The Adaptive Importance of Shoot and Crown Architecture in Conifer Trees

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American Naturalist, Vol. 143, No. 3 (Mar., 1994), 528-532.

Vol. 143, No. 3 The American Naturalist March 1994

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Most conifer tree species that dominate the high northern latitudes are evergreen and have needle-like leaves, while tree species with relatively large broad leaves are all deciduous. Sprugel (1989) concluded that the leaf, shoot, and crown architecture characteristic of conifer trees serve to enhance photosynthesis, primarily because a more upright leaf orientation generates greater sunlight penetration into the crown as well as less cold-temperature limitation to photosynthesis. Although his article is commendable for its synthetic approach, we disagree with two of the three major conclusions presented. Also, certain additional factors were not included that may be important to the functional significance of conifer tree architecture. For example, there is no mention of the potential importance of leaf, shoot, or crown structure to the survival of conifer trees during the severe winters characteristic of high latitudes.

CROWN LIGHT ENVIRONMENT

Conclusions 1 and 2 in Sprugel (1989) both emphasize the functional importance of a small leaf size, steeply angled leaf orientation, and a deeper leaf crown in conifer trees. Sprugel states that sunlight is used more efficiently because ''excess'' sunlight (greater than that needed for photosynthetic light saturation) will penetrate upper branches to leaves deeper in the crown. We disagree that sunlight penetration through upper to lower branches is an important, general feature of conifer versus broadleaf trees. In fact, the conical shape of the crown and the layered arrangement of main branches are major structural features that influence light interception in conifer trees (see Gelderen and Hoey-Smith 1986). In many species, especially fir and spruce, individual branch layers are distinct and separated by considerable vertical distances (tens of centimeters). A conical crown will create larger gaps at the top of the canopy and, thus, greater sunlight penetration and less shading of lower branches by upper branch layers. Both a conical crown and branch layering will increase sunlight interception from low sun angles, a benefit to high-latitude trees (Jahnke and Lawrence 1965; Horn 1970; Paltridge 1973; Oker-Blom and Kellomaki 1983; Terborgh 1985). A greater interception of direct-beam sunlight, with minimal depletion due to penumbral light spreading, is also characteristic of a conical crown shape where the foliated branch tips are sunlit (Smith et al. 1989; Schoettle and Smith 1991).

Very little sunlight penetrated a given branch layer in *Abies lasiocarpa* (subalpine fir) and *Picea engelmannii* (Engelmann spruce), dominant tree species of

Am. Nat. 1994. Vol. 143, pp. 528–532.

the central Rocky Mountains of the United States. Integrated daily irradiance measured at randomly selected locations just beneath a branch layer (middle and lower canopy) averaged almost 10-fold (9.6 ± 2.1 SE) less than that measured just above the adjacent, lower branch layer (W. K. Smith, unpublished data). In fact, a single sun-type shoot of either of these species passed less than 10% of the incident sunlight within its silhouette (cast shadow) boundary (Carter and Smith 1985).

We conclude that the conical crown and layered branch architecture of many conifer tree species are the primary structural characteristics responsible for efficient sunlight interception over the entire leaf crown. Thus, greater light penetration through upper branches to leaves lower in the crown, because of needle-like leaves that are oriented more vertically, is not the major factor responsible for the efficient interception of sunlight in a typical conifer tree crown, as proposed by Sprugel (1989, Conclusion 1).

LEAF AND SHOOT PHOTOSYNTHESIS

Conclusion 2 in Sprugel (1989) states that the more steeply angled leaves of conifer trees would reduce cold-temperature limitations on photosynthesis because at low sun angles (low irradiance), cold air temperatures will cause less decline in photosynthesis than if the leaf were nearer light saturation. The physiological data supporting this conclusion are shown in figure 2 of Sprugel's article. According to this figure, photosynthesis would become greater at 5°C than 20°C only when sunlight was less than about 100 μmol m^{-2} s^{-1}. However, this is an unusually low light level for coniferous forests, even for full shade (Smith et al. 1989; Chazdon and Pearcy 1991). More important, photosynthesis at such low light levels would be reduced to near 0.1 mg m^{-2} s^{-1}, less than 15% of the maximum rate predicted for light-saturated leaves at 20°C. Also, these data show that increased light levels would not improve photosynthesis substantially unless accompanied by warmer leaf temperatures (Sprugel 1989, fig. 2). In more general terms, the evolution of greater limitation to one resource (e.g., sunlight) so that limitation to another (e.g., temperature) is diminished would only be tenable if photosynthesis and annual carbon gain increase (Schulze 1982; Gower and Richards 1990). We believe that the scenario proposed by Sprugel is not the correct interpretation of the benefits of upright, needle-like leaves to conifer tree photosynthesis. We propose that benefits of conifer architecture do result from needle-like and upright leaves, but for quite different reasons.

There is evidence that conifer leaf and shoot architecture may be adaptive for increasing leaf temperatures to nearer optimal levels for photosynthesis, often well above air temperature (Smith and Carter 1988). Needle temperatures in several subalpine conifers were well above air temperature during much of the day and, as a result, were closer to optimum temperatures for photosynthesis. This warming is due to a decrease in air flow around individual needles that are tightly packed and, thus, a decrease in convective heat exchange. Other studies have also reported conifer needle temperatures well above air temperature for fully sunlit shoots as well as for leaves of other species with densely packed leaf arrangements (see citations in Smith and Carter 1988). Any tight packing of individual needles along a stem, shoots on a branch, or branches within a crown can generate an additional aerodynamic warming, especially if mutual shading is minimized. At the shoot level, this warming occurs even though many needles are angled steeply to the incident sunlight. Sun shoots of many conifer tree species typically have a more tightly clustered and upright arrangement of needles than shoots developing in shade, as well as higher leaf temperatures. It is also relevant that a needle-like leaf geometry will minimize mutual shading for virtually any leaf orientation, even for densely packed needles. As a result, there is a substantial increase in the potential for photosynthetic carbon gain per unit stem length (Carter and Smith 1985; Smith et al. 1991). Thus, the needle-like leaf structure, upright leaf orientation, and tight packing generates a large number of leaves per stem length on the sun-exposed branch tips, minimal mutual shading, and warmer leaves. Additional warming of needle temperatures in conifer trees was also due to the clustering of lateral shoots within a given branch layer of the crown (W. K. Smith and W. T. Simons, unpublished manuscript) or due to whole-crown effects, such as krummholz mats of upper timberline conifers (Hadley and Smith 1989). A characteristic feature of tightly packed leaves in any arrangement is that greater leaf warming can occur at lower incident sunlight because of reduced convective heat exchange.

The interpretations above contrast with Sprugel's (1989) conclusion that more vertical, needle-like leaves serve primarily to increase sunlight penetration into the crown and reduce incident sunlight on individual leaves so that cold temperature limitations on photosynthesis are minimized. It seems illogical that the evolution of a strong light limitation would occur so that temperature sensitivity was reduced, unless the net result was an increase in annual carbon gain. If there is an advantage for reducing sunlight incidence on conifer needles, it may stem from the well-documented effects of concurrent cold temperatures and high light on photoinhibition of photosynthesis (Sakai and Larcher 1987). However, incident light is already substantially reduced at the leaf surface, without orientation effects, because of the characteristically curved leaf surface evident in the cross-sectional geometry of conifer needles (Jordan and Smith 1993). In fact, the only way small cylindrical leaves can warm in sun to the level of a larger broadleaf would be to increase packing without mutual shading (W. K. Smith and W. T. Simons, unpublished manuscript).

WINTER CONDITIONS

The adaptive significance of conifer leaf, shoot, and crown structure may be most important for winter rather than summer growth conditions. Although a conical crown with tightly packed, needle-like leaves may maximize sunlight interception, leaf warming, and photosynthesis, these structural features could be most important for withstanding the severe shear forces and snow loading that occur in winter. Evergreen tree species with larger broad leaves are virtually nonexistent in habitats with severe winters. This is not surprising when one considers the effects of winter wind and snow deposition on a crown composed of large broadleaves. In contrast, the mechanical strength of the conifer needle has been documented (Niklas 1991), as well as the capabilities of a conical crown with a layered branch configuration for withstanding wind shear and snow loading (see Tranquillini 1979; Sakai and Larcher 1987 for reviews). Despite these apparent capabilities, significant foliage loss in coniferous forests due to winter wind shear may still be an important selective pressure not fully appreciated (Grier 1988).

Conifer needle mortality from cuticle abrasion (blowing snow) and subsequent desiccation has been reported for upper timberline trees (Tranquillini 1979; Hadley and Smith 1986, 1987, 1989) and the upper canopy of trees within relatively closed stands of subalpine forest (Hadley and Smith 1990). Cuticle damage was always greater on the exposed, windward sides of individual shoots and leaf crowns. For upper timberline trees, snow cover during winter was crucial for new shoot survival and is enhanced by the snow-collecting capabilities of the krummholz mat growth form (Hadley and Smith 1989). A similar finding has been reported for the leaves of young *Larix lyallii* (alpine larch) that are maintained for one winter and the subsequent growing season in this otherwise deciduous conifer tree (Richards and Bliss 1986). We have also observed a rather remarkable capability for snow accumulation on the foliated shoots and branches of many conifer tree species. This capability could certainly reduce the potential for cuticle abrasion during winter. In addition, snow accumulation on branch tips of *Abies lasiocarpa* and *Picea engelmannii* resulted in significant needle warming at night when radiative cooling reduced exposed branches without snow to over 6°C below air temperature (W. K. Smith and J. H. Hadley, unpublished data). This measurement period was fairly typical of the coldest nights of the winter when severe winter storms are followed by nights with clear skies and, often, the lowest minimum air temperatures of the year (< −30°C). Thus, the snow-collecting capabilities of exposed branch tips may also be adaptive for avoiding extreme temperature minimums.

SUMMARY

In summary, we believe that the primary adaptive significance of the characteristic leaf, shoot, and crown structure of conifer trees is not because a more vertical leaf orientation of a needle-like leaf results in greater light penetration through upper branches to those lower in the leaf crown or less low-temperature limitation to photosynthesis at lower incident light (Sprugel 1989). Instead, the tight packing of needle-like leaves on individual shoots, along with the conical crown shape and layered arrangement of branches, may be essential for survival during winter, the most stressful period of the year. However, evidence suggests that these same structural features may also enhance summer carbon gain by increasing direct sunlight interception, leaf warming, and photosynthesis per unit of stem biomass.

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Submitted May 20, 1992; Revised April 5, 1993; Accepted May 20, 1993

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Associate Editor: F. Stuart Chapin III