

DOES PHOTOSYNTHETIC BARK HAVE A ROLE IN THE PRODUCTION OF CORE VS. OUTER WOOD?

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ABSTRACT

This paper hypothesizes a correlation in some species between the cambial age of transition from core (juvenile) to outer (mature) wood and the cambial age of transition from photosynthetic to non-photosynthetic bark. Secondly, this paper hypothesizes that the relationship is causal: a signal produced in relation to the photosynthetic bark affects wood development a few millimeters away. It is further hypothesized that the photosynthetic periderm is replaced by a non-photosynthetic one at light levels below its light compensation point. In *Tsuga heterophylla* and *Pseudotsuga menziesii* var. *menziesii*, the cambial age at which the first periderm dies (the base of photosynthetic bark) ranges from 16 to 33 and 12 to 43 years, respectively, for four Oregon Coast Range populations. These values are in the same range as the cambial ages of transition from core to outer wood, as shown by literature values and data reported here on tracheid length in *T. heterophylla*. In both species, the cambial age at the base of the live crown is not coincident with, nor consistently higher or lower than, the height of the lowest photosynthetic bark. Data presented here are consistent with the photosynthetic bark hypothesis of formation of core wood, but manipulative studies are needed to further explore the relationship.

Keywords: Core wood, crown wood, wood quality, tracheid length, fiber length, periderm, tracheid, juvenile wood, cambium, phellogen.

INTRODUCTION

In softwoods, the wood produced near the pith often has different anatomical, mechanical, and drying properties than the wood produced farther from the pith, giving a tree a zone of core wood (also called juvenile wood) surrounded by a sheath of outer wood (also called mature wood). Core wood is generally inferior to outer wood for structural applications because of its lower strength and stiffness; its increased warp, bow, and crook during drying; and its higher longitudinal shrinkage (Senft et al. 1985) due to the ultrastructure of its cell walls. The shorter rotations and more rapid growth that are anticipated for trees in the future are likely to increase greatly the proportion of core wood in the timber resource.

This paper introduces a correlative and then

a causative hypothesis relating core wood production to the type of bark overlying the cambium for two coniferous species, *Tsuga heterophylla* (Raf.) Sarg. (western hemlock), and *Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco (Douglas-fir).

- 1) The zone of the tree covered by photosynthetic bark is correlated with the zone of the tree that is currently producing core wood.
- 2) A signal produced in relation to the photosynthetic bark prevents outer wood from forming (or, perhaps, causes core wood to be produced). This signal is produced within millimeters of the vascular cambium. Where the light environment drops below

the photosynthetic bark's light compensation point, a new periderm is initiated. This periderm performs no photosynthesis.

Photosynthetic bark referred to in this paper is the green tissues immediately underneath the surface on the younger part of trunks and branches. These tissues may include the pheloderm produced by the first phellogen, or the interior-lying cortex, a primary tissue.

The second hypothesis is motivated by the issue of why the living plant produces core wood, and what the development signals are that cause the transition from core to outer wood. Surprisingly little research has gone into understanding core wood's function in living trees or the biological mechanisms that induce its formation. Most research into core and outer wood has focused on how these zones influence properties or value of the forest products (e.g., Megraw 1985; Maguire et al. 1991; Cown 1992), where the zones occur on the bole (e.g., Cown and McConchie 1980; Fukazawa 1984; Yang et al. 1994), how growth conditions affect their distribution (e.g., Clark and Saucier 1989), and the extent to which their properties are heritable (e.g., Cown and Parker 1979; McKimmy and Campbell 1982; Zobel and van Buijtenen 1989; Vargas-Hernandez et al. 1994).

This paper presents the cambial ages at which the photosynthetic bark is replaced by the first deep periderm, and compares this to the age of transition from core to outer wood, both from literature values and from data using tracheid lengths in western hemlock. The live crown hypothesis of core/outer wood formation (Larson 1962, 1969) explains wood quality in terms of distance from the foliage, considering foliar vigor and the plant's phenology. The most simplistic interpretation of the live crown hypothesis is that core wood is produced within the live crown and outer wood is produced below the base of the live crown. This paper also presents data on the cambial age at the base of the live crown, to allow comparison of the live crown and the photosynthetic bark hypotheses, and to permit discus-

sion of experimental manipulations to test between them.

MATERIALS AND METHODS

Cambial age at the base of photosynthetic bark (age_{pb}) and the base of live crown (age_{lc})

Ten western hemlock trees (in monoculture) and 10 Douglas-fir trees (in a stand of 80% Douglas-fir/20% western hemlock) were studied from a 34-year-old plantation (planted at 2 years old) at current densities of 450 stems/ha in the Siuslaw National Forest in the Coast Range, Oregon (longitude 123°57'W, latitude 44°25'N, 400 m elevation). After estimating tree height from the ground, a person on a ladder determined the height of the lowest photosynthetic bark. This was done by nicking the surface to get below the outer tissues and looking for green coloration. A core was then taken from that height on the bole to learn the cambial age (number of growth rings from the pith) at the base of photosynthetic bark (age_{pb}), which could also be defined as the cambial age of the stem where the second periderm forms and the first photosynthetic periderm dies.

The cambial age at the base of photosynthetic bark (age_{pb}) and the cambial age at the base of the live crown (age_{lc}) were also determined for 85 Douglas-fir trees from the McDonald-Dunn Forest of Oregon State University (longitude 123°15'W latitude 44°35'N, 120 m elevation) in the Oregon Coast Range. The trees were in a 55-year-old natural stand at 200 stems/ha. Age_{pb} and age_{lc} were determined by coring the bole at the base of the photosynthetic bark or live crown to learn the corresponding cambial ages. Height to live crown was defined as the height to the lowest point on the bole with ≥ 2 live branches.

Age_{pb} was studied also in western hemlock from Oregon State University's Blodgett Tract (longitude 123°20'W, latitude 46°05'N, 325 m elevation). The stand, predominantly western hemlock, currently had 300 stems/ha (> 20 cm dbh) but had been thinned 3 years prior to the study. Six trees were felled that appeared to

TABLE 1. Cambial ages of the lowest photosynthetic bark (age_{pb}) and the base of the live crown (age_{lc}) on boles of *Tsuga heterophylla* and *Pseudotsuga menziesii* var. *menziesii* trees from three sites in the Coast Range, Oregon (mean \pm s.e.). Maximum and minimum values are given in parentheses.

	n	Tree age (yr)	Age _{pb} (yr)	Age _{lc} (yr)
<i>Tsuga heterophylla</i>				
Siuslaw	10	38	18.6 \pm 1.0 (16–26)	no data
Blodgett	5	52.0 \pm 1.1 (50–56)*	25.6 \pm 3.2 (17–33)	28.0 \pm 0.8 (27–31)
<i>Pseudotsuga menziesii</i>				
Siuslaw	10	38	22.4 \pm 0.9 (17–28)	no data
McDonald-Dunn	85	55	26.4 \pm 0.7 (12–43)	31.2 \pm 0.7 (19–45)

* Breast height age.

vary in the height of base of photosynthetic bark (actually chosen by the top of the scaly bark, which is visible from the ground). Suppressed trees and those with forks or other unusual form were avoided. Tree height and the height to the base of the photosynthetic bark were measured. Disks were removed every two meters (described below), and age_{pb} was interpolated from ages of the disks.

Wood quality in relation to photosynthetic bark and live crown

Average tracheid length was used as an indicator of core vs. outer wood (e.g., Yang et al. 1986) as a means of learning whether the transition from core to outer wood occurs near the same cambial age as age_{pb} , age_{lc} , neither, or both. The height to live crown was measured for the six felled western hemlock trees from Blodgett. Then disks were taken from stump height, every 2 meters along the bole, and at breast height. The cambial age of each disk was determined by counting its growth rings, and then one sample of latewood for each of the outer three growth rings (separately) was removed with the aid of a chisel, hammer, and razor blade. At any height, therefore, data were acquired on three growth rings. The latewood was macerated, then stained with 1% aqueous safranin. Forty tracheid lengths/growth ring were obtained from the macerations using an Apple Macintosh-based image analysis system and NIH Image software (Rasband 1992). The operator points to each end

of unbroken tracheids on the digitized image, and the computer records their length. Thus, the operator decides which tracheids to use, eliminating broken or clumped tracheids. One tree was removed from the study because its growth rings were too narrow to sample. For a second tree with narrow growth rings, one maceration per disk was made for the outer three growth rings pooled. Cambial ages of the base of live crown (age_{lc}) were interpolated from height/age relationships of the disks.

RESULTS

Cambial age at the base of photosynthetic bark (age_{pb})

In western hemlock, age_{pb} ranged from 16 to 33 years, averaging 19 and 26 years, in the Siuslaw and Blodgett, respectively (Table 1). In Douglas-fir, age_{pb} ranged from 12 to 43 years, averaging 22 and 26 years, in the Siuslaw and McDonald-Dunn, respectively (Table 1).

Cambial age at the base of photosynthetic bark (age_{pb}) vs. at the base of live crown (age_{lc})

The cambial age at the base of the photosynthetic bark (age_{pb}) explains very little of the cambial age at the base of the live crown (age_{lc}) in the trees in this study. For the 85 Douglas-fir trees from the McDonald-Dunn Forest, the correlation was significant at $P < 0.01$ but with an r of only 0.37 (Fig. 1).

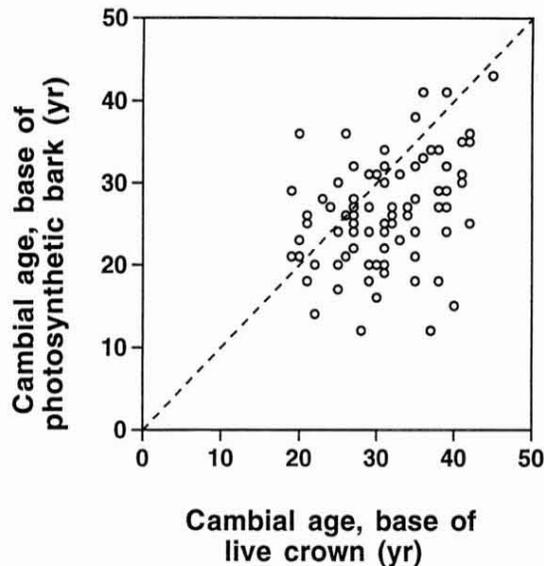


FIG. 1. Cambial age of the base of live crown vs. base of photosynthetic bark for 85 *Pseudotsuga menziesii* var. *menziesii* trees from McDonald-Dunn Forest, Coast Range, Oregon. The dotted line is where the cambial age of the base of live crown equals the cambial age of the base of photosynthetic bark.

Wood quality in relation to height of photosynthetic bark and live crown

In western hemlock, tracheid length of the outer rings increased from the base of the bole for a few meters, leveled off, and then declined toward the top of the tree (Fig. 2). This decline, an indicator of core wood, occurred near the location of both the base of the photosynthetic bark and the base of live crown. The five individuals varied with respect to whether the base of the photosynthetic bark or the live crown was higher (compare, for example, their relative locations in Fig. 2A and D). The standard errors for tracheid lengths were generally <0.1 mm, and did not extend beyond the plot symbols on the figure.

DISCUSSION

Cambial age at the base of photosynthetic bark (age_{pb})

The ages of bark transition were in the approximate range of the ages of wood transition

usually reported in the literature. This study found transition ages of 16–33 years for western hemlock. The only literature values found for transition age in western hemlock were for variation in specific gravity in western hemlock by distance from the pith, not age (Krahmer 1966). That report concluded that the wood in the first 5 cm from the pith had higher specific gravity than the wood beyond that, and from graphs shown, this could represent ages from roughly 13 to 35 years.

This study found bark transition ages for Douglas-fir of 12 to 43 years (averaging 22 and 26 years in the two stands), similar to reported values for wood transition. For Douglas-fir, Abdel-Gadir et al. (1993) found that the average cambial age at which mature wood formed was 27 to 37 years at breast height, depending upon the property considered ($n = 360$ trees from Wind River, WA). For wood specific gravity, the cambial age of transition from core to outer wood ranged from 11 to 37 years, with an average of 25 years ($n = 180$ trees from Wind River, WA, Abdel-Gadir and Krahmer 1993). For those trees, the mean ages of transition ranged from 22 to 29 years for the ten provenances studied, and 17 to 30 years for the 30 half-sib families studied (where all members of a half-sib family have one parent in common and the other parent unknown). For stand-grown Douglas-fir trees from British Columbia, Di Lucca (1989) found that the transition age for specific gravity was 23 ± 6 years (mean \pm SD, $n = 37$), with a range from 11 to 48 years.

Wood quality in relation to height of photosynthetic bark and live crown

The cambial age at the base of photosynthetic bark was similar to the cambial age at the base of the live crown in Douglas-fir and neither consistently higher nor lower, indicating the difficulty of distinguishing the causal signal through correlations without experimental manipulation. With the low number of trees tested and the low magnitude of variation in age_{pb} and age_{lc} , it was not possible to con-

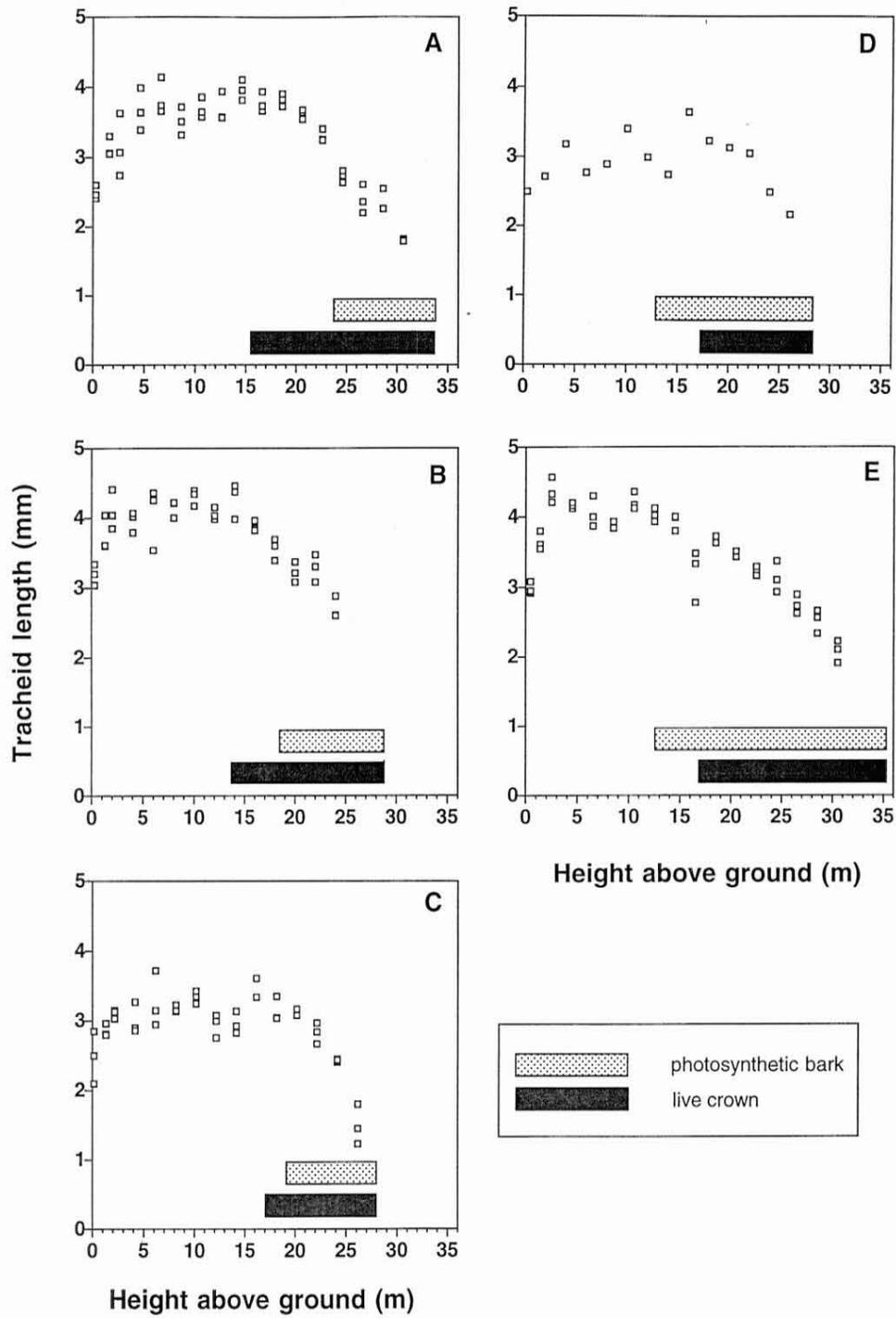


FIG. 2. Tracheid length, zone of photosynthetic bark, and zone of live crown as a function of height above the ground for boles of *Tsuga heterophylla* trees. At any height, tracheid lengths are shown separately for each of the outer three growth rings (40 measurements/growth ring), except for tree D, for which the three outer rings are combined. Standard errors are smaller than the plot symbols.

clude whether age_{pb} or age_{lc} was better correlated with the change in wood quality (indicated by tracheid length).

Current paradigm: live crown.—The current view of core wood production states that core wood is produced in the vicinity of the live crown and that outer wood is produced beyond the region influenced by the crown. This live crown hypothesis of core wood production is further elaborated to include theory on width to which cells develop (dependent on season-dependent auxins, manufactured in the canopy) and the degree to which the cell walls thicken (dependent on rate of division and the season-dependent availability of photosynthate; e.g., see Larson 1962, 1969; and discussions on p. 5 of Megraw 1985, Di Lucca 1989). According to the hypothesis, the developmental fate of a tracheid should depend on its location relative to the crown, and on the time of year.

Di Lucca (1989) compared the height of the wood transition to the location of the base of the live crown for specific gravity in 37 Douglas-fir trees. The height of wood transition was lower than the height of live crown; but the values became closer as the trees became older: for trees averaging 23, 30, and 37 years old, height of the core/outer wood transition was lower than the live crown by an average of 10.5, 9.3, and 3.8 m, respectively. Thus, Di Lucca concluded that the live crown hypothesis was unable to explain the location of the transition zone from core to outer wood. However, his criterion for live crown was more restrictive than the hypothesis required (not taking into account lengths of branches, quantity and vigor of foliage), and in general terms, there are many observations consistent with the live crown hypothesis (e.g., Aloni and Zimmermann 1983).

Proposed mechanism: photosynthetic bark.—At a stem's tip, the outer tissues (external to the phloem) originate at the apical meristem. They include cortex (which may be photosynthetic), and epidermis. As the xylem increases in diameter, the outer tissues must increase in circumference. This is accomplished, usually after several years of stem growth, by products

of the first periderm (the meristematic phellogen and its products, the phellem and the phelloderm). The first phellogen arises from parenchyma cells within the cortex, epidermis, or even phloem (reviewed in Srivastava 1964, p. 227; Borger 1973) (Fig. 3A). The phellem (cork), produced to the exterior, differentiates and then dies and becomes air- and water-impermeable. Any tissues external to a phellem layer will die because their supplies are cut off from the plant. The phelloderm, produced to the phellogen's interior, can contain chlorophyll and can fix measurable quantities of CO_2 (e.g., Foote and Schaedle 1978). While not always apparent, this first phelloderm, or perhaps the interior-lying cortex, often functions photosynthetically for up to several decades. A stem with only a first periderm usually appears smooth. In some cases it is green, and in other cases green only if it is nicked, depending on the thickness and opacity of the overlying layers. In some conifers, stems with only one periderm will have visible resin pockets (resin blisters).

In most woody species additional periderms arise internal to the first periderm, this time from the parenchyma cells of the phloem (Fig. 3B). There is very little information on the age at which this occurs (Srivastava 1964). After an additional periderm forms, bark photosynthesis must cease: supplies are cut off to the first phelloderm (now external to the current phellem), and the light level is too low for pho-

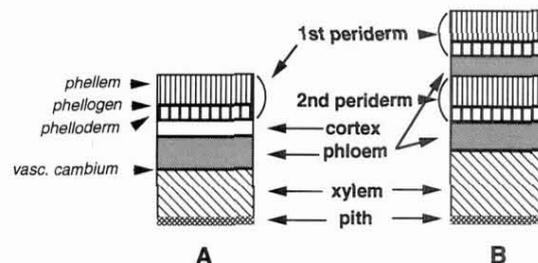


FIG. 3. Bark development and anatomy. A). Stem with only one periderm. The phelloderm and/or cortex may be photosynthetically active. B). Stem after formation of a sequent phellogen. The phellogen from the first periderm dies, and the phelloderm (if formed) from the sequent periderm, is not photosynthetically active.

tosynthesis in the new phelloderm. After development of these "deep" periderms (including second and "sequent" ones), the bark is usually brown or scaly, and has no turgid resin pockets.

The light compensation point is that photon flux density at which the carbon fixed just equals that required by the photosynthetic organ (leaf, bract, branch, fruit, etc.) for self-maintenance (Larcher 1980, p. 102). It is often stated that a plant may allow an organ to senesce when its light environment falls below the light compensation point for some period of time. A codicil of the argument is that the organ may be subsidized with carbon from elsewhere, allowing it to live until it reaches a light threshold below that of the light compensation point. This statement has been hard to test empirically because both the light compensation point and the light level in the canopy are temporal and spatial averages, but the scale at which a tree averages them is unknown. It is likely that the second periderm forms where the light environment has declined below a threshold value which could be near the periderm's light compensation point, or lower or higher, depending on the individual or species.

How might the first periderm affect wood development? Its photosynthetic contribution to the *plant's* carbon budget is probably low and results mostly from recycled carbon (from respiration elsewhere in the stem), but its contribution to the *bark's* carbon budget may be quite significant (reviewed in Schaedle 1975). Perhaps more importantly, the first periderm is very close to the vascular cambium and connected to it by rays. Hormonal control of wood differentiation is far from completely understood (reviewed in Little and Pharis 1995), and it is possible that a small amount of a product of photosynthesis or some other substance related to maintenance or development of the photosynthetic apparatus could affect the wood's development. My hypothesis is that a chemical signal related to photosynthesis by the first periderm causes formation of core wood (or prevents formation of outer wood).

Just as suggested by the live crown hypothesis (Larson 1962, 1969), this chemical signal could be an auxin: auxins are found in the cambial zone of actively-growing 50-year-old *Pinus sylvestris* trees (Sundberg et al. 1993) and auxins are produced in the cytosol of chloroplast-bearing cells from *P. sylvestris* needles (Sandberg et al. 1990).

The photosynthetic bark hypothesis suggests that the location of the core/outer wood transition is systematically and causally related to the photosynthetic/non-photosynthetic bark transition (the location of formation of the second periderm). The cambial age of the transition should vary by habitat and cultural treatment, and could well vary by genotype. However, Olesen (1982) states that in some species the change in bark type with height is due to cyclophysis (maturation of the apical meristem) rather than a change induced by the lateral meristem. Also, some species appear to have first periderms for too long (*Abies*) or too short (*Quercus*) a period to affect the wood quality discussed here and so it is unlikely that the mechanism acts in those species.

The location of the two transitions need not be spatially coincident for a number of reasons. First, the signal may affect adjacent tissues, such as tissue on the opposite side of the stem or centimeters above or below the bark transition. Secondly, the cambial response may be dose-dependent, and thus be related to bark characteristics nearby as well as at some distance. Thirdly, it could take years for the cambial initials to take on their final configuration once a signal is stopped. These last two proposals explain how a discrete signal like presence/absence of photosynthetic bark could drive a gradual transition in wood properties that could take a decade or more to occur.

If core wood is produced for hydraulic and mechanical reasons rather than as an unselected result of development, then photosynthetic bark is well-located to act as an environmental sensor. The local light environment is probably highly correlated with the environment in which core wood is advantageous to the plant: light parts of the tree are the most

subject to wind and are the nearest to transpiring foliage. A darker location would be correlated with a lower part of the canopy or bole, or denser stand, where wind is less likely, the stem may be stouter, and the foliage is farther from the stem (so water demands are spatially and temporally dampened).

Discrimination between photosynthetic bark and live crown mechanisms.—One way to further study these phenomena would be to compare available genetic material (from progeny tests) with early vs. late ages of transition from core wood to outer wood to see whether they had high vs. low bases of photosynthetic bark, respectively. A second approach would be to manipulate the lowest branches. Removal of lower live branches or of their buds should accelerate production of outer wood if the live crown mechanism governs core vs. outer wood production, but should have no effect on wood quality if the photosynthetic bark mechanism is responsible. Additionally, shading the stem should accelerate outer wood production for the photosynthetic bark mechanism but have no effect if the live-crown mechanism holds.

Significance.—If photosynthetic bark does prove to be correlated with the quality of wood produced at a height, this information could be used in several ways. Silviculturists and tree breeders could use this bark characteristic as a non-destructive indicator of wood quality. Ecologists and physiologists could pursue research on signals and their consequences for wood and/or bark development.

Little is known about how bark photosynthesis affects plant growth, and bark may well be playing more roles than we have understood. Comstock and Ehleringer (1990) showed that young woody stems effectively scavenged respired (“recycled”) CO₂. Ballaré et al. (1990) showed that stem elongation of forbs is responsive to light environments sensed by the stems themselves. Lev-Yadun and Aloni (1993) reported that topped trees resprout according to a different pattern depending on whether the bark in the cut region was smooth or furrowed. More research is needed to learn to what extent the bark is influencing the quality,

quantity, and distribution of woody biomass, and to elucidate the varied roles played by tissues in the plant stem.

CONCLUSIONS

The location on the stem where the second periderm is produced and bark photosynthesis stops may be near the location where there is a transition from production of core wood to outer wood. Two types of data support this statement.

1) The age of transition from photosynthetic to non-photosynthetic bark is in the same range as reported values of transition ages from core to outer wood for Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) and western hemlock (*Tsuga heterophylla*).

2) Crown-to-root profiles of tracheid length (as a proxy for changes in wood quality, with short tracheids indicating the core zone) in western hemlock show a transition from core to outer wood in the same vicinity on the vertical axis of the trunk as the transition from photosynthetic to non-photosynthetic bark.

Data reported here are unable to distinguish between the hypothesis that the transition to outer wood occurs as a result of the crown becoming increasingly distant from the cambium as the crown lifts (the live crown hypothesis), or as a result of photosynthetic bark becoming shaded and replaced with non-photosynthetic bark (the photosynthetic bark hypothesis); manipulative studies are needed. Further study is merited to explore this hypothesis that a photosynthetic layer in the periderm, only millimeters from the vascular cambium and connected to it through rays, produces signals that influence the type of wood that is produced.

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