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W.K. Smith
G.A. Carter

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W.K. Smith
G.A. Carter

Department of Botany
University of Wyoming
Laramie, Wyoming

SHOOT STRUCTURAL EFFECTS ON NEEDLE TEMPERATURES AND PHOTOSYNTHESIS IN CONIFERS[1]

WILLIAM K. SMITH AND GREGORY A. CARTER[2]

Department of Botany, University of Wyoming, Laramie, Wyoming 82071-3165

ABSTRACT

Greater needle packing (number of needles per unit stem length) among shoots of *Picea engelmannii* (Parry ex. Engelm.), *Abies lasiocarpa* ([Hook] Nutt.), and *Pinus contorta* (Engelm.) collected at sun-exposed locations resulted in leaf temperatures (T_l) that were well above air temperature (T_a) and which were closer to optimum for maximum photosynthesis under field conditions. Maximum photosynthesis in these species occurred at leaf temperatures well above mean maximum T_a during most of the summer growth period. An approximate doubling in needle packing on sun shoots of these species, however, led to an estimated temperature enhancement of daily photosynthetic carbon gain of 21 to 36% compared to estimations assuming $T_l = T_a$ for the entire day. Elevated T_l due to needle packing may lead to substantial increases in summer carbon gain for conifers experiencing cold-limited, short growth seasons.

NUMEROUS ADAPTATIONS involving leaf size, shape, absorptance to solar irradiance, and orientation properties that have important influences on leaf temperature and photosynthesis are now recognized for a variety of broadleaved species (Gates, Alderfer, and Taylor, 1968; Taylor, 1978; Smith, 1978; Ehleringer and Mooney, 1978; Begg, 1980; Ehleringer, 1980). Comparatively little research of a similar nature has been reported for plants with narrow leaves or leaflets arranged in distinctive configurations on individual shoots, such as found commonly among needle-leaved coniferous tree species (Kramer and Clark, 1947; Levernz and Jarvis, 1979, 1980; Oker-Blom, Kellomaki, and Smolander, 1983; Carter and Smith, 1985). As an example, greater needle packing in conifer sun shoots substantially increased photosynthesis per unit stem length with only minimal decreases in photosynthesis per needle due to mutual shading and/or orientation effects (Carter and Smith, 1985). We report here on an additional influence of needle packing in conifers which resulted in an increase in needle temperatures to more optimum levels for photosynthesis throughout much of the summer growth period. Data are reported for the three dominant conifers of the central Rocky Mountains, USA (Engelmann spruce, *Picea engelmannii* Parry ex. Engelm.; subalpine fir,

Abies lasiocarpa [Hook] Nutt.; lodgepole pine, *Pinus contorta* Engelm.).

MATERIALS AND METHODS—In all of the following field studies (Medicine Bow Mountains, southeastern Wyoming, USA, 41°21′N, 106°10′W), photosynthetic measurements were taken using either an open-flow CO_2 exchange system with temperature-controlled leaf cuvette and an infrared gas analyzer (Anarad model 410) or a closed-flow portable photosynthesis system (model LI-6000, LI-COR, 4421 Superior St., Lincoln, Nebraska). (See Carter and Smith, 1985, for more details.) The closed-flow system did not enable temperature regulation, but instead was used to sample shoots at various times of the day when shoot temperatures were different, but incident sunlight levels were above levels required to saturate photosynthesis. In all cases, mean leaf conductance values to water vapor (indicating degree of stomatal opening) varied by no more than ±18% and were always ≥2.5 mm s⁻¹. Sun shoots were defined as those growing at locations receiving at least 70% of the total clear-day solar irradiance (horizontal sensor) compared to shade shoots that received less than 20% (LICOR 190S quantum sensors and Campbell Scientific CR7 data loggers).

The temperature response for net photosynthetic CO_2 uptake was measured for a total of 13 shoots from 6 individual spruce trees, 15 shoots from 6 trees of the fir, and 9 shoots from 4 trees of pine during the summers of 1982–1986 (all years combined). All measurements of net photosynthetic CO_2 uptake (μmol CO_2 m⁻² s⁻¹) were determined either over continuous 2–6 hr periods using the controlled-en-

vironment leaf cuvette or from hourly mea-
surements over entire days using the LI-6000
portable photosynthesis system. Individual
shoot tips (approximately 10–20 cm) were
placed inside the gas exchange cuvette with the
plane of the main shoot axis oriented perpen-
dicular to the incident sunlight. Additional
needle temperatures in the field were measured
by wrapping fine-wire (0.024 mm) thermocou-
ples around the midpoints of from 3–10 in-
dividual needles per shoot selected at random
out of approximately 70–150 total needles per
shoot tip. Air temperatures were always mon-
itored as ambient conditions at least 4 m away
from measurement trees and at the same ap-
proximate height off the ground as for mea-
sured shoots (midcanopy for young saplings
approximately 2–3 m in height). All data of
leaf temperatures or photosynthetic assimila-
tion were pooled according to species and av-
eraged over 1-hr time intervals during the day.

The specific influence of needle packing on
needle temperatures was also evaluated in the
laboratory using detached, nontranspiring (sto-
mata closed) shoots within 2 days after de-
tachment. Detached shoots were positioned in
their natural field orientation and exposed to
irradiance levels that closely approximated
natural sunlight during midsummer (1,240 ±
68 W m^{-2} at Solar Noon) using an overhead
incandescent light. Needle temperatures were
monitored using fine-wire thermocouples
(0.083 mm diameter) wrapped tightly around
needle midpoints. Thermocouples were at-
tached to up to 20 randomly selected needles
(8–20) on single shoot tips that ranged in length
from 12–22 cm (166–309 total needles). A fan
was used to generate windflow perpendicular
to the main axis of the shoot. A hot-wire ane-
mometer connected to a strip-chart recorder
was used to measure wind speeds and compute
turbulence intensity at the center and imme-
diately windward of the shoot (approximately
2 cm from needle tips). The fan speed was
regulated to generate approximately 30 cm s^{-1}
(28 ± 9 SD) representing low wind conditions
of morning at midcanopy heights and 3.0 m
s^{-1} (3.1 ± 0.4 SD) for the windier conditions
typical of afternoon. These values were chosen
to approximate mean values of actual wind
speeds measured for 37 representative days in
summer (6 June–4 Sept., 1979–1984) when
mean maximum daily air temperatures were
within ±2 C of 12-yr average values for a given
date (1964–1976, Wyoming Solar Observa-
tory). Mean wind speeds during morning (0800–
1000 hr) ranged from 21–116 cm s^{-1} with
$\bar{x}$ = 33 ± 22 and during the afternoon (1300–
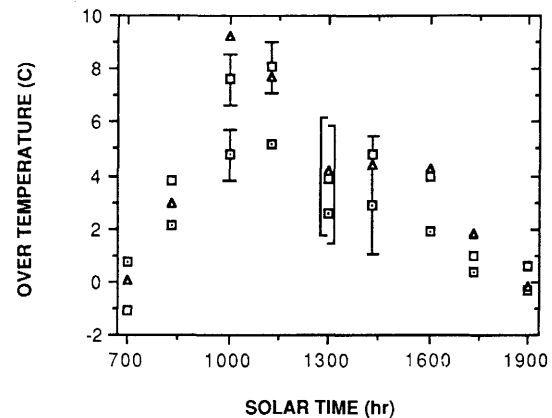1500 hr) from 0.92–6.7 m s^{-1} with $\bar{x}$ = 2.6

Fig. 1.   Individual leaf overtemperatures (leaf temper-
ature – air temperature) measured for *Picea engelmannii*
(□), *Abies lasiocarpa* (△), and *Pinus contorta* (▣) during
the summers of 1982–1986. Each point is the mean of all
measurements (N = 16–39) taken within one hour before
and after the indicated time over 12 days in June, 11 days
in July, and 9 days in August (32 total days). All sampled
days had mean maximum air temperatures that were with-
in ±2.5 C of a 12-yr average (1964–1972) for each cor-
responding day (12-yr data are from a standard weather
station located within 1.1 km and ±80 m elevation of all
research sites, Wyoming Solar Observatory, 1986). Ver-
tical bars are greatest 95% confidence intervals for each
data set.

(±1.1) m s^{-1}. Both the lower and higher fan
wind speeds generated Turbulence Intensities
(0.46 ± 0.8) that were not statistically different
(ANOVA, α = 0.05) and which approximated
values measured under field conditions (Smith,
1980; Nobel, 1981).

RESULTS AND DISCUSSION—Shoots that grew
in locations with a high exposure to sunlight
(sun shoots) had considerably greater needle
packing than for shoots in shaded locations.
Mean needle packing of each species for 15 sun
shoots collected from 5 different trees (total
N = 75) was 21 ± 3 needles/cm in the spruce,
22 ± 2 for the fir, and 19 ± 3 in the pine,
compared to 15 ± 2, 12 ± 2, and 11 ± 1,
respectively, for shade shoots. Similar in-
creases in needle packing have also been cor-
related with sun exposure as well as increasing
elevation in other conifer species (Muller-Stoll,
1954; Zelawski and Niwinski, 1966; Delucia
and Berlyn, 1984).

Although the small diameter of conifer
needles has led investigators to assume a close
coupling of needle and air temperature (Jarvis,
James, and Landsberg, 1976), considerable data
now suggest that conifer needle temperatures
in the field may increase substantially over am-
bient air temperature (Volwinckel, Oechel, and
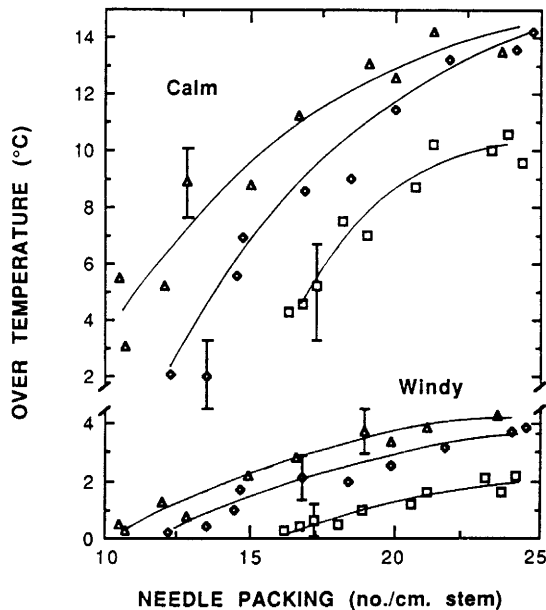Bell, 1975; Christersson and Sandstedt, 1978;

Fig. 2. Leaf overtemperatures ($T_1 - T_a$) vs. the degree of needle packing (number of needles per cm stem length) under simulated. full-sun field conditions in the laboratory. *Calm* refers to an early morning windflow of ≈30 cm s^{-1}; *windy* is for an experimental wind of ≈3.0 m s^{-1}, typical of afternoon periods. Please see text for justification of selected wind and irradiance levels. Ten different shoot tips were monitored for each species with ten needles per shoot measured for temperature changes. Vertical bars are greatest 95% confidence intervals for each data set. *Picea engelmannii* (◇), *Abies lasiocarpa* (△), *Pinus contorta* (□).

Smith, 1980; Hadley and Smith, 1983, 1985, 1987; Price and Petzold, 1984; Vanderwaal and Holbo. 1984; Kaufmann, 1985). Over past summers (1982–1986), we compiled a relatively large number of needle temperature measurements on sun-exposed shoots (south-facing canopy) of a spruce, fir, and pine species (Fig. 1). Maximum overtemperatures (leaf air) of 8 C occurred by about 1000 hr with a substantial decline to about 4 C overtemperatures beginning at noon and continuing until late afternoon. Even on initially clear days a major portion of the summer is characterized by afternoons that have a considerable accumulation of advective cloud formation over the mountain ranges. These clouds begin to develop by middle to late morning and continue to form until sunset. This cloud formation was partially responsible for the drop in mean overtemperatures at about noon, although sporadic, high overtemperatures continued to occur throughout most of the day (Fig. 1). The higher wind speeds and air temperatures of the afternoon period also contributed to the consid-

erably lower mean overtemperatures compared to morning conditions.

Simulating natural shoot orientations, sunlight exposure, and wind flow in the laboratory resulted in leaf overtemperatures under the calm wind speed (Fig. 2) that were similar to values measured during morning in the field (Fig. 1). The higher wind speed regime resulted in relatively small overtemperatures (<4 C) even at the greatest needle packing. A strong relationship between overtemperatures and needle packing was evident for each of the three species. The spruce and fir had more similar response patterns, although fir needle temperatures were significantly warmer at a given needle packing level. Lodgepole pine had considerably smaller overtemperatures and a narrower variation in needle packing among the collected shoots (Fig. 2).

In the absence of any photosynthetic effects due to less efficient sunlight interception (Carter and Smith, 1985), we evaluated the effect of increased needle packing on daily photosynthesis due to potential influences on needle temperature. The temperature ranges for maximum photosynthesis (90% of maximum rates under saturating light) for all three species were well above the mean maximum T_a recorded during much of the summer growth season (Table 1). Optimal photosynthetic temperature ranges for all species averaged 14.1–25.1 C, although the mean maximum T_a during corresponding intervals was only 15.8 C. Moreover, the computed length of time that individual shoots were within the temperature range for maximum photosynthesis averaged only 30% of the day (26–32%) if needle temperatures were hypothetically assumed equal to T_a, compared to 58% (49–65%) when actual needle temperatures were used to estimate photosynthesis (Table 1). Field measurement of needle temperatures of the 15 fir shoots in Table 1 resulted in a mean daily needle temperature of 6.6 C above T_a (0900–1600 hr) with a range of 1.8–14.4 C for periods when shoots were receiving direct sunlight. Computed increases in total daily CO_2 assimilation for fir shoots with actual needle temperatures vs. the same shoots with needle and air temperatures equal ranged from 26–35%, for an average increase of 29% (Table 1). It is noteworthy that the greatest overtemperatures occurred in the field during morning when T_a tends to be much lower than the mean maximum for the day. Moreover, maximal stomatal opening and carbon gain occur most frequently during the morning hours before water stress develops in midafternoon (Smith, 1985). Minimizing any cold temperature limitation to photosynthesis

TABLE 1. *Importance of elevated needle temperatures to conifer shoot photosynthesis in* P. engelmanni *(S),* A. lasiocarpa *(F), and* P. contorta *(P) during the summers of 1982–1986. Measured temperature ranges for maximum photosynthesis (= 90% of maximum rates), mean maximum ambient air temperatures that occurred during the corresponding periods of photosynthetic determinations, and the percent of the day (0800–1800) that* A. lasiocarpa *shoots would have been within their temperature ranges for maximum photosynthesis as computed for measured (Actual) needle temperatures and if needles were hypothetically equal to air temperature* (T_a), *according to the temperature-photosynthesis response curves measured that day. Plus and minus values are 95% confidence intervals*

| Period | Species | Number of shoots | Temperature range for maximum photosynthesis | Mean maximum daily air temperature (°C)[b] | Maximum photosynthesis (% of day) | | Percent increase in daily CO_2 uptake[a] |
					Actual	T_a	
9–23 June	S, F, P	2, 2, 2	13–22, 15–24, 13–25	13.8 ± 2.3	64	32	26
1–16 June	S, F, P	3, 3, 2	14–24, 14–26	15.6 ± 1.9	59	30	29
16–24 July	F	2	14–26	16.7 ± 1.6	56	29	33
1–14 July	S, F, P	2, 2, 1	15–27, 14–25, 13–24	17.4 ± 1.8	65	32	35
16–28 July	S, F. P	2, 2, 2	16–26, 15–26	16.9 ± 1.6	49	26	20
17–24 Aug	S, F, P	4, 4, 4	15–26, 14–24, 16–23	14.6 ± 1.9	53	31	29
	$\bar{x} =$		14.1–25.1	15.8 ± 1.2	58	30	29

[a] Each value is computed for the indicated number of fir sun shoots only.
[b] 12-year means (1962–1974, Wyoming Solar Observatory; see text).

would be especially advantageous during the morning vs. afternoon periods.

In a seasonal study of photosynthesis in *Pinus contorta,* air temperatures also appeared to be well below optimum ranges for maximum photosynthesis throughout much of the year (Tranquillini and Turner, 1961). More recently, Delucia and Smith (1987) also found that optimal leaf temperatures for photosynthesis in *Picea engelmannii* measured during the summers of 1984 and 1985 were also well above mean maximum air temperatures during much of summer.

Increased needle packing in sun shoots, the frequent elevation of needle temperature above T_a due to needle packing in more sun-exposed shoots, and the correspondingly high temperature ranges for maximum photosynthesis (well above mean maximum daily T_a) suggest strongly that needle packing is important for increasing carbon gain over much of the growth season in these coniferous species. Similar elevations in leaf temperatures due to leaf clustering have been reported for other plant species living at high latitudes or elevations (alpine) where cold air temperatures and short growth seasons prevail (Krog, 1955; Warren-Wilson, 1957; Salisbury and Spomer 1964; Mohlgaard, 1982; Smith et al., 1983). Reported increases in conifer needle packing with greater elevation (Delucia & Berlyn, 1984) may also serve to compensate for the relatively steep air temperature lapse rates associated with mountain habitats. Needle packing in these coniferous species could represent a method of elevating leaf temperatures to enhance photosynthetic performance that is antithetical to the large undertemperatures and enhanced photosyn-

thesis reported for broadleaved desert species (Smith, 1978). The clustering of individual leaves along stems or petioles can provide an uncoupling of leaf and air temperatures that has not been systematically evaluated among different plants or habitats.

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