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Tailoring Fiber Properties to Paper Manufacture: Recent Developments

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TAILORING FIBER PROPERTIES TO PAPER MANUFACTURE: RECENT DEVELOPMENTS

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ABSTRACT

Opportunities for more closely matching wood and fiber properties to end-use requirements are manifold and have long been recognized. Until recently, many approaches to capitalize on such opportunities were only hypotheses; few were being implemented. Benefits had not been realized due to long rotations for most US commercial tree species. Only general approaches, e.g., plantation management, were yielding returns. Other approaches are now providing or are poised to provide increased control over wood variability and quality. For example, plantations established with seed from early southern pine breeding are nearing harvest or are being harvested; stems are straighter and have finer, flatter branches. Reduced reaction wood and greater uniformity are the result. Brazilian scientists have more than doubled growth of *Eucalyptus* hybrids while also adjusting specific gravity to desired levels, narrowing its range of variability, and increasing cellulose content. This paper describes similar developments from across the spectrum of research and development. Examples range from classical breeding through silvicultural practices to harvesting and wood preparation in the woodyard. Possibilities for further manipulation via cloning, molecular genetics, and genetic transformation are also reviewed.

INTRODUCTION

Forestry operations would be most effective if trees were tailored to match specific end-uses. To move toward closer matches, organizations charged with designing, breeding, growing, and harvesting trees must be aware of activities and needs elsewhere in the manufacturing continuum (Figure 1). Similarly, those responsible for pulping and papermaking must be alert to effects of their needs and actions on others.

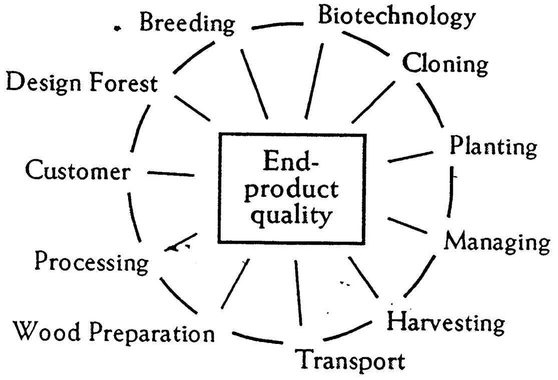
Much research has been devoted to raising forest productivity. Rapidly growing plantations are now the rule in many regions. Uncertainties about how wood from forests planted today will be used at harvest continue to inhibit efforts to modify wood and fiber properties. Biologically altering such properties requires knowledge of which are important and whether change can be accomplished more economically than by adjusting processing technology.

Deciding which properties to manipulate is difficult since the pulp and paper industry uses a wide variety of raw materials and manufactures an ever widening array of products. That different paper grades have contrasting requirements suggests that developing a universally acceptable set of wood and fiber properties is near impossible. Characteristics such as wood uniformity and paper strength, however, are common to many products.

The overall goal of this paper is to alert participants in the continuum to accomplishments in and opportunities for biological manipulation of wood and fiber properties, particularly those affecting wood uniformity and paper strength. As a first step, important properties were identified from basic and applied investigations of relationships between wood, fiber, and paper properties. The next step and main focus involve analysis of findings from research, development, and application in several phases of the manufacturing continuum: Breeding and Cloning; Management and Silvicultural Practices; and Harvesting and Wood Preparation. Finally, prospects for manipulation via Biotechnology are reviewed.

Effects on optical and other properties are mentioned only briefly. Chemical composition is discussed only as concerns lignocellulosic constituents; extractives are not considered. The general term fiber is used inclusively for softwood tracheids and hardwood fibers. When considered, other cell types, e.g., vessel elements, are mentioned separately. Discussion generally concerns tree species of commercial importance in the USA. Where necessary, however, examples are drawn from other countries.

Figure 1: The paper manufacturing continuum: End product quality depends upon individual and joint actions.



RELATIONSHIPS BETWEEN WOOD, FIBER, AND PAPER PROPERTIES

Breeding, growing, and harvesting trees with wood and fiber properties well suited to paper manufacture is complicated by competing needs of the paper and solid wood products industries. Properties contributing to bending stiffness are valued in lumber manufacture, whereas others seem critical to paper strength. Indeed, tree species ideal for manufacture of strong papers often are less suited for lumber production, and specialized strains may be needed to satisfy both customers (1).

Certain wood supply characteristics are valuable regardless of product. Cost is critical, since wood is so large a component of manufacturing expense (2). Assured supply across seasons and years is likewise important. Uniformity is also a key feature (3) in view of its impact on processing efficiency and product quality. Toward satisfying these needs, organizations responsible for breeding and growing trees have concentrated on traits such as growth, form, and pest resistance. Direct efforts to improve wood and fiber properties received lesser emphasis. Uncertainty as to importance of individual properties provided cause to defer or take only minor action (4).

Conflicts also occur within the pulp and paper industry since choice of pulping process and paper grade are influenced by wood and fiber properties. Selection of mechanical pulping process, for example, depends on tree species (5). With regard to products, the smooth, low-porosity papers demanded by printers require thin-walled fibers that readily collapse upon drying. In contrast, stiffness and compressive strength of paperboard varies with fiber wall thickness (1). Nonetheless, properties influencing paper strength seem important regardless of product.

Several methods have been used to identify wood and fiber properties critical to strength (6). Theoretical approaches designed to identify physical and chemical attributes governing tensile strength provide a useful starting point. The Page equation defines tensile strength in terms of individual fiber and bond strengths (7). Individual fiber or zero span tensile strength was seen as a function of fibril angle, natural or artificial defects, and lignin content (8). Bond strength was attributed to contact area between fibers and adhesion capability of fiber surfaces. Contact area was considered a function of fiber flexibility and conformability, which in turn depend on fiber dimensions such as length, perimeter, and coarseness. Adhesion capability was said to be associated with hydroxyl groups in cellulose and hemicellulose molecules.

Further analysis defined five principal pulp properties: fiber length, coarseness, wet compactability, intrinsic fiber strength, and cohesiveness (9). Coarseness and wet compactability were seen as functions of fiber wall thickness. Intrinsic fiber strength was attributed primarily to degree of cellulose polymerization and secondarily to fibril angle. Cohesiveness was considered a function of hemicellulose content.

More applied approaches, relying on multiple regression analyses, have also been used to relate paper strength to wood and fiber properties. An added advantage of such approaches is that they can easily be used to evaluate changes in one or more paper properties caused by breeding or silvicultural practices. An early example showed that several strength properties of handsheets made from slash pine (*Pinus elliottii*) kraft pulps were determined by zero-span tensile strength, fiber length, specific gravity, and proportion of juvenile wood (10). Similar analyses of kraft pulps from various *Eucalyptus* species and hybrids indicated that number of fibers per gram, pentosan content, and basic density were useful in modeling tensile strength, bulk, air resistance, and roughness (11). Also, tensile, burst, and tear strengths, stretch, and density of handsheets of kraft pulps from second-growth Douglas-fir (*Pseudotsuga menziesii*) varied with basic density, fiber length, coarseness, and quantities of long fibers (12).

The investigations reviewed above have varying outcomes, clearly illustrating complexity of relationships between paper strength and the properties of wood and fiber. Conflicting findings are expected in view of the diversity of tree species and products (11), and their prevalence underscores need for intensive interaction among participants in the manufacturing continuum (Figure 1).

For purposes of the present report, the collected findings also indicate that contributing wood and fiber properties can be reduced to relatively few, e.g., fiber length, fibril angle, and cellulose, hemicellulose, and lignin contents, and uniformity. Wood specific gravity or basic density is involved via its dependence on fiber dimensions such as wall thickness. Other properties may be involved, but the foregoing appear to be the most important of those that are also amenable to control by breeding, growing, and harvesting. In keeping with our purpose, these properties are discussed in ensuing sections from the standpoint of whether or not and to what extent they can be manipulated.

METHODS TO IMPROVE FIBER QUALITY AND PROPERTIES

Classical Tree Breeding

Classical tree breeding seeks to create trees with lasting improvement in growth, adaptability, and pest resistance. Wood and fiber properties are not often included as traits of primary importance; i.e., they seldom receive the same priority or emphasis as growth. Even so, prospects for improvement are good.

Manipulating wood and fiber properties has a place in breeding and is a useful tool for the future. Indeed, simple selective mating of straight trees gives offspring with reduced defects and reaction wood. Also, opportunities for improvement become more easily exploitable as harvest rotations become shorter. Acquiring knowledge as to how wood properties are inherited and how they can be improved is thus both prudent and necessary. Indeed, interest in the US has risen in recent years largely as a result of the desire to shorten softwood rotations and to develop systems for intensively managed short-rotation hardwoods.

Specific gravity.

Specific gravity or basic wood density is of key importance in the manufacture of both paper and solid wood products. As noted above, specific gravity contributes to paper strength in a variety of ways. Similarly, strength of solid wood products varies directly with specific gravity. Relative ease of measurement has fostered use of specific gravity as an index of wood quality.

Though generally viewed and manipulated as a single trait, specific gravity is a composite dependent primarily upon proportions of late to early wood, fiber size and number, and fiber wall thickness. In softwoods, proportions of latewood and thickness of latewood fiber walls appear to have greatest influence. Specific gravity of hardwoods is governed by these factors and also by proportions and sizes of vessel elements and other cell types. Chemical composition is contributory in all species but to an uncertain extent.

Contributing factors can vary together or independently of one another, and individual trees can have similar specific gravities for different reasons. High specific gravity in loblolly pine (*Pinus taeda*) is due to a high proportion of latewood with thick fiber walls. A high specific gravity *Eucalyptus* hybrid could have an elevated number of fibers with narrow lumens and relatively thin and flexible fiber walls.

Given the potential for variable responses, specific gravity can be altered by changing one or more contributing factors. Breeding to enhance paper strength therefore requires understanding what is changed and how that in turn affects paper properties.

Variation in specific gravity among and within species is significant and more than adequate for progress via classical breeding. Degree of genetic control is also strong. Heritability, or the ratio of genetic to total observable variance, ranges from 0.4 to 0.7, values as high or higher than those for any other trait of commercial interest in both softwoods and hardwoods. Summary tables of heritability values for various species are available (13, 14, 15).

Several considerations have prevented tree breeders from exploiting such opportunities on a larger scale (16). Prominent among these in the case of loblolly pine is the tendency of most organizations to seek development of an all-purpose tree. Cost is also a factor. Determining specific gravity costs considerably more than assessing growth. Also, correlations between growth and specific gravity tend toward the negative, and continued breeding for growth may decrease specific gravity.

Individual traits are often independent of or only loosely correlated with one another. Under these circumstances, breeders can secure improvement in both by expending some additional effort to identify, test, and breed more trees. The task is eased when two traits are correlated positively and strongly; i.e., significant numbers of trees are likely to excel in both traits. Should traits be correlated negatively, however, simultaneous improvement is difficult if not impossible.

Correlations between specific gravity and other characteristics vary greatly. Correlations with percentages of latewood and fiber wall thickness are positive and strong. As mentioned above, however, associations with growth are worrisome in that they range from slightly negative to slightly positive in most species (13, 14, 15). Given the small size of such correlations in certain species, breeders may be able to produce strains with desirable combinations of productivity and specific gravity (13). Even under the best circumstances, however, breeding for several traits is expensive. The marginal gain provided by including specific gravity in efforts to improve dry wood weight of loblolly pine was not considered worthwhile (17). This outlook is changing, however, as pine rotations are shortened; breeding to increase both growth and specific gravity seems warranted.

Concerns also have been expressed by hardwood breeders (18). Rather strong and negative correlations were found between specific gravity and growth in *Populus deltoides*, and simultaneous improvement was considered impractical. Given the greater impact of growth on profitability, breeding efforts seemed better focused on productivity. Such findings, however, are not universal, and breeding of some *Eucalyptus* hybrids has yielded considerable improvement in both growth and specific gravity (19 , 20).

As noted above, specific gravity is a complex trait, and changes in it could result from one or more causes. Thus, increasing specific gravity may not yield better wood and fibers (21). Uncertainties are greatest in hardwoods where specific gravity is more complex than in softwoods. Changes in vessel element numbers and sizes may be involved (13, 14). Additional work is needed to discern what changes occur as specific gravity is altered and how they affect pulp and paper properties.

One reason for lack of knowledge about such changes is that older methods for assessing wood and fiber properties either cannot identify causative factors or can do so only at great cost. Newer techniques and instrumentation may permit analyses of underlying causes (12 , 22).

Given that anatomic outcomes accompanying changes in specific gravity are not always understood, other approaches to altering the trait are worth considering (21). Lignin has a lower specific gravity than cellulose. If breeding or other approaches could be used to reduce lignin content, specific gravities would increase in proportion to cellulose, and fewer changes in wood anatomy might result. This may be one way that the new techniques of molecular genetics can assist classical tree breeding.

Fiber length.

Genetic variability in and genetic control of fiber length in most commercially important species is sufficient for improvement (13, 14, 15).

That opportunities for improvement have not been exploited with great frequency may result in part from the belief that improvement will not have significant impact. That is, increasing fiber length beyond roughly 2 mm does little to increase tear strength of kraft paper (13). Similarly, lengthening fibers beyond a certain threshold is not likely to enhance tensile strength (23). Thus, a 10 percent increase for a species with a mean fiber length of 1 mm may not be cost effective (13). Also, softwood fiber lengths typically average 3 mm, well above the minimum required for desirable strength in most products. In such species, efforts to improve fiber length could dilute effectiveness of breeding for other more important traits. On the other hand, breeding may be warranted in species or situations where mean fiber lengths are at or near 2 mm. Rapidly growing softwoods with high proportions of juvenile wood represent one possible situation.

A summary of research in softwoods (13) indicates that fiber length is negatively, though weakly, correlated with several other wood properties, including specific gravity. Associations with growth typically are positive and fairly strong.

Not nearly as much research has been done on correlations with other traits in hardwoods. Available data on major North American hardwoods suggest little or no association with specific gravity and rather strong, positive relationships with growth (14). As an example, a significant positive correlation was found between fiber length and growth in aspen (*Populus tremuloides*), and trees with long fibers at early ages had longer fibers when mature (24).

Another genetic approach to improving fiber length involved creation of triploid hybrids between *P. tremuloides* and *tremula* (25). Fiber lengths were at least nine percent longer than those of native aspen, and several paper properties were enhanced. Renewed emphasis on poplar hybridization in recent times has produced numerous rapidly growing hybrid clones. Whether fiber properties will be enhanced like those in aspen remains to be seen. The potential nevertheless is present, and increased research seems imperative in view of the increasing importance of hardwoods.

Fibril angle.

Few data are available on genetic variability and inheritance of fibril angle (13). Generally positive associations with other traits (for example fiber length) infer moderate genetic control. Lack of data no doubt results from difficulty and cost of measurement. Early methods for measuring such properties were expensive, slow and tedious, and limited in accuracy (12). Recent advances may yield more data as well as new insights into relationships with paper quality. As an example, an automated system for measuring softwood basic density, fiber wall thickness, and coarseness is being adapted to analyze hardwoods (22) and measure fibril angle (26).

Cellulose, hemicellulose, and lignin content.

Despite importance to papermaking, little is known about genetic variability and control of cellulose, hemicellulose, and lignin contents of major tree species. Difficult, expensive, and inaccurate measurement methods seem the main reasons for this lack of information (13).

Early research in softwoods disclosed only minor variation in holocellulose contents among loblolly pine families (27). Variation among trees within families, however, was quite large and partially heritable. Classical breeding was deemed impractical, but substantial gains seemed achievable through cloning outstanding trees. These and related findings were reaffirmed in a later review (19), which emphasized gains obtained via cloning. Specifically cited was outstanding improvement of *Eucalyptus* hybrids by Aracruz Florestal S.A. in Brazil. This organization sought to increase growth, specific gravity and cellulose content (19, 28). Pulp yields rose from 47 to 51 percent. Concomitant increases in uniformity, most certainly, reduced harvesting and processing costs.

As a contrasting example, minor genetic variation and control of holocellulose content was found for eastern cottonwood (*Populus deltoides*) clones (18). Variation in α-cellulose content was larger and under greater control; both variability and heritability were considered sufficient for breeding. Also found, however, was a negative correlation with growth. Simultaneous improvement was not considered practical; i.e., efforts to improve cellulose content were seen as likely to reduce gains in growth. Correlation matrices nevertheless are imperfect, and screening more individuals could yield clones excelling in both quantity and quality. The issue thus reduces to economics and how much processors are willing to pay for the additional effort required to improve quality.

Pentosan concentration, an approximation of hemicellulose content, has been evaluated in a number of species. A review of early research (14) disclosed only nominal variation in poplar species and hybrids. Though statistically significant in some instances, the limited variability was considered inadequate for breeding. In contrast, a recent analysis of nine *Eucalyptus* clones showed significant variation and rather strong genetic control (20). Further research on genetic control and implications for pulp and paper quality is warranted.

That natural variation in lignin content exists among and within species has been known for some time (13, 21). Investigations of genetic variation and control, however, are more recent. Lignin content of aspen (*Populus tremuloides*) families varied significantly, but the range was quite small, roughly three percentage points (29). Similar ranges have been found in loblolly pine (30) and black locust (*Robinia pesudoacacia*) (31). These and related investigations also show only weak genetic control. One exception is the strong genetic control found recently in improved *Eucalyptus* clones (20). In general, classical breeding does not seem a useful approach for modifying lignin content.

An analysis of the potential for improving wood properties (21) provided evidence, empirical and experimental, that genetic control of lignin content is independent of that governing holocellulose contents and specific gravity. Manipulating lignin quantity and quality, using the tools of molecular genetics, was considered feasible and not likely to have detrimental effects on wood formation.

Opinions differ about ease and utility of altering lignin quantity and quality, but prospects are tempting, and benefits could be significant. Given the millions of tons of wood pulped annually in the US, even a small reduction in lignin content would have tremendous impact on pulp yields and processing costs. Accordingly, several organizations have initiated research on molecular approaches; developments on this front are summarized in a succeeding section.

Regardless of approaches taken to manipulate lignin and/or cellulose, fast, accurate, and inexpensive methods are needed for measuring change. In general, older methods are not especially accurate and tend to be expensive and time-consuming (13). Some recent innovations offer much promise. Near-infrared reflectance spectroscopy of powdered wood was used to estimate pulp yield and cellulose content of several pine species (32). A similar approach was used to predict pulp yields and soda charge in soda pulping of *Eucalyptus* species. (33). Utility was also confirmed recently in our laboratory. Lignin contents, specific gravities, and growth rates of loblolly pine were estimated from 12 mm-increment cores. New techniques that are accurate, rapid, and inexpensive and that rely on small nondestructively collected samples open the way for manipulating cellulose and lignin contents and perhaps even specifying pulping and bleaching conditions.

Uniformity.

Classical breeding has helped lessen natural wood variability. Much more, however, can be done.

Given the importance of reaction wood to pulping properties, tree straightness and form were among the first traits considered for improvement by early tree breeders (13). Crooked trees contain larger quantities of reaction wood than straight ones. Similarly, branch size and angle directly affect knot and associated reaction wood quantities as well as amounts of resin and bark in nearby wood. Straightness and form were easy and inexpensive to assess and proved to be as strongly inherited as growth. Trees were therefore bred for straightness as well as for fewer and finer branches emerging at right rather than acute angles from the stem. Straight, small-limbed trees from early genetic tests produced greater pulp yields and tear strength than did crooked trees with large diameter branches (34). Plantations of improved trees are now being harvested; amounts of reaction wood have been reduced.

Improved resistance to fusiform rust, caused by *Cronartium quercuum* f.sp. *fusiforme*, further illustrates the impact of breeding on uniformity. This disease, often considered the most serious pest of southern pines, kills young trees and reduces wood quality in surviving trees (35). In wood near infections, fiber length and specific gravity are reduced, fibers are thin-walled and deformed, latewood fails to form, and resin content is increased. Wood supplies containing numerous infected trees require more chemicals for pulping and bleaching and also yield less pulp than those from healthy trees (36). Southern pine breeders have been culling susceptible trees from breeding populations for some years. Thus, plantations now have greater resistance (37); mortality, damage, and defects are lower.

Several other approaches to increasing uniformity and/or developing specialized strains are being implemented or could be pursued. For example, heritabilities for specific gravity of both juvenile and mature wood are high, and genetic correlation between the traits is positive and strong (38). Given such relationships, breeders could increase juvenile wood specific gravity without adversely affecting that of mature wood. Another tack, advocated in the past for raising juvenile wood specific gravity, involves simply breeding for higher specific gravity (39, 40). An option for the future centers on breeding for earlier transition from juvenile to mature wood (40, 41). Some degree of genetic control over age of transition has been found in certain species.

On other fronts, extensive testing has shown that offspring from certain trees perform better at some locations than at others. Organizations with large land bases and associated seed and seedling production facilities collect seed from such trees, keep it separate during seedling production, and then plant the seedlings where they will best grow. This so-called family block planting procedure was first instigated to increase return on investments in breeding by maximizing productivity. The combination of growth on optimal sites and heightened genetic relatedness should also yield more uniform harvests. Since such harvests are likely to differ in quality, they can be allocated to highest end use.

This practice is being taken to a yet higher level by replacing random pollination during seed production with a technique called supplemental mass pollination (42). Mass control pollination, a more rigorous technique, is also being used. In the family block planting scheme outlined above, only the female side of the seedling family is controlled and known. By collecting pollen from an individual male and applying it en masse to a selected female, both sides are controlled, and genes for a particular trait or traits can be collected together more efficiently. Coupling this technology with family block planting can further raise productivity, increase uniformity, and enhance fit to end use.

Prospects for enhancing uniformity and developing special strains are also aided by dividing breeding populations into so-called breeding groups or lines. This strategy was initiated to control relatedness across generations (43). When trees are bred together, even in random pairs, the number of unrelated individuals available for future breeding is reduced by one half. Inbreeding can be a problem in many species, and measures are taken to control it. To reduce impacts of inbreeding on growth, southern pine breeders have divided breeding populations into subgroups. As breeding moves across generations, inbreeding is permitted within groups. For purposes of seed and seedling production, however, only one or a few individuals are chosen for use from each group. Seedlings for commercial planting thus result from outcrossing among unrelated individuals and are less likely to suffer ill effects of inbreeding. With the overall breeding population split into subgroups, breeders also have the opportunity to select for one trait in one group and perhaps another in other groups (44). This could yield seedlings with unique combinations of traits. Breeding group technology, directed pollination, and family block planting constitute major steps not only toward increasing productivity and uniformity but also toward development of specialized strains. Managing, harvesting, and processing stands established with these combined technologies will provide valuable lessons for eventual application of clonal forestry.

Even greater leverage for increasing uniformity can be obtained by coupling cloning technologies with classical breeding. By producing numerous genetically faithful copies of outstanding trees, cloning eliminates variability maintained by the sexual cycle and permits establishing entire stands with one tree. Variability among trees can be greatly reduced. As one example, variation in specific gravity among members of a loblolly pine clone was only 29 percent of that among seedlings from the same family (45).

Cloning technologies also make possible capturing heritable variation that cannot be exploited by classical breeding. Cellulose content, for example, seems inherited more strongly at the individual tree than at the family level. Recent advances in cloning technologies are reviewed in a following section.

More data on changes in variability are needed, especially as concerns variation among trees relative to that within trees. Until more is known, importance to other parts of the manufacturing continuum (Figure 1) will be uncertain. In addition, the full economic benefits of increased uniformity will not be appreciated.

Silvicultural Practices

The shift toward intensive management of US softwoods has been underway for roughly five decades. Plantation acreage and productivity have expanded tremendously. Movement toward plantation management of hardwoods has been slower but has been accelerating in recent years. Intensively managed plantations yield 50-100 percent more volume per unit area per year than natural stands. Not to be overlooked, however, are concomitant increases in uniformity. Control of spacing and stocking at planting have contributed to straightness and desirable branching patterns, thereby reducing quantities of reaction wood. Also, plantations established with seedlings adapted to their environments are more uniform as well as more productive. Harvesting trees and stands of similar size and age has also increased uniformity; quantities and distribution of juvenile wood are more predictable than in harvests from natural stands.

Plantation management has increased yields and returns on investment, but concerns have arisen about wood quality, especially that of fast-grown softwoods. Since more trees are being harvested earlier, raw material supplies contain higher proportions of juvenile wood. Variation between juvenile and mature wood is most pronounced in softwoods such as loblolly pine and Douglas-fir. Differences are less noticeable in northern softwoods and most hardwoods (13, 46). In species with large differences, juvenile wood lacks latewood and has lower specific gravity, shorter fibers, larger fibril angles, thinner fiber walls, and more reaction wood. Accordingly, pulp yields are lower and several paper strength properties are reduced. On the other hand, tensile strength and paper properties affecting printing quality are improved. All things considered, wood derived from rapidly growing softwoods is not undesirable. It differs from that in older trees and forests and is well suited for manufacture of many paper grades, some of which are different than those formerly manufactured. In response to increasing harvests of younger trees, process technologies have been adjusted. Changes will continue as trees with large amounts of juvenile wood will remain the norm.

The seeming disadvantage of high juvenile-mature wood ratios can be turned to an advantage. Differences are predictable in southern pines, and processors can divide trees of similar age into segments having different specific gravities for manufacturing of products giving highest returns. Systems for accomplishing this are discussed below in the section on harvesting and handling. As noted above, breeding technology can be used to diminish juvenile-mature wood differences and improve juvenile wood quality.

Once a plantation has been established and is growing well, forest managers must strive to maintain growth. Undue fluctuation in growth rates can affect wood quality and increase variability. Prominent among tools for governing growth in developing stands are thinning and fertilization. These are discussed below as a result of their widespread use and potential effects on wood quality.

Thinning is done to provide more growing space for individual trees by removing some, usually slow-growing, trees to reduce competition for light and other resources. Thinning does not raise total stand productivity but does allow harvesting trees that would otherwise be lost to competition and mortality. Also, trees left after thinning have more resources, thereby growing larger and more valuable for manufacture of solid wood products. Thus, growers benefit from timely thinning through both early returns generated by thinning and greater growth and value of the remaining trees.

Given the desire to increase size and value, thinning may not be done with wood and fiber quality in mind. Instead, timing tends to be governed by market prices, tax considerations, and availability of labor and time. Wood quality can be affected adversely when such factors cause thinning to be done too heavily, too early, or too late.

Impacts of thinning on wood and fiber quality are several. Removing large numbers of trees at early ages increases crown and branch size. Trees removed in thinning generally will be relatively young, with high proportions of juvenile wood. Trees left after thinning should grow faster than and be harvested earlier than those in unthinned stands. If harvested at the same age, final harvests should contain more mature wood than otherwise. On the other hand, harvesting thinned stands at especially young ages would yield trees with larger proportions of juvenile wood.

Specific gravity and fiber length are reduced by thinning, but not to a great extent or for very long (13). Nevertheless, changes in these properties can be expected as growth accelerates after thinning and then slows as trees enlarge in size and begin competing again. Thinnings timed to maintain growth are likely to dampen magnitude of such shifts.

Fertilization of both softwood and hardwood stands is routine in many regions, since forest lands are often of low fertility. Nitrogen is the most common limiting element, and its addition typically raises volume productivity. Economic returns are quite favorable. Some reduction in specific gravity occurs, but losses in this regard are outweighed several fold by large gains in volume growth. Even so, effects of fertilization on wood properties are greater and longer lasting than those of thinning (13). Earlier applications can increase crown and branch size, thereby raising reaction wood quantities above those encountered in unfertilized trees. Similarly, several light applications are likely to maintain growth without having much effect on wood properties. Applying the same total amount at one point in time, however, can have significant effects on specific gravity and fiber length.

In softwoods, fertilization appears to affect specific gravity by increasing proportions of earlywood relative to latewood, thereby decreasing specific gravity for several years (13). Moreover, fertilization often results in thicker fiber walls in earlywood and thinner fiber walls in latewood. Thus, carefully timed fertilization could maintain growth and decrease variation within annual rings.

Information on fertilization of hardwoods is limited, and outcomes are not nearly so clear. In several investigations fertilization increased uniformity of both growth and wood properties (46). Fertilization generally increases dry wood production, despite some reduction in specific gravity (13). Effects in ring porous hardwoods are likely to mimic those in softwoods; i.e., accelerated growth is associated with reduced specific gravity, shorter fibers, and thinner fiber walls.

In summary, plantation management and practices such as thinning and fertilization have improved returns from forestry operations, and considerable research has been devoted to explaining their impact on wood and fiber properties. Perhaps too little effort, however, has been given to characterizing their potential for manipulating such properties in desired directions, i.e. toward enhanced uniformity and higher quality. Viewed in another dimension, development of specialized strains and short rotation plantations for pulp production, is likely to render thinning unnecessary and fertilization more important. Understanding effects of this intensified management on wood and fiber properties seems critical. Such research seems especially urgent in hardwoods, given their anatomical complexity and increasing importance as raw material. Greater knowledge of cambial activity and factors controlling it seems a useful starting point (47).

Harvesting and Wood Preparation

Eliminating harmful practices during harvesting and handling in the woodyard can do much to ensure raw material quality and uniformity (48). Time lags between harvest and delivery hinder bark removal and reduce brightness and yield. Paper strength can also be lessened. Variation in tree species, age, and size, moisture content, and decay can have dramatic effects on process efficiencies and product quality (48). Chip quality is also important, and major efforts to ensure consistent size and cleanliness have been implemented in recent times. Continued improvement is possible but can only be achieved by interaction among those responsible for the several activities (Figure 1).

Awareness of wood supply source, nature, and age has stimulated segregation of differing types of wood in the woodyard prior to processing (49). Dividing individual trees into segments based on specific gravity allows optimal utilization of the predictable variation in distribution of juvenile and mature wood within trees (50). Systems for classifying, chipping, and storing loblolly pine thus provide for separate processing of low-specific gravity chips from tops and young plantations, high-specific gravity chips from sawmill residues and older trees, and chips from stems of intermediate and variable specific gravity (51).

Such systems have become more comprehensive and sophisticated in recent times. Basic density in radiata pine (*Pinus radiata*) varies with position in and age of individual trees and with geographic origin of the trees (51). Segregation of wood supplies according to basic density permits the processing of chips having similar densities as well as of directed mixtures of chips with differing basic densities. Benefits include greater uniformity during production of typical commodity products and manufacture of niche products.

Expected increases in juvenile wood content also prompted suggestions to separate second-growth Douglas-fir wood supplies on the basis of juvenile and mature wood content (12). Chips can be stored and used separately or blended in proportions best suited to pulping conditions and product specifications.

Systems for classifying, segregating, and directed processing of wood supplies are becoming commonplace in many regions. Most are used with species having abrupt transitions from juvenile to mature wood. In view of the potential for increased efficiency and quality, advantage should be taken of opportunities to further improve such systems and extend them beyond the woodyard. Extension may be facilitated by new instrumentation for automated assay of basic density (22). Characterizing stands slated for harvest in terms of basic density and related properties could allow scheduling harvests such that deliveries would be more uniform and that changes could be predicted in advance. In the future, faster and more comprehensive assays for separation by basic density, or perhaps by other properties, could enable growers to earn returns varying directly with suitability of their harvests for different products.

Biotechnology and Molecular Genetics

As described above, classical breeding has made the trees of today, particularly softwoods, more productive, straighter, and more pest resistant as well as more uniform and of better quality than those from wild stands. Though effective, such technologies are expensive and long term. Several southern pine generations have passed en route to the so-called super trees now being planted. Perhaps 15 or more years are required to breed and produce seed of a new generation in many species. Given the promise of biotechnology and molecular genetics, trees of tomorrow should be even better, have traits not now available, and be produced faster. Described below are several means by which biotechnology and molecular genetics can decrease the time required to identify or create and mass produce desirable trees.

Cloning.

Many commercial tree species are cloned by rooting cuttings collected from branch tips or stump sprouts. After treatment with growth hormones, cuttings are rooted in greenhouses or nurseries, grown to proper size, and planted like seedlings. As in all cloning processes, the method conserves genetic attributes of the original tree by asexually regenerating many individuals from one. Bypassing the sexual process avoids the dilution occasioned by random formation and combination of sperm and egg. Another advantage is time savings. Rather than wait for seed production, growers can regenerate large numbers of genetically identical trees for testing and move into production as quickly as results are available. Time to planting can be one-third or less that required to produce seed. Rooted cuttings are used routinely to establish highly productive *Eucalyptus* stands with individual clones matched to site and manufacturing needs (52). Similar methods are used commercially for cottonwood and its relatives in the US, and large acreages of short-rotation poplars are being grown by industrial concerns in the Pacific

Northwest and Mississippi River Valley. Rooting success varies among species, and the method is not yet practical for many softwoods such as loblolly pine (53). Recent summaries of research on both US hardwoods and softwoods are available (54).

One problem with rooted cuttings is that superior trees are best selected at or near harvest age. By then, rooting becomes difficult; i.e., efficiency declines, sometimes dramatically, with age. Cell and tissue culture methods offer one means to circumvent this difficulty. Cells or tissues, often taken from immature seeds of superior trees, are grown in liquid or solid cultures in the laboratory. Astute applications of growth hormones are used to foster growth. Changes in hormone regimes are then used to stimulate formation of shoots (organogenesis) or embryos (somatic embryogenesis). In organogenesis, shoots are harvested, rooted, and planted as described above. In somatic embryogenesis, embryos are grown to sizes similar to those in seed, germinated in the laboratory or greenhouse, and then planted just like seedlings from conventional nurseries.

Cultures can be held in cold storage (55, 56) until the original donor trees have been proved superior. The combination of organogenesis and cold storage is being used operationally with radiata pine in New Zealand (55). Similar procedures are being evaluated for loblolly pine (53).

Research on somatic embryogenesis has progressed rapidly in recent years, and it seems the preferred technology for cloning softwoods. Among advantages over rival methods, the technology yields larger numbers of seedlings, greater ease of cold storage, generally more normal growth, and greater uniformity within clones. Field trials are underway for several spruce species (*Picea* spp.) (57), radiata pine (56), Douglas-fir (58), and loblolly pine (53). Loblolly pine seedlings have also been produced in our laboratory. On the hardwood front, field trials have been established with a number of species, one prominent example being yellow poplar (*Liriodendron tulipifera*) (59). Additional information on these techniques is available in proceedings of recent symposia (54, 60, 61).

Somaclonal variation.

Beyond simply cloning superior trees, cell and tissue culture also offers potential for large scale and low cost creation and/or selection of useful variants in the laboratory. Some examples of potentially useful strains produced via genetic change in culture include poplars' resistance to foliar and canker diseases caused by *Septoria musiva* (62). Cultures of hybrid poplars, noted for rapid growth, yielded plants that have been more resistant than the donor clones for more than six years in field trials. Although field trials to verify resistance require considerable time, several resistant clones were produced within only one year of initiating the research. Attempts to produce variants with altered wood and fiber properties may be worthwhile.

Genetic maps and markers.

Classical breeding relies on the wide variability naturally extant in most forest trees. Sorting this variability to identify outstanding individuals requires lengthy testing over numerous environments. Most traits of commercial value (for example, volume growth) are quantitative in nature and seem governed by many genes with minor effects and variable modes of inheritance. Accurate identification of superior trees, as a result, is difficult. Also, superiority, until recently, has been judged only as trees approach rotation age. Advances in breeding technology have reduced time requirements by more than 50 percent, but several years are still required, even for short rotation trees such as *Populus* and *Eucalyptus*. Genetic maps and markers could enable breeders to document presence of desirable genes at any age, thereby increasing accuracy and saving time.

In general, the order of genetic information, DNA sequences, on chromosomes is more similar for related than for unrelated individuals. This order is somewhat shuffled during sexual reproduction, but DNA sequences or genes close to one another tend to remain in their original orders. Accordingly, knowledge of sequences can be used to determine if they are associated with particular traits and if individuals and/or their relatives have a particular gene or genes (63). A variety of techniques have been developed to identify DNA sequence commonalities, and several are being used to create genetic maps for and to identify genetic markers in forest trees (64).

In just the last few years, genetic maps have been prepared for a variety of softwood and hardwood species and used to locate DNA sequences or chromosomal segments, so-called quantitative trait loci (QTLs), that control or at least are correlated with important traits (60, 61, 65). QTLs have been identified for leaf morphology, phenology, growth, branching pattern, stem taper, frost tolerance, disease resistance, rooting ability, and specific gravity. Several organizations are seeking to apply QTLs in marker-assisted selection; i.e., early identification of individuals superior for important traits such as specific gravity (20, 66). Such applications may be aided by new developments in automated assessment of factors contributing to specific gravity (22).

Variations on the technology could also be used to isolate outstanding trees within families for cloning, to identify trees having complementary QTLs for mating, to create specialized strains, to verify identity of superior trees in breeding and planting programs, and to prevent theft of proprietary breeding or planting stock. Eventual creation of highly improved strains could make such applications critical. Indeed, the future could bring brand name clones, for which breeders and growers demand premium payment.

Genetic maps and markers clearly hold much promise. The technology, however, is young and largely unproved. Much research remains to be done, especially as concerns economic returns from marker application relative to those from classical breeding. Both approaches are expensive, but the molecular approach requires more specialized facilities and personnel. Benefits may be best realized via cooperatives supported by numerous clients.

Genetic transformation.

Should genes for a desired trait not exist in a species slated for breeding, genetic transformation can be used to secure them from other organisms and insert them in the tree or trees in question. Genetic transformation may also save time; i.e., the sexual process and long generation intervals of classical breeding could be bypassed.

Several methods for genetic transformation of trees are in use (59, 67), and a number of genes have been inserted and expressed in trees. The first such achievement involved a gene that conferred herbicide tolerance on hybrid poplar (68). Indeed, poplar species and hybrids have become model systems for transformation as a result of the ease with which they can be manipulated in and regenerated from cell and tissue cultures (69). Transformation is becoming more routine with many species; reports in the proceedings of three recent symposia (60, 61, 65) show that a variety of marker and useful genes have been inserted in a wide array of commercially important trees. In our laboratory, a system for transforming cottonwood (70) is being used to study effects of a gene for enhancing synthesis of a growth hormone associated with cambial activity.

Transformation and other molecular genetic techniques can be adapted to alter expression of existing genes; i.e., to increase or decrease the activity of genes underlying traits of interest. This involves isolating the genetic system in question, making copies of the genes and their controlling elements, synthesizing genetic constructs that enhance or obstruct expression of the native genes, and then inserting these into the tree.

Though far from routine, such procedures are being used to retard synthesis of lignin precursors, limit deposition of lignin, and alter softwood lignin to resemble more closely that of hardwoods. The range of species and lignin properties being investigated can be glimpsed in the proceedings of two symposia held in late 1994 (61, 65). As one example of progress, lignin contents were reduced by 5 to 12 percent following transformation of tobacco plants with an obstructing construct patterned after a gene for lignin synthesis in aspen (71). Efforts are underway to determine if similar effects will occur after transformation of aspen.

A number of significant barriers must be cleared before genetically transformed trees enter commerce. Not the least of these are more efficient and reliable systems for cloning. This and related impediments seem particularly severe for softwoods, e.g., loblolly pine (67). The critical nature of these needs is underscored when one contemplates the large number of trees used in the classical breeding programs. Transforming and regenerating a useful proportion of such trees represent a major undertaking.

Another, and far from minor, obstacle to commercialization of genetically transformed trees is concern over consequences of their release into the environment. This stems mainly from the possibility that genetically transformed trees will spread so-called foreign genes. To minimize such risks, genetically transformed trees probably will have to be rendered sexually sterile, and at least one laboratory has instigated research on identifying and inserting genes for sterility along with other useful ones (72). Such research could yield significant side benefits; i.e., eliminating reproductive structures would make greater quantities of energy, water, and nutrients available for wood and fiber production.

Just when forest biotechnology will yield returns remains uncertain. As evidenced above, however, much progress has been made on cloning, genetic mapping, marker assisted selection, and genetic transformation. Even so, gaps in understanding of forest tree genetics, physiology, and biochemistry continue to limit progress. Molecular applications will be limited until more is known about the genes underlying valuable traits and especially about mechanisms governing time and place of gene expression. Sustained support for such research is necessary if benefits of these exciting and rapidly evolving technologies are to be realized in a reasonable time frame.

SUMMARY AND CONCLUSIONS

The foregoing review indicates the feasibility of manipulating wood and fiber properties via biological methods. Numerous opportunities are yet to be exploited.

Concerning classical breeding, genetic variation and control is sufficient to improve most traits, for example, specific gravity. Prospects are limited for modifying chemical composition. Correlations between such traits and growth may restrict progress, but the evidence is mixed. More information is needed, especially for hardwoods. Opportunities for improving juvenile wood properties are good, and breeding strategies are available to produce specialized strains. Technological advances have reduced generation intervals, but time and cost remain major disadvantages of classical breeding.

Intensive silvicultural practices have lessened wood variability by reducing proportions of reaction wood. Thinning and fertilization are being used to increase growth and value, and the latter practice may find use as a means for reducing variability within and among annual rings. Future plantations may well be managed even more intensively than those of today; i.e., specialized strains will be bred for and grown on short rotations.

Technology is available to increase uniformity of wood deliveries by segregating harvests according to age and juvenile wood content. Next steps involve refinements to lower costs and foster application to a wider array of products. Improved analytical techniques could help extend application from woodyard to forest.

Biotechnological approaches hold promise for manipulating wood and fiber properties faster and to greater extents than classical breeding. Technologies for cloning superior trees can significantly increase both productivity and uniformity; several methods are being used. With time, these and others will be extended to widely planted softwood species. Genetic maps and markers could improve accuracy and speed with which superior trees are identified for breeding. Some further research is needed to establish reliability and cost effectiveness. Genetic transformation promises to yield traits not now available (for example, herbicide tolerance) and the ability to suppress activity of genes controlling traits such as lignin synthesis. Commercialization, however, awaits refinement of available methods and means to ensure that genetically transformed trees do not have undue environmental consequences.

Continued support of research can be expected to provide specialized strains and practices that improve end product quality. Parallel emphasis on improved productivity should also help offset increased costs caused by reduced harvests from public lands and tightened regulation of private lands.

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