

Fiber length in young hybrid *Populus* stems grown at extremely different rates

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Abstract: Length of libriform fibers was measured in rings 2–7 at breast height in 7-year-old hybrid poplar stems from two clones (11-11, a *Populus trichocarpa* Torr. & Gray × *P. deltoides* Bartr. ex Marsh. hybrid; and D-01, of unknown taxonomic identity) grown in a controlled test of three spacings (0.5, 1.0, and 2.0 m) on an irrigated and fertilized site in western Washington. In each clone, samples included a very wide range of cambial growth rates, with ring widths from 1 to 19 mm. Growth rate, expressed in several ways, had no consistent effect on fiber length within rings of the same age for rings 2–6. For ring 7, however, there were positive correlations between most growth rate measures and fiber length. Whole-disk fiber length increased with overall growth rate as measured by stem diameter; this apparent anomaly is caused by the fact that fast-growing trees have more of their basal area concentrated in rings further from the pith than do slower growing trees, and these rings have longer fibers compared with rings closer to the pith.

Résumé : La longueur des fibres ligneuses simpliciponctuées de tiges de peuplier hybride âgées de 7 ans provenant de deux clones (11-11, un *Populus trichocarpa* Torr. & Gray × *P. deltoides* Bartr. ex Marsh. hybride et D-01 d'identité taxonomique inconnue) a été mesurée à hauteur de poitrine dans les cernes annuels 2 à 7. Les tiges provenaient d'un dispositif d'essai de trois espacements (0,5, 1,0 et 2,0 m) sur un site irrigué et fertilisé de l'ouest de l'État de Washington. Pour chaque clone, les échantillons couvraient une très large gamme de taux de croissance cambiale avec des largeurs de cernes de 1 à 19 mm. Le taux de croissance, exprimé de différentes façons, n'a pas eu d'effet conséquent sur la longueur des fibres à l'intérieur des cernes du même âge pour les cernes 2 à 6. Cependant, pour le cerne 7, il y avait des corrélations positives entre la plupart des mesures de taux de croissance et de longueur des fibres. La longueur des fibres pour les disques entiers augmentait avec le taux de croissance total mesuré à partir du diamètre de la tige. Cette anomalie apparente est due au fait que les arbres à croissance rapide ont une plus grande proportion de leur surface terrière concentrée dans les cernes plus éloignés de la moelle que dans le cas d'arbres à croissance plus lente, ces cernes ayant des fibres plus longues comparativement aux cernes situés plus près de la moelle.

[Traduit par la Rédaction]

Introduction

Hybrid poplar trees have received considerable attention during the past decade in the northwestern United States as a source of fiber for pulp production. Industrial owners have established thousands of acres of clonal poplar plantations, and additional plantings are planned in the region. Crosses between eastern cottonwood (*Populus deltoides* Bartr. ex Marsh.) and black cottonwood (*Populus trichocarpa* Torr. & Gray) have resulted in very productive clones and are the most common hybrids planted. Plantations are typically located on agricultural land and are grown on short rotations of 6 or 7 years (Stettler et al. 1988; Heilman et al. 1991).

Because wood produced in these plantations is destined for pulp and paper products, and because the majority of the wood cells are libriform fibers (hereafter referred to as fibers), fiber

length is a wood-quality characteristic of importance (Horn 1978; Amidon 1981). The focus of this paper is fiber length, rather than other characteristics important to pulp and paper, such as proportion and dimensions of vessel elements and proportion of broken fibers. Previous studies have reported on fiber length variation in *Populus* species and their hybrids. Numerous studies report an increase in fiber length with rings from the pith in *Populus* (Kennedy 1957; Holt and Murphey 1978; Murphey et al. 1979; Yanchuk et al. 1984; Bendtsen and Senft 1986). The implication of this pattern is that wood from trees grown on short rotations will have a shorter average fiber length than wood from older trees.

It is less clear how fiber length is affected by growth rate or the silvicultural practices that influence growth. Some studies report that fiber length increased with faster growth (Johnson 1942; Kennedy 1957; Kennedy and Smith 1959; Cech et al. 1960; Einspahr and Benson 1967; Posey et al. 1969; Yanchuk et al. 1984). Most of these studies were conducted with wood samples collected in natural stands, and growth rate differences generally were associated with differences in genotype (different stands), geographic location or site, and calendar year(s) during which the fibers were produced; exceptions were two reports concerning mean fiber length from either 1-year-old coppice sprouts (Kennedy 1957) or first-year shoots from cuttings or seeds planted in a nursery (Cech et al. 1960). Other studies, including most of the more recent studies using younger material from carefully tended hybrid poplar

Received October 31, 1997. Accepted February 2, 1998.

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Table 1. Range of growth rate measures and libriform fiber lengths in rings 2 and 7 from the pith in two *Populus* clones.

Characteristic	Clone D-01		Clone 11-11	
	Ring 2	Ring 7	Ring 2	Ring 7
Ring width (cm)	0.5–1.4	0.1–1.2	0.8–1.7	0.1–0.7
Basal area increment (cm ²)	0.3–3.1	0.3–18	1.3–5.1	0.3–9.3
Circumference increase (%)	175–400	2.8–17.4	133–576	1.5–13.5
Fiber length (mm)	0.59–0.74	0.79–1.05	0.56–0.71	0.85–1.09

plantations, report no effect of growth rate or silvicultural treatment on fiber length (Marton et al. 1968; Holt and Murphey 1978; Murphey et al. 1979; Phelps et al. 1982; Snook et al. 1986). One report documented an increase in fiber length with irrigation, but diameter growth was unaffected although height growth was increased (Einspahr et al. 1972). One study suggested a negative relationship between ring width and fiber length in 20-year-old hybrid poplar clones (Babos and Fillo 1970); this finding was attributed to a higher proportion of earlywood (which contained shorter fibers) in fast-growing than in slow-growing trees. Given these conflicting reports, we decided to conduct a detailed examination of the relationship between growth rate and fiber length in *Populus* hybrid clones grown in a controlled research trial in the Pacific Northwest.

Methods

Plant materials

Material for this study came from a hybrid poplar test plantation designed for a biomass fuel program, and is described in detail by DeBell et al. (1996). This source of material was ideal for study, because trees manifesting a very wide range of growth rates were available. They were similar in age to trees being harvested under current operational regimes, and some were of equivalent size. Also, within each clone, genetic variation was eliminated as a source of variation in fiber length between trees. The plantation includes two clones (D-01, 11-11) grown at three square spacings (0.5, 1.0, and 2.0 m), replicated three times. The D-01 clone is of unknown taxonomic identity; the 11-11 clone is a *P. trichocarpa* × *P. deltoides* hybrid. These two clones differ markedly in phenology, form, branching characteristics and growth rate; stem biomass yield at age 7 averaged 58 and 110 Mg/ha for D-01 and 11-11, respectively (DeBell et al. 1996).

The plantation was established from cuttings in spring 1986. All environmental conditions were closely controlled and very uniform. Fertilizer was applied prior to planting at rates equivalent to 100 kg/ha N, P, and K. An additional 100 kg N/ha was applied in May 1988 and again in March 1992. All plots were irrigated periodically with a drip system during each growing season and maintained in weed-free condition by herbicide application and hoeing.

Eighteen trees of each clone were harvested in December 1992, when the trees were 7 years old. The trees were selected from all spacings to represent the full range of diameters at the site; sample trees averaged 9.5 cm diameter at breast height and ranged from 4 to 16 cm. We cut one disk at breast height (1.3 m) from each harvested tree. The disks were kiln-dried to prevent decay and stored until fiber length measurements could be made.

Laboratory sampling and measurements

In the laboratory, stem radii to the outer boundary of each ring were measured to the nearest 0.5 mm. Disks in which not all seven rings could be identified, primarily the extremely small disks, were excluded from the study.

After the radius measurements were completed, a radial strip 5 mm wide, extending from pith to bark, was cut from each disk. The strips were split into individual rings, from which matchstick-sized subsamples were cut using a razor blade. Five subsamples were removed at even intervals across the radius of the ring, but their relative positions were not tracked. For a few very narrow rings, the ring was divided into four subsamples.

The subsamples were macerated in sodium chlorite and acetic acid, then stained with safranin-o to improve contrast for microscopic viewing. Libriform fibers from each subsample were mounted in glycerine on microscope slides. Fiber lengths were measured using an Apple Macintosh based image analysis system consisting of a video camera on a microscope that sent signals to a digitizing card in an Apple Macintosh computer. The software NIH Image version 1.42 (Rasband 1992) displayed the image and allowed calibration from pixels to microns. With the slide's image on the computer monitor, we used a mouse to locate the two ends of a fiber, and the software calculated fiber length. This method allows the operator to choose fibers that are unbroken and to search across the slide until sufficient measurements have been obtained.

Twenty unbroken fibers were measured on each of the five slides per ring, for a total of 100 fibers/ring (25 fibers/slide were measured for rings with only 4 subsamples). From these data, an average fiber length was calculated for each ring.

We characterized growth rate in three different ways, as ring width, annual basal area increment, and percentage circumference increase. In the following equations, r_1 is the inner boundary of the ring and r_2 is the outer boundary.

$$[1] \quad \text{Ring width} = r_2 - r_1$$

This value is the most common expression of growth rate in wood quality studies.

$$[2] \quad \text{Annual basal area increment} = r_2^2 - r_1^2$$

This value represents the actual amount of wood produced at a given height in the tree.

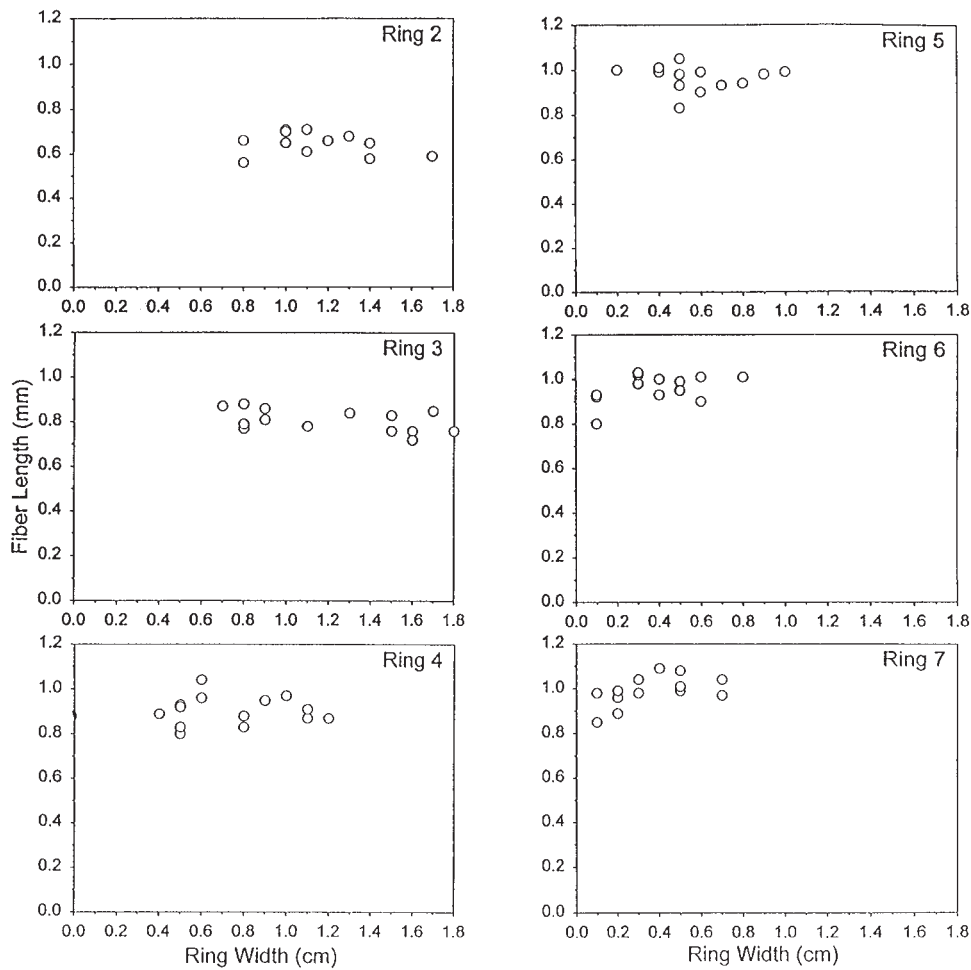
$$[3] \quad \text{Percent circumference increase} = [(r_2 - r_1)/r_1] \times 100$$

This value is intended to be an index of the number of number of new cambial cells required as the stem increases in girth. Bannan (1960) has shown that the average length of cambial initials is reduced by division to produce new cambial cells.

Data analysis

Because the first annual ring has an inner radius of zero and cannot be used in eq. 3 above, we conducted the analyses for effects of growth rate on rings 2–7 only. We analyzed relationships between fiber length and growth rate within rings produced during the same year with linear regressions, taking $p = 0.05$ as the level of significance. We also calculated a whole-disk average fiber length by weighting individual ring fiber lengths by ring areas. In addition, average values for several ring and disk characteristics were calculated for the three largest, three smallest, and three medium trees of each clone. These average values were plotted to examine differences in trends between fast- and slow-growing trees.

Fig. 1. Average libriform fiber length as related to width of growth ring for rings 2–7 at breast height in *Populus trichocarpa* × *P. deltoides* clone 11-11. On any panel, each data point represents a different individual.



Results and discussion

There was an extremely wide range in both growth rate and libriform fiber length within either clone (Table 1; also see ranges of values in Figs. 1, 2, and 3). Nonetheless, there was no consistent relationship between the two within individual rings produced during the years 2 through 6 (Table 2, Fig. 1). Both clones had some rings that showed statistically significant relationships between some measures of growth rate and fiber length, and most of these significant relationships were positive. In the majority of cases for these rings, however, fiber length was not significantly related to growth rate. Conversely, fibers produced in year 7 were positively correlated to all expressions of growth rate for clone D-01 and to two of three measures for clone 11-11 (Table 2).

These results for effects of growth rate on fiber length within rings produced in the early years were consistent with other results reported in the literature. Although some research on 1-year-old material suggested a positive influence of growth rate on fiber length in poplar (Kennedy and Smith 1959; Cech et al. 1960), most studies with young, intensively cultured poplars have concluded that growth rate, or silvicultural practices that influence it, have no effect on fiber length (Marton et al. 1968; Holt and Murphey 1978; Murphey et al.

Fig. 2. Mean whole-disk fiber length as a function of stem diameter at breast height for 7-year-old trees from cuttings of two *Populus* clones, D-01 (unknown parentage; solid circles and heavy line) and 11-11 (*P. trichocarpa* × *P. deltoides*; open squares and thin line). Each data point represents a different individual.

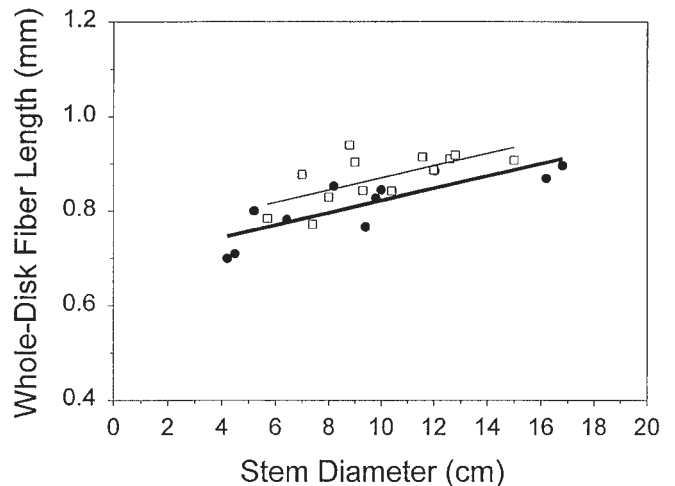


Fig. 3. Mean sample characteristic as a function of ring number from the pith and diametric growth rate for *Populus trichocarpa* × *P. deltoides* clone 11-11 (each value represents the mean for six individuals). (A) Stem diameter; (B) ring width; (C) ring area as percentage of basal area; (D) libriform fiber length.

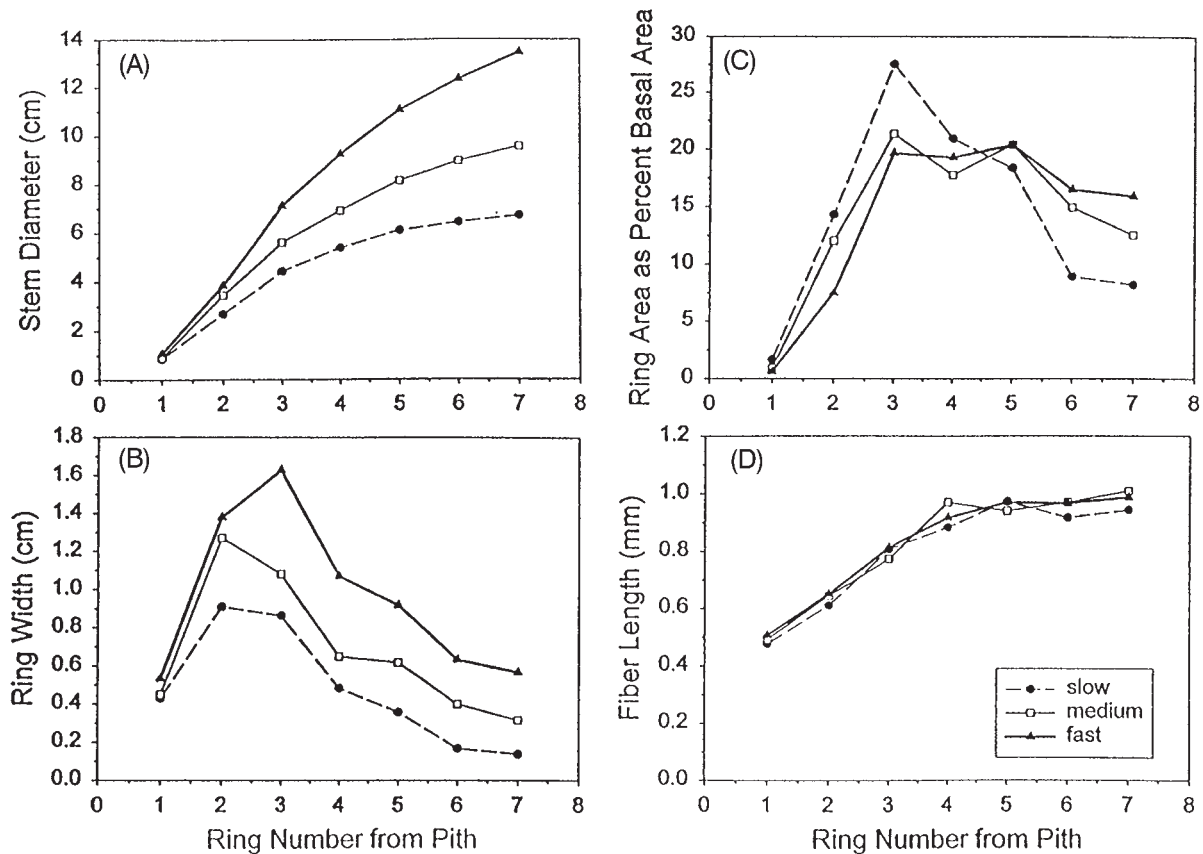


Table 2. Results from regression of libriform fiber length on three measures of growth rate.

Clone	Measure of growth rate	Ring number					
		2	3	4	5	6	7
D-01	Ring width (cm)	0.01 (+)	0.90	0.04 (+)	0.54	0.21	0.02 (+)
	Basal area increment (cm ²)	0.01 (+)	0.44	0.07 (+)	0.44	0.32	0.01 (+)
	Circumference increase (%)	0.75	0.07	0.02 (+)	0.91	0.16	0.04 (+)
11-11	Ring width (cm)	0.29	0.11	0.95	0.62	0.18	0.04 (+)
	Basal area increment (cm ²)	0.25	0.40	0.94	0.64	0.26	0.13
	Circumference increase (%)	0.83	0.01 (-)	0.44	0.77	0.13	0.02 (+)

Note: Values are the probabilities that the regression slopes are significantly different from zero. The plus and minus signs in parentheses are the slopes of the regression lines for significant *P* values.

1979; Phelps et al. 1982; Snook et al. 1986). Several studies conducted primarily with older material from natural stands did find a positive correlation, however (Johnson 1942; Einspahr and Benson 1967; Posey et al. 1969; Yanchuk et al. 1984). At least some portion of the inconsistencies among findings may be related to real differences (or the ability to detect them) between relationships in the juvenile versus mature core.

We had expected to find a negative effect of rate of circumference increase on fiber length, given existing knowledge about lateral divisions and how they may affect the length of cambial initials, i.e., cambial initials are shorter when the rate of anticlinal division is high (Bannan 1960). But there are sev-

eral possible reasons why there was no significant negative relationship between rate of circumference increase and fiber length in our study. First, the rate of anticlinal division is not directly correlated with circumference growth. The number of anticlinal divisions exceeds the number required for increase in cambial circumference (Bannan 1960; Evert 1961). In both gymnosperms and angiosperms the rate of production is also accompanied by a high rate of loss (Philipson et al. 1971). This suggests that there may not necessarily be more production of new initials with high versus low rates of cambial division. Second, postcambial cell elongation of fibers in hardwoods averages 140% (Panshin and deZeeuw 1980); one measurement for *Populus* (species not listed) indicated 84% (Bailey

1920). Therefore, differences in length of cambial initials could be masked by differences in degree of fiber extension during maturation.

In contrast to the individual ring results, whole-disk average fiber length of both clones increased with growth rate as measured by stem diameter (Fig. 2). Although the clones have different average fiber lengths, the rate of increase in fiber length with stem diameter was nearly equal in both clones. Both regressions were highly significant; size (hence cumulative growth rate) accounted for more than 40% of the variation in fiber length of clone 11-11 and nearly 70% of the variation in clone D-01 ($r^2 = 0.43$ and 0.69 , respectively). Although such relationships may appear anomalous to results from individual ring analyses, they are consistent if we consider trends in both growth rate and fiber length over time in trees grown at different rates. These trends are displayed in Fig. 3 for slow-, medium-, and fast-growing trees of clone 11-11 only, but the patterns for clone D-01 mirror the patterns shown.

By age 7, the differences in annual growth rate had created substantial differences in stem diameter between the fastest- and slowest-growing trees (Fig. 3A). Ring width was generally greatest at ring 2 for medium- and slow-growing trees and greatest at ring 3 for fast-growing trees, and then it decreased gradually in trees of all growth rates (Fig. 3B). When ring area was graphed as a percentage of total cross-sectional area, trends were markedly different for fast- versus slow-growing trees. In the smaller trees, maximum ring area occurred at ring 3 and then decreased markedly; however, in the larger trees, maximum ring area occurred at ring 5 and subsequently decreased only slightly (Fig. 3C). The relevance of these differences becomes apparent when trends in fiber length are considered (Fig. 3D); older rings have longer average fiber lengths. Because faster growing trees have more of their basal area in older rings (Fig. 3C), and older rings have longer fibers, the average whole-disk fiber length is greater for faster growing trees. This difference amounts to about 0.13 mm in average whole-disk fiber length over the range of disk sizes we measured.

Summary and implications

Our data indicate that fiber length within rings produced at the same age and during the same growing season is unrelated to growth rate of *Populus* during the first 6 years of growth; thus, growth rate of short-rotation poplar can be increased without concern that fiber length may be negatively affected. Furthermore, we found positive correlations between growth rate and fiber length in rings produced at age 7, and many previously cited reports of positive relationships were based on samples collected from older trees. Fiber length differed significantly by clone and increased with ring age, indicating opportunities to influence fiber length through selection of clonal material and by choice of rotation age. In short-rotation cultural regimes, faster growth will most likely increase mean fiber length, because a greater proportion of wood is contained in older (outer) rings of fast-growing trees than of slow-growing trees. We believe that this general relationship will hold for most cultural practices (e.g., increased growing space and supplemental nutrition) that are applied to enhance growth rate.

Acknowledgments

This research was supported by a special USDA grant to Oregon State University for wood utilization research. The plantations were established with funds provided to the USDA Forest Service PNW Research Station's silviculture team at Olympia, Wash., from the U.S. Department of Energy through Interagency Agreement No. DE-A105-810RZ0914. We thank Mark Lavery for help in fiber length measurements.

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