average tree conductance could
be estimated. Approximately 75 min were required to complete one
set of measurements.

Total needle surface areas for use in calculating conductance
were obtained by drying the needles at 75 C for at least 3 days
and then calculating leaf area using a dry mass to area
conversion. This relationship was developed using
geometrically-determined areas.


## RESULTS AND DISCUSSION

Late spring and early summer in 1982 at both the 3200 m and
2860 m sites were characterized by cool temperatures and frequent
rain or snowstorms. Due to cool temperatures, the heavy winter
snowpack persisted in 1982 until mid-June at the lower site and
late July at the higher site. These factors combined to maintain
high soil moisture conditions throughout the summer with minimum
recorded soil water potentials being -.07 MPa (8/19) and -.06 MPa
(7/11) at the higher and lower sites, respectively (Table 1).
Frequent rain and snow greatly reduced the number of days during
which it was possible to obtain complete diurnal conductance
curves, with four such curves being obtained at the higher site
and three at the lower site.

Diurnal conductance patterns

Stomatal conductance ($g_{wv}$) for all species at both the high and low elevation sites was usually highest during the early morning period (approximately 0800 solar time) and gradually decreased until early evening when final measurements were made (Figs. 1 and 2). Spruce and fir conductances were typically not significantly different ($\alpha$ = .05) on a diurnal basis, although spruce conductance tended to be higher (Figs. 1 and 2). Lodgepole pine conductance was consistently greater than spruce or fir conductance on a diurnal basis (Fig. 2), beginning in early July.

Since $\psi_{soil}$ and $T_{soil}$ did not vary appreciably during the day and all complete diurnal curves were obtained on essentially clear days, the observed conductance patterns were probably a result of diurnal changes in $T_{air}$ and/or SVD. Multiple non-linear regression equations of the form

$$g_{wv} = e^{(b_0 + b_1\ SVD + b_2\ SVD^2 + b_3\ T_{air} + b_4\ T_{air}^2)}$$

were tested separately for each species on each date at both sites. Results of these regression analyses were often similar between species at a given site on a given date with regard to the most important components of the resulting model. However, the structure of the resulting equations was usually different between sampling dates. Therefore, no specific equation can be given for predicting diurnal changes in $g_{wv}$. In general, however, saturation vapor deficit (as SVD or $SVD^2$) was the variable most often of greatest importance in the generated equations (16 out of 23), and was significant (p = .05) in the equations 22 out of 23

times. Average $r^2$ values obtained when regression equations were of the form

$$g_{wv} = e^{(b_0 + b_1\ SVD)}$$

or

$$g_{wv} = e^{(b_1\ SVD^2)}$$

were .30 and .23 for spruce and fir at the higher site, and .35, .26, and .15 for spruce, fir, and pine at the lower site, respectively. Air temperature (as $T_{air}$ or $T_{air}^2$) was significant in the equations 7 out of the 8 days used in modelling diurnal conductance at the higher site, but only 7 out of the 15 days modelled for the lower site.

Although the $r^2$ values were less than 0.4, the importance of SVD in 22 out of the 23 equations probably is an indicator of the greater influence of SVD than $T_{air}$ on needle conductance. Higher $r^2$ values for equations predicting diurnal changes in $g_{wv}$ probably could have been obtained by accounting for photon flux striking the branch tips (Kaufmann 1982a).

The possibility that increasing leaf water stress caused the observed diurnal decreases in $g_{wv}$ seems unlikely, since our minimum recorded midday (1400) XPP's (-1.3 and -1.1 MPa for spruce and fir, respectively, at the higher site, and -1.2, -1.4, and -1.3 MPa for spruce, fir, and pine respectively, at the lower site) were relatively high compared with values reported by Running (1980a, -1.8 to -2.0 MPa). Our values were also greater

than the minimum values reported by Kaufmann (1982a) (-2.2, -1.9, -1.8, and -2.3 MPa for spruce, fir, pine and aspen, respectively), who reported that XPP's of -2.2 to -2.3 MPa were necessary to reduce aspen leaf $g_{wv}$ to one-half of the still high $g_{wv}$'s attained at -1.5 to -1.7 MPa XPP. Our XPP data therefore seem to support the suggestion that increases in SVD were primarily responsible for the observed diurnal decreases in $g_{wv}$.

## Changes in maximum conductances

Freezing minimum nighttime air temperatures apparently reduced mean maximum conductances ($g_{wv}^{max}$) in both spruce and fir in May and June at 3200 m (Fig. 3). During this period, $g_{wv}^{max}$ for both species was less than half that which occurred following the onset of consistently non-freezing nights. On days following freezing nights, fir $g_{wv}^{max}$ was usually close to zero, whereas spruce $g_{wv}^{max}$ averaged 0.6 mm s$^{-1}$. This was a highly consistent difference (Fig. 3). The $g_{wv}^{max}$ values usually occurred during the 0800 measurement at either site following non-freezing nights, and generally increased for each species from late June until mid-August (Figs. 3 and 4). The highest mean conductances recorded during the summer were 7.1, 6.3, and 8.7 mm s$^{-1}$ for spruce, fir, and pine, respectively, at the lower site (August 18), and were 4.1 and 3.9 mm s$^{-1}$ for spruce and fir, respectively, at the higher site (August 3). The lower site $g_{wv}^{max}$ values are higher than any reported so far for conifer species.

Mean maximum conductances for spruce and fir were nearly identical at each site on mornings following non-freezing nights throughout the summer (Figs. 3 and 4). Lodgepole pine consistently

had greater $g_{wv}^{max}$ than spruce or fir at the lower site from early July through mid-August (Fig. 4).

In attempting to relate $g_{wv}^{max}$ to various environmental variables, the data were tested for significant fits to several non-linear multivariate equations. Results of these regression analyses indicate that, of the models tested, an equation of the form

$$g_{wv}^{max} = e^{(b_0 + b_1\, T_{soil} + b_3\, SVD + b_3\, T_{soil}^2 + b_4\, SVD^2)}$$

predicts most accurately maximum needle conductance for all species at either site (Table 2). The $r^2$ values for the above relationship are .31 and .54 for spruce and fir, respectively, at the higher site and .83, .75, and .81 for spruce, fir, and pine, respectively, at the lower site.

It is interesting to note that $r^2$ values are much higher for the species at the 2860 m site, and that soil temperature (as $T_{soil}^2$ or $T_{soil}$) was most important in the model at 2860 m whereas SVD (as SVD or SVD + $SVD^2$) was most important at 3200 m (Table 2). It appears that at the higher site, $g_{wv}^{max}$ was most sensitive to fluctuations in SVD whereas at the lower site increasing $T_{soil}$ was most highly correlated with $g_{wv}^{max}$ during the summer. The most probable explanation for these differences seems to be that at 40 cm depth, $T_{soil}$ at the 3200 m site was never greater than approximately 7.5 C (Fig. 5), whereas the maximum $T_{soil}$ (40 cm) measured at 2860 m was 9.5 C (Fig. 6). The higher $r^2$ values were obtained with data from the 2860 m site, indicating a good fit to an exponential-type curve with $T_{soil}$ as the most important model

component, and suggesting a threshold relationship of $g_{wv}^{max}$ to above-freezing $T_{soil}$.  Kaufmann (1975) reported that root resistance in young Engelmann spruce trees became significant below 7.5 C, and Running (1980b) reported a similar threshold for lodgepole pine at approximately 7 C.  Our data would seem to agree with these results, because a rapid increase in $g_{wv}^{max}$ at the lower site is apparent in the same temperature range (Fig. 6).  It is also interesting that Running (1980b) observed these $T_{soil}$ effects to be significant mainly when soil water was not limiting, as was the case in the present study.  In addition, since fir $g_{wv}^{max}$ data fit the equation as well as spruce and pine data, it would seem that a similar root resistance response to $T_{soil}$ exists in fir if a root resistance threshold is indeed the phenomenon indicated by the regression relationships.  The lower $r^2$ values obtained with data from 3200 m may result therefore from poor fit of the data to an exponential equation due to the lack of exponential increase in $g_{wv}^{max}$ caused by below-threshold $T_{soil}$.

As an explanation of large increases in $g_{wv}^{max}$ based on soil temperatures rising above a threshold of approximately 7.5 C is supported to some degree by $XPP^{max}$ (early morning) data (Table 3). $XPP^{max}$ increased gradually at 3200 m, though more sporadically at 2860 m over the summer as $T_{soil}$ increased (Table 1), possibly indicating increased overnight trunk recharge rates with decreasing root resistance to water uptake.  Greater $XPP^{max}$ later in the summer would then partially explain the observed increases in $g_{wv}^{max}$, and thus the high correlation of $g_{wv}^{max}$ with $T_{soil}$.

CONCLUSIONS

Leaf conductance to water vapor loss was measured under conditions of high soil moisture and predominantly on clear days. Given these conditions, results indicate that variations in SVD are most important in controlling diurnal variations in $g_{wv}$. This finding is in agreement with the results of Running (1980a), as well as with Murphy and Ferrell (1982) who found summer conductance of Douglas fir to be related largely to vapor pressure deficit.

Our data also indicate that soil temperature was important in effectively regulating maximum needle conductance over the summer. Our early-morning XPP ($XPP^{max}$) data lend some support to this possibility, since $XPP^{max}$ generally increased over the summer along with $T_{soil}$ and $g_{wv}^{max}$. This could indicate the limiting of $g_{wv}^{max}$ following non-freezing nights by lower $XPP^{max}$, which may in turn be caused by higher root resistance to water uptake induced by soil temperatures below approximately 7 C.

It seems reasonable to expect differences between maximum conductances at higher and lower elevation sites based on the persistance of cooler soil temperatures at the higher elevations. Relationships between $T_{soil}$ and root resistances to water uptake have been accurately described for young Engelmann spruce (Kaufmann 1975) and lodgepole pine (Running 1980b). Our data along with that of Fahey (1979), Kaufmann (1982b, 1975), Running (1980a, b), and Smith et al. (unpublished data) lead us to hypothesize that the occurrence of maximum stomatal conductances greater than approximately 0.5 mm s$^{-1}$ is dependent on minimum nighttime air temperatures ($T_{air}^{min}$) rising above freezing in late spring, and

conversely, that decreases in $g_{wv}^{max}$ to below this approximate
level are due to decreases in $T_{air}^{min}$ to freezing in the fall.
However, between these periods and given optimal light and soil
moisture conditions, it is hypothesized that $g_{wv}^{max}$ is limited to
below maximum possible levels until soil temperature rises above
approximately 7 C.  In higher elevation spruce-fir forests, soil
temperatures may never rise far above this apparent threshold
level, thus $g_{wv}^{max}$ in these forests may never reach values as high
as in forests at lower elevations.  With the acquisition of
additional field data relating $g_{wv}^{max}$ to $T_{soil}$ under non-limiting
light and soil moisture conditions, a more accurate description of
this relationship can be formulated.  The results provide a basis,
however, for adapting the hydrologic simulation model (H2OTRANS)
to spruce-fir forests in Wyoming (Running et al. 1982).

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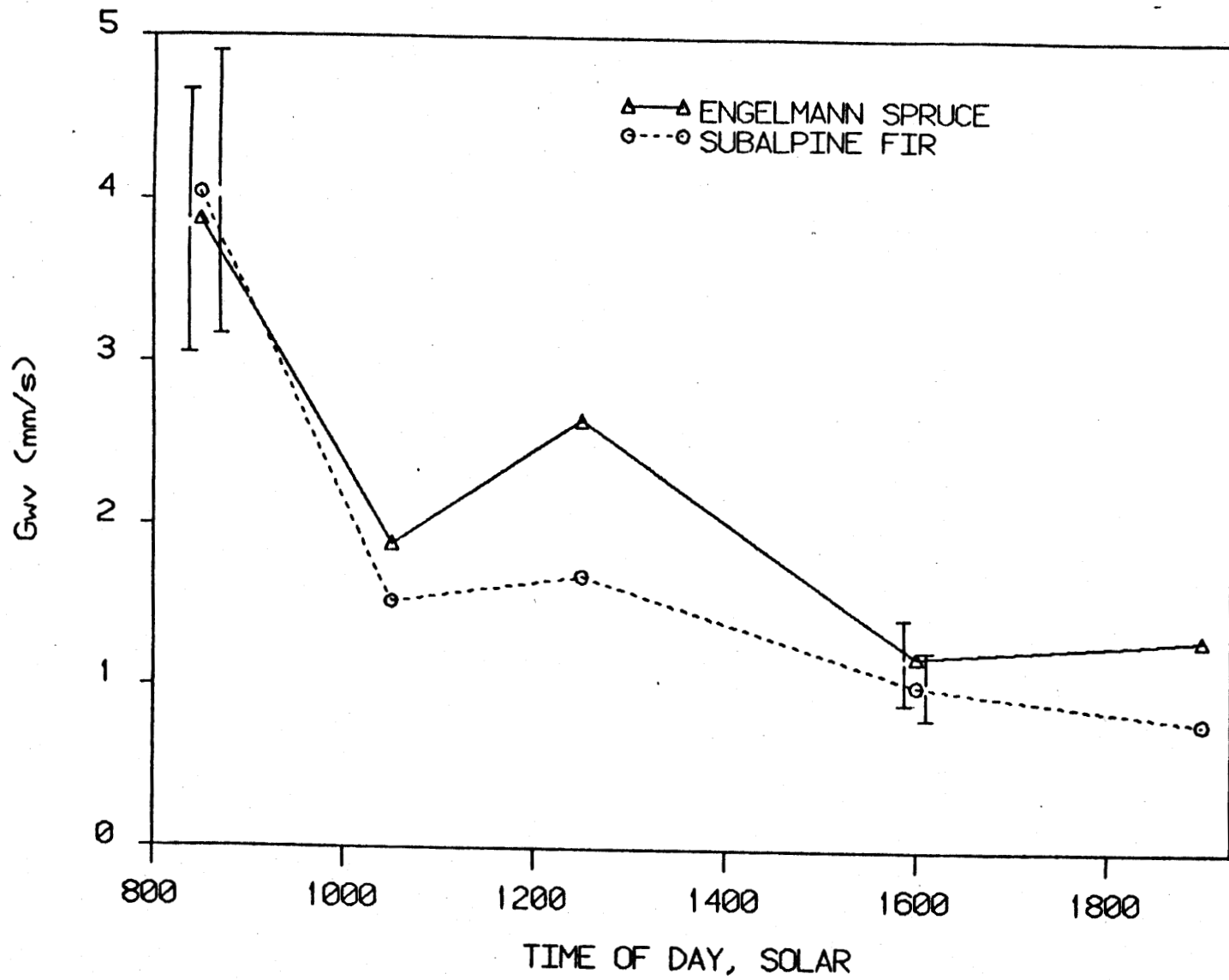     with desert plants.  Oecologia (Berl.) 41: 109-122.

Figure 1. Mean conductance versus solar time, August 3, 1982, 3200 m elevation. Brackets represent 95 percent confidence intervals.
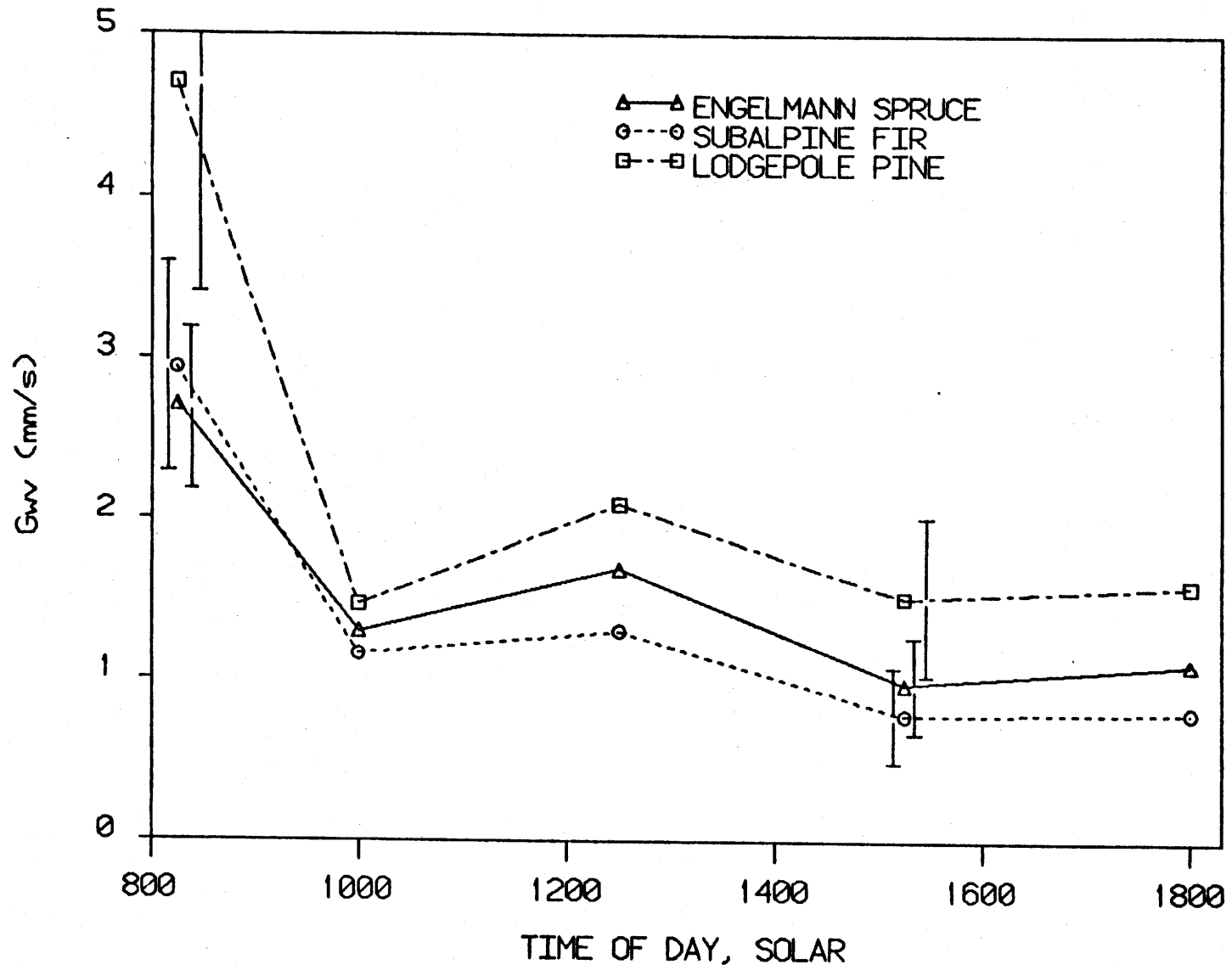
Figure 2. Mean conductance versus solar time, July 31, 1982, 2860 m elevation. Brackets represent 95 percent confidence intervals.
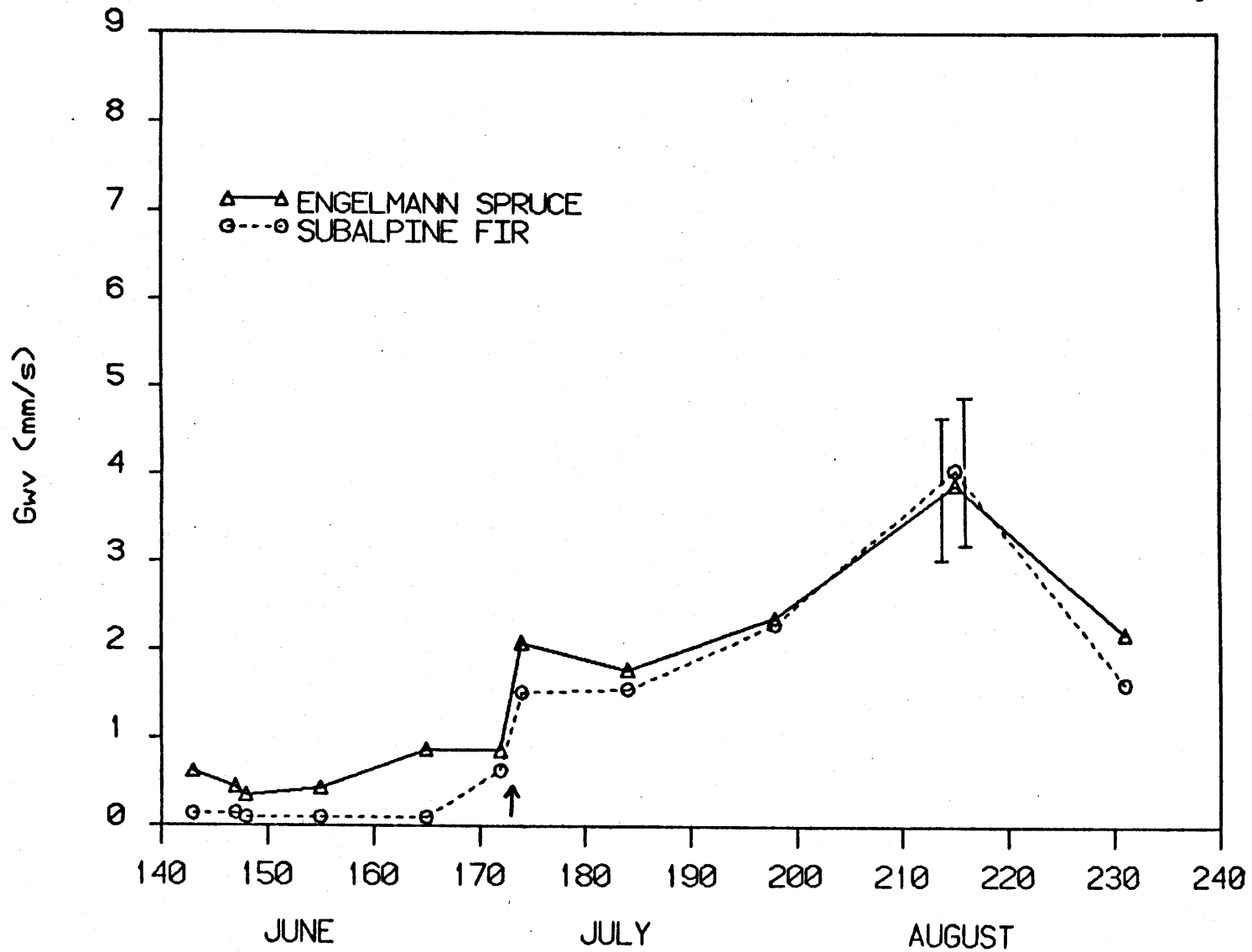
Figure 3. Mean maximum conductance versus Julian date, summer, 1982, 3200 m
elevation. Brackets represent maximum 95 percent confidence intervals.
Each point is a mean of 12 early-morning observations (usually 0800 h).
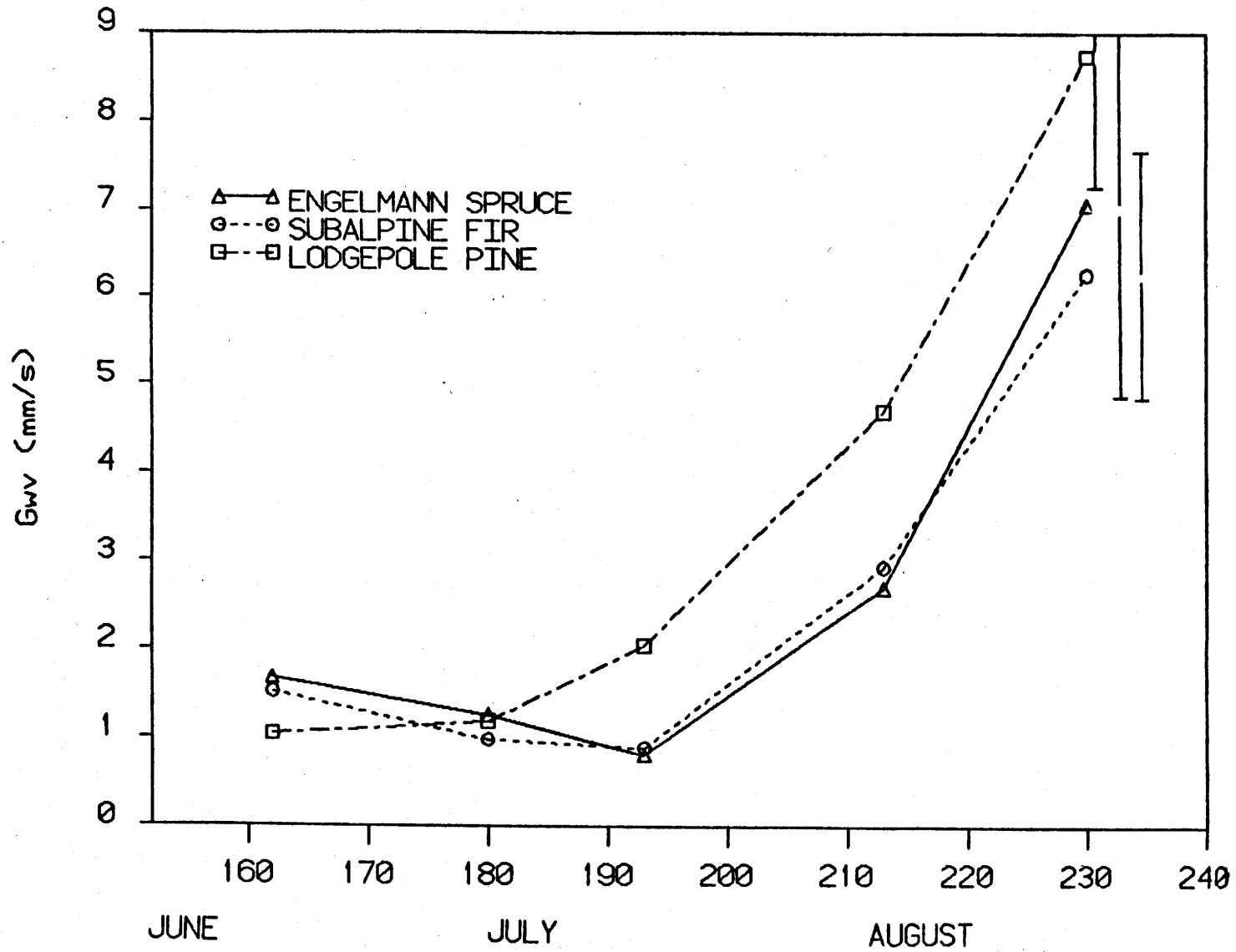Arrow indicates onset of consistently freezing nights.

Figure 4.   Mean maximum conductance versus Julian date, summer 1982, 2860 m
elevation.   Brackets represent maximum 95 percent confidence intervals.
Each point is a mean of 8 early-morning observations (usually 0800 h).
All points follow non-freezing nights.

Figure 5. Mean maximum conductance versus soil temperature, summer 1982, 3200 m
elevation. Brackets represent maximum 95 percent confidence intervals.
Each point is a mean of 12 early-morning conductance observations
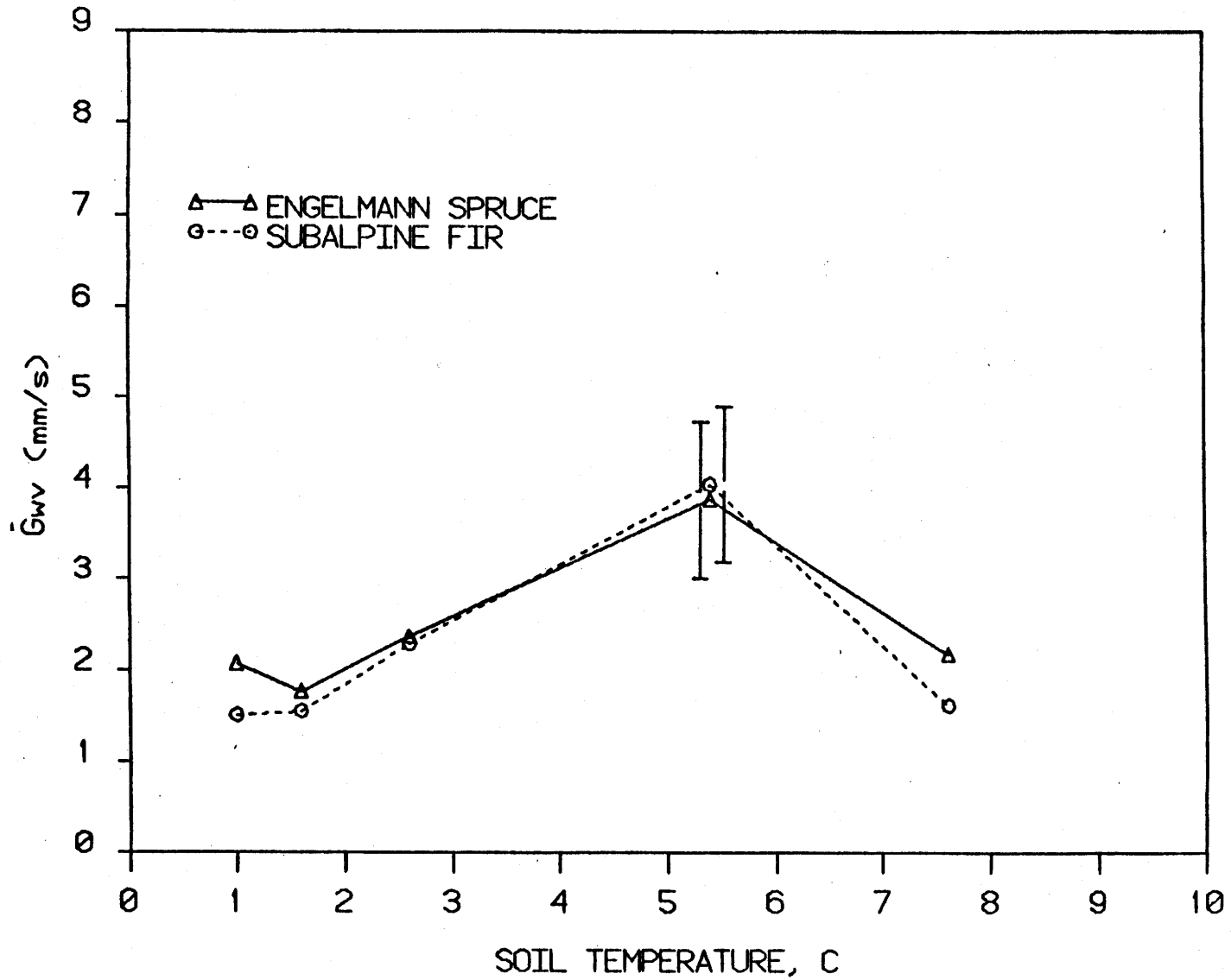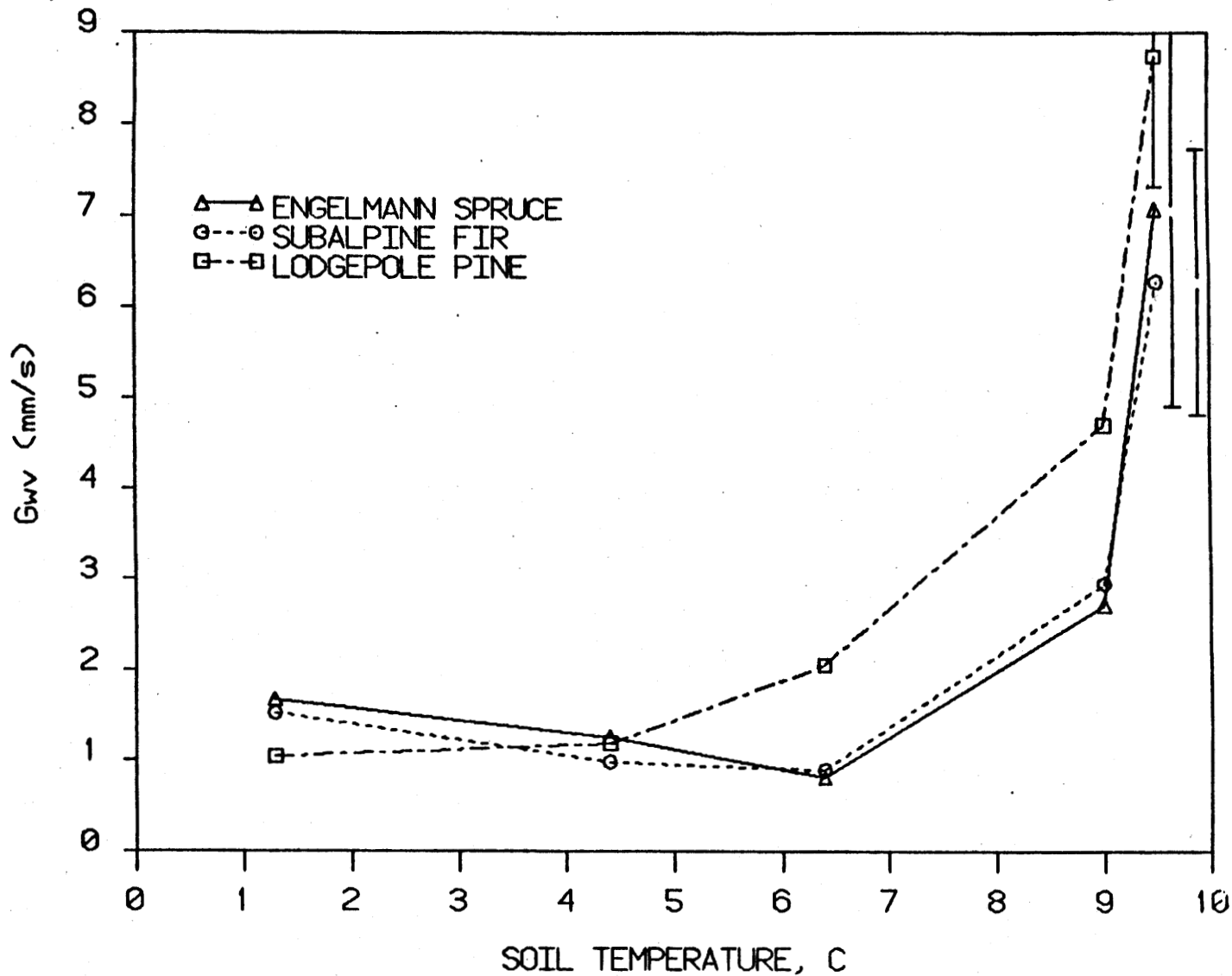(usually 0800 h).

Figure 6. Mean maximum conductance versus soil temperature, summer 1982, 2860 m elevation. Brackets represent maximum 95 percent confidence intervals. Each point is a mean of 8 early-morning conductance observations (usually 0800 h).

Table 1.  Soil temperature, water potential, and minimum and maximum

   air temperatures, summer, 1982.

| Site | Date | $T_{soil}(°C)$ | $\psi_{soil}(MPa)$ | $T_{air}^{min}(°C)$ | $T_{air}^{max}(°C)$ |
|---|---|---|---|---|---|
| 3200 m | 5/22 | -- | -- | -3.0 | 12.0 |
| | 5/26 | -- | -- | -2.5 | 12.0 |
| | 5/27 | -- | -- | 2.0 | 12.0 |
| | 6/4 | 1.1 | -.05 | -3.0 | 9.0 |
| | 6/14 | -- | -- | 3.0 | 9.0 |
| | 6/17 | 0.8 | -.03 | 1.0 | 10.0 |
| | 6/21 | -- | -- | -1.0 | 12.0 |
| | 6/23 | 1.0 | -- | 2.0 | 12.0 |
| | 7/3 | 1.6 | 0.0 | 4.0 | 16.0 |
| | 7/17 | 2.6 | -.04 | 3.0 | 16.0 |
| | 8/3 | 5.4 | -.04 | 7.0 | 16.0 |
| | 8/19 | 7.6 | -.07 | 9.5 | 18.5 |
| 2800 m | 6/1 | 1.0 | -.01 | 0.0 | 8.5 |
| | 6/3 | 0.0 | -.03 | -1.0 | 8.5 |
| | 6/10 | 1.3 | -.04 | 1.0 | 13.0 |
| | 6/28 | 4.4 | -.05 | 3.0 | 19.5 |
| | 7/11 | 6.4 | -.06 | 5.5 | 22.5 |
| | 7/31 | 9.0 | -.03 | 7.0 | 20.5 |
| | 8/18 | 9.5 | -.05 | 9.5 | 22.0 |

Table 2.  Comparison of $r^2$ values for equations relating $g_{wv}max$ to various environmental factors and XPP.

| Model Tested[1] | | Significant (p = .05) variables $(r^2)$[2] | |
|---|---|---|---|
| | | 3200 m site[3] | 2860 m site[4] |
| 1. $g_{wv}^{max} = e^{(T_{soil} + SVD + T_{soil}^2 + SVD^2)}$ | Spruce | SVD + SVD$^2$ + T$_{soil}$ <br> (.31) | Tsoil$^2$ + Tsoil + SVD <br> (.83) |
| | Fir | SVD + SVD$^2$ + T$_{soil}^2$ <br> (.54) | T$_{soil}^2$ + T$_{soil}$ <br> (.75) |
| | Pine | -------------------- | T$_{soil}^2$ + T$_{soil}$ <br> (.81) |
| 2. $g_{wv}^{max} = e^{(T_{soil} + XPP + SVD + T_{soil}^2 + XPP^2 + SVD^2)}$ | Spruce | SVD + SVD$^2$ + XPP <br> (.32) | T$_{soil}^2$ + T$_{soil}$ + SVD <br> (.83) |
| | Fir | SVD + SVD$^2$ + T$_{soil}^2$ <br> (.54) | T$_{soil}^2$ + T$_{soil}$ <br> (.73) |
| | Pine | -------------------- | T$_{soil}^2$ + T$_{soil}$ <br> (.81) |
| 3. $g_{wv}^{max} = e^{(T_{soil} + T_{air} + SVD + T_{soil}^2 + T_{air}^2 + SVD^2)}$ | Spruce | SVD + T$_{air}^2$ <br> (.30) | T$_{soil}^2$ + T$_{soil}$ + T$_{air}$ +SVD <br> (.83) |
| | Fir | SVD + T$_{air}^2$ + SVD$^2$ <br> (.54) | T$_{soil}^2$ + T$_{soil}$ <br> (.75) |
| | Pine | -------------------- | T$_{soil}^2$ + T$_{soil}$ <br> (.81) |

[1]  Only models yielding the highest $r^2$ values are shown
[2]  Significant variables are listed in order of relative importance
[3]  60 observations per species
[4]  40 observations per species

Table 3.  Mean maximum (early morning) xylem pressure potentials (-MPa).

| Site | Date | Spruce | Species Fir | Lodgepole |
|------|------|--------|-------------|-----------|
| 3200 m | 6/4 | 1.0 | 1.4 | --- |
|  | 6/14 | 1.3 | 1.1 | --- |
|  | 7/3 | 0.8 | 0.8 | --- |
|  | 7/17 | 0.8 | 0.6 | --- |
|  | 8/3 | 0.5 | 0.3 | --- |
|  | 8/19 | 0.6 | 0.5 | --- |
| 2860 m | 5/21 | 1.1 | 1.6 | 0.8 |
|  | 5/30 | 0.8 | 1.0 | 0.8 |
|  | 6/1 | 0.7 | 0.8 | 0.8 |
|  | 6/10 | 1.5 | 1.5 | 1.3 |
|  | 6/28 | 1.1 | 1.0 | 1.1 |
|  | 7/11 | 0.8 | 0.7 | 1.0 |
|  | 7/26 | 0.3 | 0.3 | 0.4 |
|  | 7/31 | 0.8 | 0.8 | 0.9 |
|  | 8/18 | 0.6 | 0.7 | 0.7 |