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# Influence of Shoot Structure on Light Interception and Photosynthesis in Conifers

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## ABSTRACT

The influence of shoot structure on net photosynthesis was evaluated under field conditions for the central Rocky Mountain (United States) conifers *Picea engelmannii* (Parry ex Engelm.), *Abies lasiocarpa* (Hook) Nutt., and *Pinus contorta* (Engelm.). In all species, the greater number of needles per unit stem length on sun shoots correlated with a smaller silhouette leaf area to total leaf area ratio (STAR). Decreased STAR was due primarily to greater needle inclination toward the vertical, plus some needle mutual shading. However, photosynthesis expressed on a total leaf area basis did not decrease in sun shoots (lower STAR) but remained nearly constant at approximately 3 micromoles per square meter per second over a wide range of STAR (0.1 to 0.3). Relatively low light saturation levels of 200 to 1400 microeinsteins per square meter per second and diffuse light to 350 microeinsteins per meter per second maintained photosynthetic flux densities in inclined and/or shaded needles at levels comparable to those in unshaded needles oriented perpendicular to the solar beam. As a result, net CO<sub>2</sub> uptake per unit stem length increased as much as 2-fold in sun shoots (low STAR) in direct proportion to increasing needle density.

The importance of intercepting direct-beam sunlight in plants is evidenced by a large variety of behavioral and structural adaptations in individual leaves. Relatively few studies, however, have evaluated the implications of shoot structure on physiological processes. Recent data on conifer photosynthesis in shoots oriented at different angles to the irradiating beam have illustrated the potential importance of a complex shoot morphology in influencing shoot-level photosynthesis (6, 9). In fact, illuminating conifer shoots from all angles using an integrating sphere resulted in higher photosynthetic flux densities that were more typical of broadleaf species (12). Other workers have reported that individual conifer needles also had higher photosynthetic flux densities than for entire shoots exposed to direct beam light (5, 7).

The purpose of the present study was to evaluate the influence of the complex shoot structure found in conifers on photosynthetic flux densities under field conditions. Measurements of net CO<sub>2</sub> assimilation of individual shoots were combined with morphological measurements that estimated the influence of needle orientation and mutual shading on sunlight interception. Similar measurements were made for shoots which were experimentally modified to minimize these structural effects. Photosynthesis was measured for relatively short-needled spruce and fir species, and a longer-needled pine species, that are dominant members of the subalpine forests of the Central Rocky Mountains.

**Leaf Area and Photosynthesis.** Field measurements of plant photosynthetic flux densities are now commonly made by en-

closing a shoot, leaf, or leaf portion into a transparent chamber exposed to solar radiation and then determining CO<sub>2</sub> flux into the leaf material. For laminar leaves, photosynthetic flux densities are then usually calculated on the basis of the actual amount of leaf area intercepting direct beam radiation (11). When the direct radiation is perpendicular to the plane of the leaf, the area of the leaf shadow cast on a surface beneath and parallel to the leaf plane is termed PLA<sup>1</sup>. The PLA for thin, flat leaves closely approximates one-half TLA, and its use in calculating photosynthesis leads to consistent and comparable measurement units. However, an equally justifiable area for use in quantifying photosynthesis for species with complex leaf arrangements, such as conifers, has not been comprehensively evaluated. Previous researchers have often defined a PLA for conifers as equal to one-half TLA, or as the total projection area measured when all needles were removed from a shoot and spread on a flat surface (e.g. 3, 12, respectively).

Perhaps the most obvious difficulty in determining an appropriate leaf area for calculating photosynthetic flux density in complex-geometry shoots is mutual leaf shading. Mutual shading is due to the blocking of a leaf from direct-beam radiation by one or several other leaves. However, the problem is complicated further by the various orientations of individual leaves to the solar beam, and the resulting differences among leaves in incident photon flux density (and shadow projection area) dictated by Lambert's Cosine Law (1). The shadow area of a shoot oriented at any angle to the light beam, and cast on a surface perpendicular to the beam is also a projection area, but when mutual shading occurs among leaves, the term silhouette leaf area may be more appropriate than PLA. According to the Cosine Law, when the shoot is nonperpendicular to the solar beam, SLA represents a smaller area that would receive the same photon flux as the larger, actual leaf area that is composed of nonperpendicular and/or shaded surfaces. Under field conditions, SLA could vary significantly throughout the year, as well as diurnally, unless the shoot were perfectly symmetric relative to the solar path, or actively maintained a constant orientation to the sun. The silhouette-to-TLA ratio (SLA/TLA) quantifies the capability of a leaf or shoot to intercept direct-beam PPF. For the simple case of a very thin and flat leaf, STAR closely approximates 0.5 if the leaf is perpendicular to the irradiating beam. Values considerably less than 0.5 will occur for thicker leaves, inclined leaves, and when mutual shading occurs among leaves on a shoot.

<sup>1</sup> Abbreviations: PLA, projected leaf area; TLA, total leaf area; SLA, silhouette leaf area; STAR, silhouette leaf area/total leaf area;  $\psi_x$ , xylem pressure potential;  $J_{CO_2}$ , net photosynthesis;  $g^l$ , leaf conductance to water vapor diffusion; PPF, photosynthetically active photon flux density;  $J^{SLA}_{CO_2}$ , net photosynthesis based on SLA;  $J^{TLA}_{CO_2}$ , net photosynthesis based on TLA.

## MATERIALS AND METHODS

All study sites were located within the Medicine Bow Mountains of southeastern Wyoming (41°20'N, 106°15'W). To determine typical STAR values for individual shoots (*i.e.* the terminal 15–20 cm of a given branch) of each of the three conifer species, shoots were collected from 16 sites that ranged in elevation from 2810 to 3168 m. Shoots were chosen from mature trees (trunk diameter at human breast height [ $\approx 1.5$  m],  $>0.3$  m) of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), subalpine fir (*Abies lasiocarpa* [Hook] Nutt.), and lodgepole pine (*Pinus contorta* Engelm.) at each site to represent either 'sun' shoots that received at least 75% of the total direct sunlight available during the day or 'shade' shoots that received less than 20%. In general, sun shoots were collected from the lower portions of canopies on the south sides of trees in open environments, and shade shoots were collected from the north sides of trees which were shaded by surrounding trees.

A forest understory site at 2610 m elevation and an open site at 3080 m elevation were chosen to compare photosynthetic flux densities of natural shoots having sun (lower STAR) and shade (higher STAR) morphologies with  $J_{CO_2}$  of shoots that had been modified to increase STAR. Two southerly oriented shoots were monitored for each species at each site on saplings that were approximately 6 to 14 years old, and were 0.4 to 1.4 m in height. On one shoot of each sapling, STAR values were increased by removing needles with scissors until there remained only an approximately planar (horizontal), arrangement of nonoverlapping needles on the shoot (approximately 20–100 needles). Mutual needle shading was completely eliminated, although remaining needles varied about  $\pm 10$  degrees from the horizontal plane of the shoot. Photosynthesis was also monitored for a natural shoot located immediately adjacent to the modified shoot.

Additional measurements of  $J_{CO_2}$  for natural shoots of the three species were made biweekly from June through September 1984, on an open and understory site at 2865 m elevation. These sites were approximately midway in elevation between the clear-cut at 3080 m and the forest understory at 2610 m. Measurements of  $J_{CO_2}$  and STAR were made at the 2865 m sites to evaluate physiological differences due to sun and shade shoot structure. Photosynthesis in the previous year foliage of about 5- to 15-year-old trees (0.5–2 m in height) was measured at the 2865 m sites.

Net photosynthesis for modified and normal shoots was measured during mid-morning at the open sites to avoid potentially higher plant moisture stress, but often could not be made until early afternoon at the understory sites due to the necessity of timing measurements with sunpatch occurrence. Measurements were made during clear, warm days on August 3 and 11 at the open (3080 m) and understory (2610 m) sites, respectively, using 1-year-old needles. The experiment was repeated on August 23 and September 2 at these sites using current-year foliage on different saplings. Photosynthetic flux densities in natural and modified shoots were not measured until 12 to 53 d after needle removals.

The possible physiological effects of needle removal on remaining needles were evaluated by comparing  $\psi_x$ ,  $g^l$ , and  $J_{CO_2}$  of natural *versus* modified shoots. The intent was to measure  $\psi_x$ ,  $J_{CO_2}$ , and  $g^l$  in needles of each species both before and after adjacent needles on the stem were removed to determine if needle removals had a negative effect on the shoots. To measure  $J_{CO_2}$  and  $g^l$  in several nonshaded needles while they were still intact on natural shoots, the needles must have been at least 3 cm in length to protrude sufficiently into the gas-exchange cuvette. Thus, direct comparisons of physiology for isolated needles before *versus* after removing adjacent needles could be made only for pine. However, effects of cutting could be inferred for spruce and fir by examining the long-term physiological re-

sponses of modified shoots. For all species,  $\psi_x$ ,  $g^l$ , and  $J_{CO_2}^{LA}$  were compared for natural *versus* modified shoots 12 or 53 d after needle removals. Thus, any effects of needle removals such as possible decreased  $g^l$  or  $\psi_x$  in modified *versus* natural shoots could be determined.

Net photosynthesis and transpiration flux densities were measured with a closed flow  $CO_2$  gas exchange system (LI-COR, Inc., model LI-6000 portable photosynthesis system). The rate of  $CO_2$  depletion inside the cuvette was measured after clamping a shoot into the cuvette and orienting the shoot so that the horizontal shoot plane was perpendicular to the solar beam.  $CO_2$  depletion in the cuvette was not allowed to exceed 30  $\mu\text{L/L}$  from ambient, and needle temperatures, determined by contact with a thermocouple, remained within 5°C of photosynthetic temperature optima that were near 23°C. (G. A. Carter, W. K. Smith, unpublished data). Shoots were exposed to increasing solar PPFD using a series of gray, neutral-density fiberglass screens. Shoots were exposed to a given solar PPFD for approximately 90 s. Changes in  $J_{CO_2}$  began approximately 5 s following changes in PPFD and approached a steady-state after approximately 15 s. A Li-Cor model 190 SB quantum sensor was used to measure PPFD.

To determine if individual needles on both modified and natural shoots were light-saturated under full sunlight, a hand mirror was placed beneath the chamber, and sunlight reflected onto the underside of the shoots through the transparent chamber bottom. PPFD reflected upward in this way was approximately 400  $\mu\text{E m}^{-2} \text{s}^{-1}$ . Immediately following the completion of a photosynthesis measurement, the shoot pressure potential (estimate of xylem water potential) was measured with a pressure chamber (PMS model 1000) to check for any possible differences in  $\psi_x$  between modified and natural shoots. The shoots were then placed in plastic bags and returned to the laboratory for SLA and TLA determinations. SLA for all shoots was measured using a video area meter (Delta-T Devices, Cambridge, England), while TLA was measured using a glass bead coating technique (2, 13).

The relative significance of mutual shading due to needle overlap *versus* needle-orientation effects in reducing SLA was estimated for 12 shoots each from the 2865 m open and understory sites. Shoot SLA (when the shoot plane was perpendicular to the solar beam) was divided by the product of the cosine of the average needle angle from the stem (stem = 0 degrees) and the total PLA (measured with the video area meter) of all needles removed from the shoot and spread on a flat surface. Subtracting this fraction from 1 and multiplying by 100 gave the per cent that SLA was reduced due to needles that were oriented away from the shoot plane. These results compared favorably ( $\pm 8\%$ ) with estimates of shading by directly measuring the fraction of needle length that was in shade for randomly selected, individual needles.

## RESULTS

**Natural Variation in STAR.** Differences in STAR values for natural shoots occurred among the three species as well as between sun (open environment) and shade (forest understory environment) shoots of each species (Fig. 1a). Mean STAR  $\pm 95\%$  confidence interval for shoots collected from various locations were  $0.12 \pm 0.03$ ,  $0.15 \pm 0.04$ , and  $0.13 \pm 0.02$  for sun shoots of spruce, fir, and pine, respectively, and were  $0.18 \pm 0.03$ ,  $0.31 \pm 0.05$ , and  $0.14 \pm 0.04$  for shade shoots of each species, respectively. The greatest difference in STAR between sun and shade shoots occurred in fir (0.15 *versus* 0.31), followed by spruce (0.12 *versus* 0.18), while little difference was apparent between sun and shade shoots of pine (0.13 *versus* 0.14). For each species, the decreases in STAR characteristic of open environments were closely related to increases in needle packing, *i.e.* the number of needles per unit stem length (Fig. 1b). The greatest needle packing of approximately 25 needles  $\text{cm}^{-1}$  occurred when

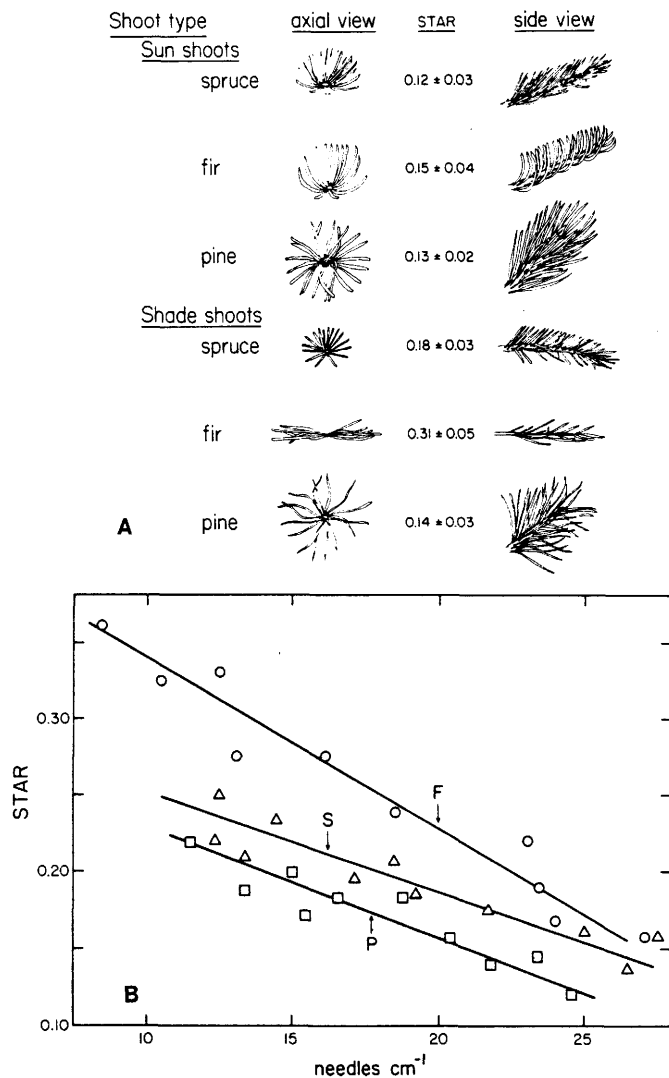


FIG. 1. A, Engelmann spruce, subalpine fir, and lodgepole pine shoots representative of open (sun shoots) and understory (shade shoots) environments. Data are mean STAR ratios  $\pm$  95% confidence intervals. B, Relationship between STAR and needle packing on shoots of spruce ( $\Delta$ ), fir ( $\circ$ ), and pine ( $\square$ ).

STAR was near 0.15 (sun shoots) while shade shoots of fir attained the lowest needle packing ( $< 10 \text{ cm}^{-1}$ ) and the greatest STAR ( $> 0.35$ ).

In addition to STAR values for natural shoots, ocular micrometer measurements of needle cross-sections revealed that the maximum needle STAR for each species was very near 0.4 ( $0.37 \pm 0.04$ ,  $0.41 \pm 0.04$ , and  $0.38 \pm 0.05$ , respectively) and not statistically different among the three species (analysis of variance,  $\alpha = 0.05$ ). Maximum STAR was thus closely approximated, particularly in the understory, by the modified shoots used in determining physiological effects of STAR. In the understory (2610 m), STAR of modified shoots ranged from 0.30 to 0.42 compared to 0.23 to 0.36 at the open site (3080 m, Table I). The lower STAR values in the open were partially due to thicker needles and thus, a greater TLA per unit needle SLA. However, some unavoidable needle curvature also served to reduce shoot SLA in the open (Fig. 1a, Table I). Natural shoot STAR values for each species at the understory (shade) site ranged from 0.14 in pine to 0.31 in fir, compared to 0.09 in pine and 0.22 in spruce and fir, respectively, at the open site (Table I).

In both the open and understory environments at 2865 m,

needle orientation effects were generally much more important than mutual shading in decreasing SLA (and therefore STAR) from maximum possible values (STAR  $\approx 0.4$ ). In the understory, 72 to 96, 92 to 98, and 41 to 67% of SLA reduction in spruce, fir, and pine, respectively, was due to needle orientations, with the remaining reduction due to mutual shading. In the open, even lower STAR shoots had an 84 to 94, 77 to 96, and 58 to 76% reduction in SLA, respectively, solely because of greater needle inclination toward the vertical.

**Effects of Needle Removals.** Due to needle lengths adequate for inserting several isolated needles into the cuvette while they remained attached to the stem, maximum  $J^{\text{TLA}}_{\text{CO}_2}$  for individual needles on pine shoots could be determined before and after modification to increase STAR.  $J^{\text{TLA}}_{\text{CO}_2}$  values before modification were similar to those for needles of modified pine shoots ( $3.5\text{--}4.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) 12 and 53 d following needle removals. Thus, in pine, photosynthesis of individual needles neither increased nor decreased after experimentally increasing STAR. Needles of spruce and fir on modified shoots exhibited only slight increases in maximum  $J^{\text{TLA}}_{\text{CO}_2}$  after 53 versus 12 d from needle removal. The result that  $J_{\text{CO}_2}$  in needles on modified shoots of spruce and fir did not decrease over long periods of time with increased daily exposure to PPFD indicates that there were no long-term solarization (chloroplast bleaching) responses of the needles (10) to the higher-light microenvironment created by removing adjacent needles. Maximum leaf conductances were also similar between modified and natural shoots. In the open environment at 3080 m, average  $g^l$  during  $J_{\text{CO}_2}$  measurements for modified shoots of spruce, fir, and pine were 2.3, 1.4, and  $1.8 \text{ mm s}^{-1}$ , compared with 1.6, 1.4, and  $1.3 \text{ mm s}^{-1}$  in natural shoots, respectively. In the forest understory at 2610 m,  $g^l$  was approximately 1.6, 1.1, and  $1.6 \text{ mm s}^{-1}$  in modified shoots and 1.1, 0.8, and  $1.1 \text{ mm s}^{-1}$ , respectively, in natural shoots. These values of  $g^l$  are typical of those measured for these species under low moisture stress during mid to late summer (G.A. Carter, W.K. Smith, unpublished data) but are somewhat below maximum values measured for these species (4). The  $\psi_x$  determined immediately following photosynthesis measurements ranged from  $-0.9$  to  $-1.4 \text{ MPa}$ , and were similar for all modified versus natural shoots of spruce and fir, and for all pine needles. Therefore, needle removals from modified shoots did not appear to result in significant changes in the water status of remaining needles.

**Photosynthesis and STAR.** Computing  $J_{\text{CO}_2}$  for natural shoots on a TLA and SLA basis resulted in quite different estimates of  $\text{CO}_2$  uptake, since SLA is always less than TLA (Fig. 2). Whereas  $J^{\text{SLA}}_{\text{CO}_2}$  increased greatly with decreasing STAR,  $J^{\text{TLA}}_{\text{CO}_2}$  remained nearly constant at 3 to  $4 \mu\text{mol m}^{-2} \text{s}^{-1}$  under full sunlight as STAR decreased from approximately 0.3 to less than 0.1. In addition,  $J^{\text{TLA}}_{\text{CO}_2}$  was similar for all sun shoots (STAR  $< 0.32$ ) regardless of species (Fig. 2).

Due to the elimination of mutual shading and the minimizing of orientational effects, shoots that were experimentally modified to increase STAR also had substantially lower  $J^{\text{SLA}}_{\text{CO}_2}$  under high light than adjacent, natural shoots with lower STAR (Table I).  $J^{\text{SLA}}_{\text{CO}_2}$  for the natural spruce shoots (both STAR = 0.22) in the open were 78 and 45% greater than for the modified shoots (both STAR = 0.28). However, maximum  $J^{\text{SLA}}_{\text{CO}_2}$  in natural shade shoots of spruce (STAR = 0.29 and 0.23) were only 24 and 41% greater than for the modified shoots (STAR = 0.39 and 0.34). Subalpine fir had lesser differences than spruce between  $J^{\text{SLA}}_{\text{CO}_2}$  values in natural versus modified shoots in the open, but very similar values in the understory (26 and 39%, Table I). Lodgepole pine had the greatest increase in  $J^{\text{SLA}}_{\text{CO}_2}$  in natural versus modified shoots in both the open and understory (104 and 170%, respectively).

Total leaf area photosynthesis of natural shoots were often

Table I. Natural and Experimentally Modified STAR and Net Photosynthesis of Shoots from a Forest Understory (Shade Shoots) and an Open Site (Sun Shoots)

Some shoots were modified to increase STAR, and changes in CO<sub>2</sub> uptake per unit SLA (J<sub>CO<sub>2</sub></sub><sup>SLA</sup>) or TLA (J<sub>CO<sub>2</sub></sub><sup>TLA</sup>) were compared to J<sub>CO<sub>2</sub></sub> of natural shoots.

Species	Date	STAR <sup>a</sup>		Maximum J <sub>CO<sub>2</sub></sub>				ΔJ <sub>CO<sub>2</sub></sub> <sup>b</sup>	
		Natural	Modified	Natural		Modified		J <sub>CO<sub>2</sub></sub> <sup>SLA</sup>	J <sub>CO<sub>2</sub></sub> <sup>TLA</sup>
				J <sub>CO<sub>2</sub></sub> <sup>SLA</sup>	J <sub>CO<sub>2</sub></sub> <sup>TLA</sup>	J <sub>CO<sub>2</sub></sub> <sup>SLA</sup>	J <sub>CO<sub>2</sub></sub> <sup>TLA</sup>		
<i>μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup></i>									
%									
Shade									
Spruce	8/11	0.29	0.39	10.69	3.10	8.59	3.35	+24	-7
	9/2	0.23	0.34	4.35	1.00	3.09	1.05	+41	+5
Fir	8/11	0.31	0.37	8.39	2.60	7.57	2.80	+26	+10
	9/2	0.28	0.39	9.29	2.60	6.67	2.60	+39	0
Pine	8/11	0.25	0.42	13.60	3.40	8.57	3.60	+78	-6
	9/2	0.14	0.30	20.71	2.90	9.00	2.70	+130	+7
Sun									
Spruce	8/3	0.22	0.28	19.77	4.35	11.79	3.30	+78	+33
	8/23	0.22	0.28	18.18	4.00	12.50	3.50	+45	+14
Fir	8/3	0.18	0.23	18.61	3.35	12.61	2.90	+52	+14
	8/23	0.22	0.25	11.82	2.60	11.40	2.85	+4	-9
Pine	8/3	0.09	0.23	35.56	3.20	17.39	4.00	+104	-20
	8/23	0.15	0.36	21.00	3.15	7.78	2.80	+170	+13

<sup>a</sup> STAR = SLA/TLA.

$$^b \Delta J_{CO_2} = \frac{J_{CO_2}(\text{natural shoot}) - J_{CO_2}(\text{modified shoot})}{J_{CO_2}(\text{modified shoot})} \times 100$$

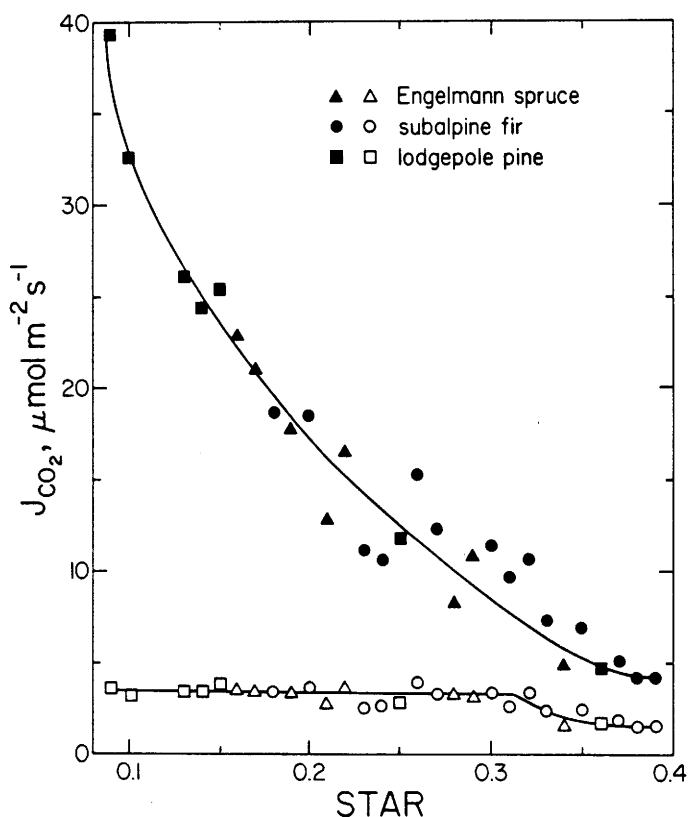


FIG. 2. The SLA (●, ■, ▲) and TLA (○, □, △) photosynthetic flux densities (J<sub>CO<sub>2</sub></sub><sup>SLA</sup> and J<sub>CO<sub>2</sub></sub><sup>TLA</sup>) in natural shoots of Engelmann spruce, subalpine fir, and lodgepole pine versus STAR.

very similar to J<sub>CO<sub>2</sub></sub><sup>TLA</sup> of the modified shoots (unshaded needles oriented perpendicular to the solar beam). In the forest understory (higher STAR), J<sub>CO<sub>2</sub></sub><sup>TLA</sup> in natural versus modified shoots differed by 10% or less (Table I). Greater differences between J<sub>CO<sub>2</sub></sub><sup>TLA</sup> in natural versus modified shoots occurred in the open environment (-20-30%) where the STAR values of natural shoots were generally less than those from more shaded environments.

The J<sub>CO<sub>2</sub></sub><sup>TLA</sup> in natural shoots was even more similar to that in modified shoots under low PPFD, especially in shade shoots (Fig. 3). The J<sub>CO<sub>2</sub></sub><sup>TLA</sup> were nearly identical in natural versus modified shoots when PPFD was below 600 μE m<sup>-2</sup> s<sup>-1</sup> in either open or understory environments (Fig. 3). In contrast, J<sub>CO<sub>2</sub></sub><sup>SLA</sup> in natural versus modified shoots was similar only under very low, diffuse PPFD (<400 μE m<sup>-2</sup> s<sup>-1</sup>), and, in the open, diverged strongly as direct beam PPFD increased (Fig. 3, Table I).

Reflecting solar radiation onto the undersides of natural and modified shoots already receiving full sunlight generally decreased J<sub>CO<sub>2</sub></sub><sup>SLA</sup> and J<sub>CO<sub>2</sub></sub><sup>TLA</sup> from values obtained just prior to use of the mirror. In cases for which photosynthesis under both direct and reflected radiation differed by more than 10% from that under only full sunlight, mirror reflection decreased J<sub>CO<sub>2</sub></sub> in 4 of 5 natural shoots (Table II). Mirror reflection decreased J<sub>CO<sub>2</sub></sub> of modified shoots in only three of six cases (Table II). Pine shoots in the open were the only natural shoots to increase J<sub>CO<sub>2</sub></sub> under mirror reflection, whereas the only modified shoots in which J<sub>CO<sub>2</sub></sub> increased under reflected radiation were in sun and shade shoots of fir, and spruce shade shoots (Table II).

DISCUSSION

The SLA and STAR parameters measure the effectiveness of a shoot to intercept solar PPFD. For the spruce and fir shoots measured here, reductions in SLA and STAR were due primarily to greater upward needle inclination, while mutual shading due to needle overlap reduced SLA by less than 20%. In pine, mutual shading and orientational effects contributed more equally to

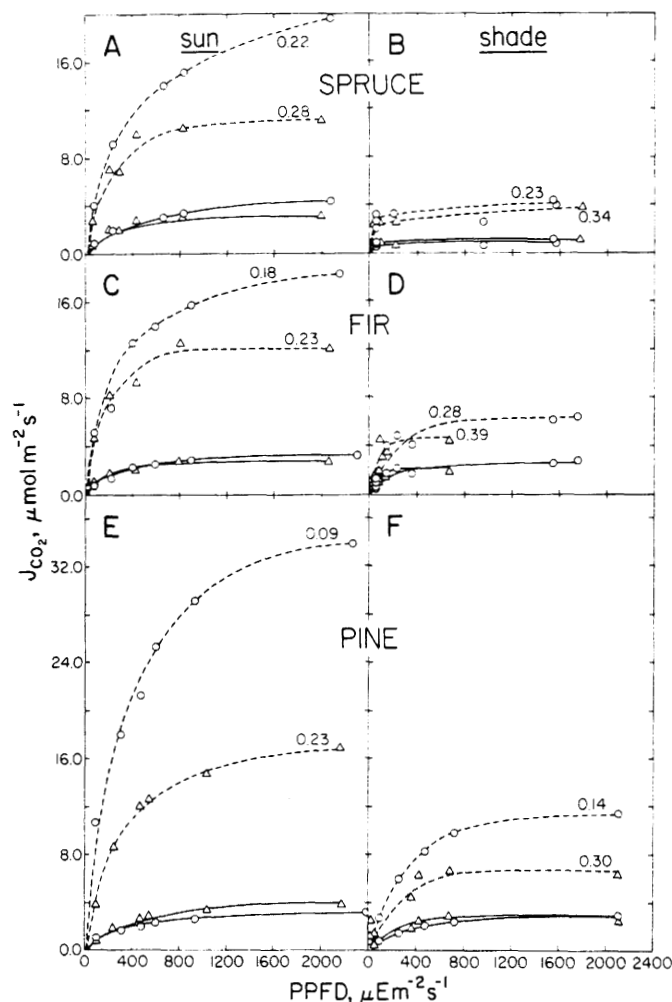


FIG. 3. Net photosynthetic flux density expressed on a silhouette leaf area (---) or total leaf area (—) basis versus PPFD in normal (O) and modified ( $\Delta$ ) shoots. Numbers on curves indicate STAR values of modified and natural shoots.

#### SLA reductions.

Because  $J_{CO_2}^{TLA}$  did not vary greatly over a wide range of STAR values (Fig. 2, except for the lower  $J_{CO_2}^{TLA}$  of shade shoots when STAR > 0.32), the photosynthetic flux densities of individual needles were apparently not closely related to shoot STAR. Thus, the steeper, vertical orientations of needles along with some mutual shading (Fig. 1a) resulted in substantial decreases in SLA and STAR but little change in maximum  $J_{CO_2}^{TLA}$  measured under high PPFD. This might be expected since the measured PPFD levels at photosynthetic saturation were considerably less than full sunlight for all shoots measured (e.g. Fig. 3). A relatively steep vertical orientation of an individual needle of 45° from the shoot plane could still result in over 1000  $\mu E m^{-2} s^{-1}$  incident on the needle surface when sunlight of 1500  $\mu E m^{-2} s^{-1}$  was incident on the shoot plane. The lower  $J_{CO_2}^{TLA}$  of shoots with STAR > 3.2 was probably due to innately lower photosynthetic capabilities in shade-acclimated understory shoots.

Maximum  $J_{CO_2}^{TLA}$  for most modified versus natural shoots differed by only 0 to 14% (Table I), and increasing incident PPFD on undersides of both modified and natural shoots either caused no change or decreased  $J_{CO_2}$  in 17 of 22 cases (Table II). The inability of most modified or natural shoots to respond to reflected PPFD with increased  $J_{CO_2}$  further suggests that most of the needle surface area of modified (higher STAR) and natural (lower STAR) shoots, including abaxial needles, was at or near

Table II. Effect of Additional Reflected Light on  $J_{CO_2}^{SLA}$  and  $J_{CO_2}^{TLA}$  in Natural and Modified Shoots under Full Sunlight

$\Delta J_{CO_2}$  represents the change in shoot  $J_{CO_2}$  (SLA or TLA) following reflection of sunlight onto shoot undersides while shoots were under full solar PPFD from the top.

Shoot Type	Date	$\Delta J_{CO_2}^a$	
		Natural	Modified
$\mu mol CO_2 m^{-2} s^{-1}$			
Shade shoots			
Spruce	8/11		
	9/2	-20	+18
Fir	8/11	-6	+21
	9/2	-4	0
Pine	8/11	-6	-14
	9/2	-10	-4
Sun shoots			
Spruce	8/3	-18	-12
	8/23	-9	-9
Fir	8/3	-13	-3
	8/23	-13	+16
Pine	8/3	+11	0
	8/23	+5	-59

<sup>a</sup>  $\Delta J_{CO_2} =$

$$\frac{J_{CO_2}(\text{full solar PPFD} + \text{mirror}) - J_{CO_2}(\text{full solar PPFD only})}{J_{CO_2}(\text{full solar PPFD only})} \times 100$$

light saturation prior to use of the mirror. Atmospheric diffuse PPFD (approximately 350  $\mu E m^{-2} s^{-1}$ ) and PPFD reflected by the ground and cuvette (110 and 200  $\mu E m^{-2} s^{-1}$ , respectively) induced appreciable photosynthesis in both open and shaded environments (Fig. 3). Furthermore,  $J_{CO_2}^{TLA}$  was similar for natural versus modified shoots under low, primarily diffuse PPFD (<400  $\mu E m^{-2} s^{-1}$ ) in both open and shade environments (Fig. 3). This suggests that needles on natural shoots were at a percentage of light saturation similar to that of the nonshaded and planar-oriented needles on the modified shoots. Thus, it appears that even the more angled or shaded needles of natural shoots received sufficient diffuse and reflected light to maintain a photosynthetic level similar to needles on the modified shoots. The similarities in  $J_{CO_2}^{TLA}$  among species having different shoot morphologies (Fig. 1a and 2) further demonstrated the ability of mutually shaded and/or angled needles to remain near light saturation.

Decreased  $J_{CO_2}$  following mirror reflections onto shoot undersides may have been due to short-term photoinhibition responses (10), and was most evident in spruce and fir (Table II). Thus, it appears that needles on sun shoots, particularly those of spruce and fir, were adapted to photosynthesize optimally when at large angles to the solar beam. However, as STAR continues to decrease, mutual shading may act to significantly decrease  $J_{CO_2}^{TLA}$ , below that of nonshaded needles (e.g. pine on August 3, STAR = 0.09, Table I).

Other researchers have attributed decreased  $J_{CO_2}$  of conifer shoots under directional light to the mutual shading that occurs among needles. However, these studies have been conducted in artificial environments, utilizing light sources with maximum radiation (frequently 1200  $\mu E m^{-2} s^{-1}$ ) well below that of full sunlight (over 2000  $\mu E m^{-2} s^{-1}$ ). Moreover, background reflection was purposefully minimized in some of these experiments (7, 8), and omnidirectional PPFD of as little as 1.5–6.0  $\mu E m^{-2} s^{-1}$  in the gas-exchange cuvette was reported (9). Thus, it appears that levels of direct, diffuse, and reflected light under field conditions in our study were much higher than in the artificial environments of previous studies. In fact, our  $J_{CO_2}^{TLA}$  were very similar (follow-

ing unit and area conversions) to  $J^{TLA}_{CO_2}$  obtained when shoots of other spruce, fir, and pine species were placed in an integrating sphere (4.3, 3.5, and 6.4  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively, 12). The higher diffuse and reflected light levels in the present study apparently minimized the effects of needle orientation and mutual shading on  $J^{TLA}_{CO_2}$ .

The advantage of a low STAR value for sun shoots and a higher STAR for shade shoots may involve both light interception and temperature effects on photosynthesis.  $\text{CO}_2$  assimilation in shade shoots is often light-limited and, thus, horizontal needle arrangements are important for intercepting direct sunlight. In general, the largest sunpatches in the forest understory occur during midday, and horizontal needles for seedlings and saplings would result in leaf surfaces nearly perpendicular to the sun's rays. In the case of sun shoots, inclination of needles upward from the stem results in a decrease in STAR, but the  $\text{CO}_2$  uptake of each needle involved still appears light saturated. In fact, there is evidence that increased needle packing in sun shoots (Fig. 1b) acts aerodynamically to elevate needle temperatures toward photosynthetic optima under field conditions (W.K. Smith, G.A. Carter, unpublished data). Also, increased needle packing along the stem in open environments would result in greatly increased carbon gain per unit stem length, since such needle packing (and decreased STAR) apparently does not decrease  $J^{TLA}_{CO_2}$  on the shoot. For example, a decrease in fir STAR from 0.3 to 0.2 would increase carbon gain per cm of stem by 70% (Fig. 1b). Thus, an ability to decrease STAR with environmental openness would seem highly adaptive for these species, particularly at high elevations near timberline where short growing seasons may greatly reduce stem elongation.

In natural shoots, maximum  $J^{SLA}_{CO_2}$  in the open environment reached values more typical of cultivated  $\text{C}_3$  and  $\text{C}_4$  plants (11). However, expression of  $J_{CO_2}$  on an SLA basis may be unjustified for purposes of comparing  $J_{CO_2}$  values between conifer shoots and broadleaves, except in the case of highly planar needle arrangements. For broadleaf species with thin leaves,  $J_{CO_2}$  is commonly computed using a PLA which is very near one-half TLA. Since a conifer PLA defined as one-half TLA is, given the present results, a constant fraction of the apparent photosynthetically effective leaf area (*i.e.* TLA), it could also be used to compute conifer photosynthesis. Using such a definition for PLA, however, would merely serve to double TLA photosynthetic flux densities. For conifers, the projected area of individual needles measured using plane projection techniques can be considerably less than one-half TLA and will vary with rotation of individual needles around their major axes (*e.g.* minimum and maximum

STAR for individual needles =  $0.07 \pm 0.02$  and  $0.38 \pm 0.11$ , respectively, in pine). Thus, computation of  $J_{CO_2}$  using such a measured PLA value could yield flux densities which are more variable than  $J_{CO_2}$  based on TLA or one-half TLA.

In summary, orientational and mutual shading effects of individual needles resulted in substantial changes in SLA and STAR but little change in  $J^{TLA}_{CO_2}$ . High diffuse and reflected sunlight levels in the field probably contributed greatly to the comparable photosynthetic flux densities of all needles on a given shoot, thus minimizing the influence of mutual shading and orientation on light interception and photosynthesis. Only in the sun shoots with the lowest measured STAR values (<0.1) did mutual shading contribute significantly to a decrease in  $J^{TLA}_{CO_2}$ . In general, needles on sun shoots of particularly spruce and fir appeared adapted to photosynthesize optimally when inclined at large angles to the solar beam. This apparent adaptation would serve to enable the greater needle packing on sun shoots, without decreasing  $J^{TLA}_{CO_2}$ . Increased needle packing would in turn increase carbon gain per unit stem length.

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