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Genetics and Improvement of Wood Properties

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Introduction

Wood quality must be defined in terms of the end product: what is good for linerboard is not necessarily good for newsprint. The most critical properties for breeding programs are usually wood specific gravity, tracheid length and microfibril angle, although many other properties are also important. In general, wood properties are strongly inherited, with heritabilities of 0.5 and up. This would make breeding for wood properties easy if they could be determined easily and cheaply. Unfortunately this is true only for wood specific gravity. Therefore, much effort has gone into developing assay methods suitable for small wood samples which can be taken from the tree with little damage.

Wood quality can be improved by silviculture and by breeding. Spacing, thinning, and fertilization all have major effects on the growth of the tree and the properties of its wood. Selective breeding also has a major impact. Traditionally, the selected trees are grafted into seed orchards, progeny tested, and rogued. The time between the start of the program and the harvest of the first trees is typically 50 years making it appropriate to breed for a general purpose tree. For species that can be vegetatively propagated another approach is feasible: clonal forestry. Using it with shorter rotations allows development of trees suitable for specific products.

What is Wood Quality?

This is a difficult question to answer. Many years ago some of the pioneers in forest tree improvement asked managers of the local paper mills what wood properties they considered desirable, and were unable to obtain helpful answers. It was not until the 1970s that breeders started to ask the right questions. The quality of any raw material is defined as its suitability for use and quality is affected by many properties. There is a wide range of products made out of wood and it is therefore necessary to define wood quality in terms of the end product. What is good for linerboard is not necessarily good for multiwall sack paper and might be disastrous for newsprint. This is the most important point to keep in mind when considering wood quality.

What Are the Important Products?

Wood products belong in two major groups: solid-wood products, and pulp and paper products. Solid-wood products include not only lumber, but also plywood, oriented strand board and particle board. They can be used for construction as well as furniture. Pulp and paper products can be produced by three major processes: the sulfite process, the kraft process, and mechanical pulping. The sulfite process is used extensively for spruces and firs. The kraft process is more flexible and can be used for most species, including almost any pine. Mechanical pulping is often used for lighter woods such as poplars, but can be used successfully for some pines. The sulfite process is very suitable for producing high quality writing papers. Unbleached kraft is used extensively for the production of linerboard and sack paper, while bleached kraft can be used for writing papers, computer paper and paper used in copy machines. Mechanical pulps are primarily used for newsprint.

What Are the Important Wood Properties?

First we must distinguish between the wood of two major groups of trees: hardwoods (essentially broad-leaved trees) and conifers. The two groups have distinctly different wood. That of hardwoods is more complex, and its most distinguishing feature is the presence of vessels the elements of which are connected to each other through large pores. Other elements include fibers, tracheids, and parenchyma. The hardwoods are further divided into ring-porous and diffuse-porous species (**Figure 1**). Conifers have tracheids, ray parenchyma, and resin ducts. The tracheids are much longer than those in hardwoods.

The wood in conifers usually has distinct springwood and summerwood, also called earlywood and latewood. Springwood has large-diameter tracheids

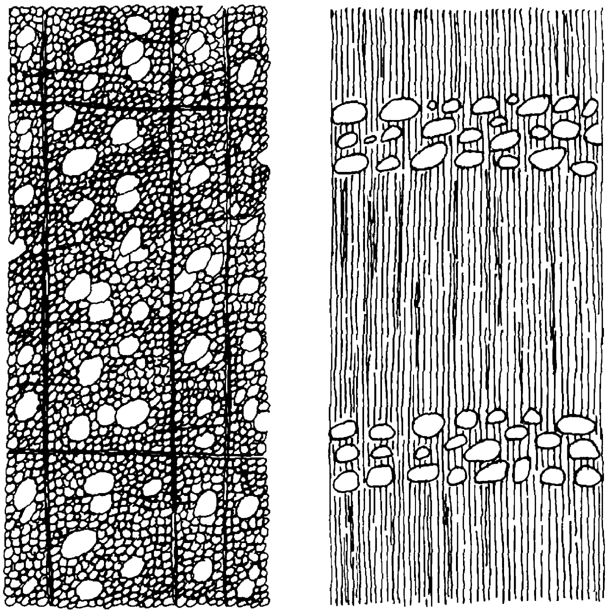

Figure 1 Cross-sections of (a) diffuse-porous and (b) ring-porous wood. From Zobel BJ and van Buijtenen JP (1989) *Wood Variation: Its Causes and Control*. New York: Springer-Verlag.

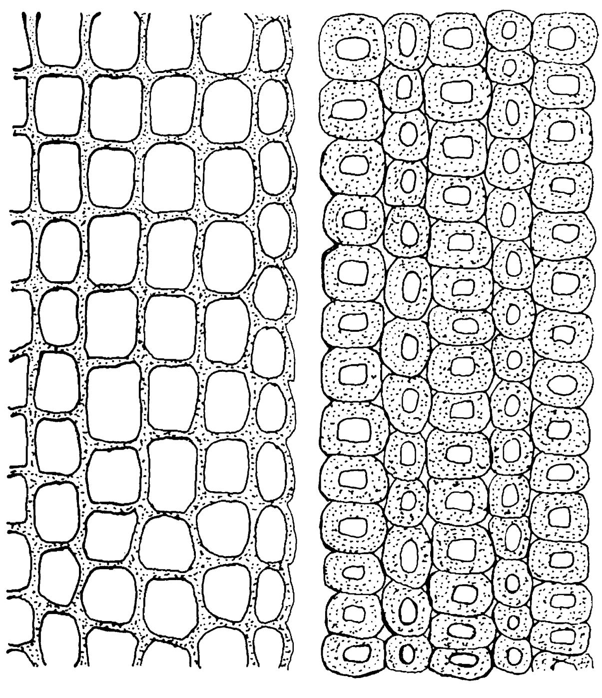

Figure 2 Cross-section of earlywood and latewood, clearly showing the difference in the cell diameter and wall thickness of the tracheids. From Zobel BJ and van Buijtenen JP (1989) *Wood Variation: Its Causes and Control*. New York: Springer-Verlag.

with thin walls and looks light on a cross-section of wood, while summerwood has narrow, thick-walled tracheids and looks dark (**Figure 2**). The most important wood properties are wood specific gravity (dry weight divided by green volume), latewood percentage, tracheid length, tracheid diameter and wall thickness, microfibril angle (the angle of inclination of the cellulose microfibrils to the long axis of the tracheid), grain spirality (the angle of the tracheids to the vertical axis of the stem), and the chemical composition of the wood.

Techniques for Determining Wood Properties Using Small Samples

In a breeding program it is most important to evaluate wood quality without destroying the tree, and much effort has been expended over the years to develop techniques to make determinations on small wood samples. The favorite method is to remove one or more small radial cores (increment cores, ≤ 10 mm diameter) from the tree, which can be used for determinations. Methods have also been developed to pulp these on a very small scale and determine the pulp and papermaking properties. It is also relatively easy to determine anatomical properties on these samples. Almost all the important properties listed earlier can be determined from an increment core. Also, new high-throughput techniques have been developed recently such as near infrared (NIR) spectroscopy, image analysis, computer tomography, X-ray densitometry, X-ray diffraction, and pyrolysis molecular beam mass-spectrometry which allow very large numbers of chemical analyses on these small samples. Several techniques have been incorporated in the Silviscan equipment developed by Robert Evans at CSIRO, Australia (**Figure 3**). These approaches are ideal for a breeding program where large numbers of individuals must be screened quickly and cheaply.

Silvicultural Improvement of Wood Properties

Spacing

The initial spacing in plantations usually has no direct effect on specific gravity and tracheid length. A wider spacing results in larger juvenile cores. In spruce closer spacing results in better pulp yield and sometimes in greater strength. On sites where water availability is a problem, wider spacing may lead to a higher wood specific gravity.

Thinning

Thinning removes the poorer quality trees and therefore increases the quality of the timber left for the final harvest. Thinning removes trees that contain little of the higher quality wood (outerwood) that is formed after the first few rings from the pith, and

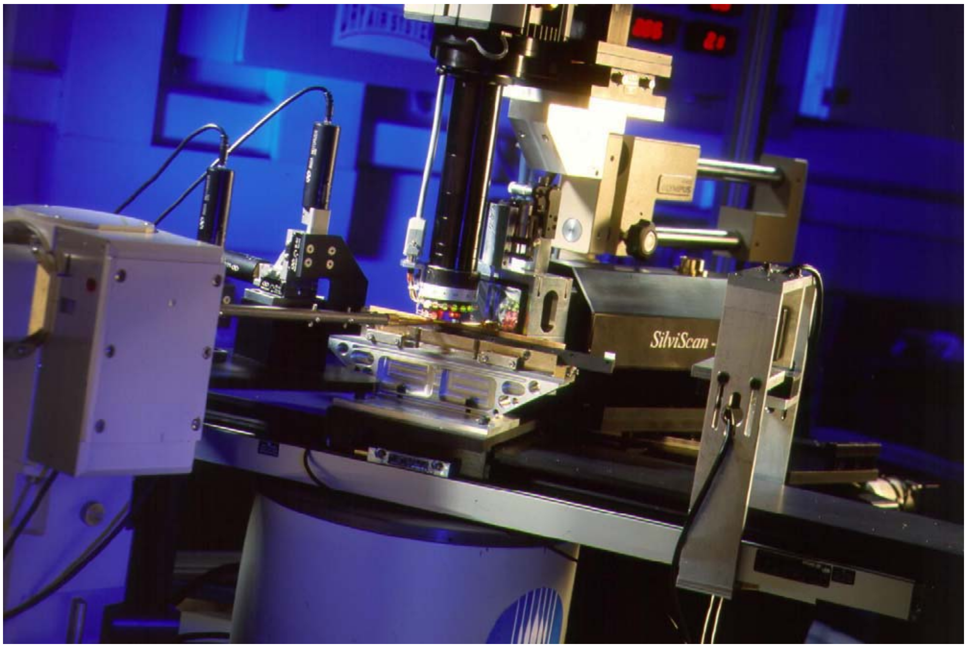

Figure 3 The SilviScan® instrument combines X-ray densitometry, diffractometry and image analysis to measure a variety of properties in a single wood sample. Photograph courtesy of CSIRO.

enhances production of such wood in the remaining crop. The effect of thinning is greatest in ring-porous species, less in diffuse-porous species, and least in conifers. Specific gravity and tracheid length are not much affected.

Fertilization

In general, soil fertilization has more effect on wood of conifers than of hardwoods. In particular, nitrogen fertilization decreases wood specific gravity in conifers and its effect may last 5–10 years. It also decreases tracheid length and increases earlywood production. To get the benefits of increased growth, while minimizing the adverse effects on wood properties, nitrogen fertilization should be light and frequent. The overall effect of fertilization both in hardwoods and conifers is beneficial, since the increase in volume more than offsets the loss in wood specific gravity. The effects of phosphorus and potassium are less pronounced than that of nitrogen. One should note that the effect of fertilization depends greatly on soil conditions. Obviously the effect is greatest when there is a nutrient deficiency.

Genetic Control of Wood Specific Gravity

The Components of Wood Specific Gravity

Wood specific gravity is a complex trait with many contributing factors. The major factor is usually the latewood percentage. Another important component is the cell wall thickness in the earlywood and the latewood. The diameter of earlywood tracheids is also important, but the diameter of the latewood tracheids is less so. The packing density, which is the specific gravity of the cell wall material itself, contributes to the actual density, but not to the variation among trees, since it is rather constant at $1.54\,g\,cm^{-3}$. Extractives and insoluble deposits are the final components, which are particularly important in the heartwood.

Inheritance of Wood Specific Gravity in Conifers

Genetic variation among provenances Trends in genetic variation among provenances, if present at all, are usually weak. Specific gravity tends to be lower with increasing latitude and altitude. In the southern pines in natural stands wood specific gravity increases from the northwest to the southeast following the rainfall patterns in the southern USA. Genetic trends, determined by growing different provenances in the same location, are in the opposite direction. Clinal patterns are expected in the southern USA, the northeastern USA, and the boreal regions. This is not true, however, in the western USA with its mountainous topography. There, broad trends are expected to be less common except for elevational differences.

Tree-to-tree variation in wood specific gravity The literature on genetic differences among trees is abundant and is only outlined here. Narrow-sense heritabilities for wood specific gravity range from 0.4 to 0.7 in both corewood and outerwood. Low specific gravity species, such as Virginia pine, spruce, and silver fir, tend to have somewhat lower heritabilities than high specific gravity species such as the hard pines, larch and Douglas-fir. In general, the specific gravity of corewood and outerwood are well correlated, with genetic correlations frequently above 0.7. This makes it possible to select for specific gravity at an early age. For species that can be vegetatively propagated, the broad-sense heritability can be substantially higher than the narrow-sense heritability, which can be important for clonal forestry.

Inheritance of Wood Specific Gravity in Hardwoods

Not as much is published on the inheritance of specific gravity in hardwoods as in conifers, but the information is still substantial. Most of the work was done on eucalypts and poplars, with some on other species. In general, wood specific gravity is inherited quite as strongly in hardwoods as in conifers. In the eucalypts and poplars the heritability of specific gravity tends to range from 0.6 to 0.8, while in oak it ranges from a little below 0.4 to almost 0.6. In sycamore reported values range from 0.7 to 0.8. Juvenile–mature correlations in hardwoods are as high as in conifers.

Genetic Control of Other Wood Properties

Latewood Percentage

Differences between earlywood and latewood are so strong that they should often be evaluated separately. A fair amount of information is available on the relationship between latewood percentage and specific gravity, but far less on the genetics of it. There is no general trend in the earlywood : latewood ratio, although the higher latewood percentage is usually associated with high wood specific gravity. The heritability of latewood percentage is rather variable with reported values ranging from 0.25 to over 0.9. The narrow-sense heritability is often around 0.5, while the broad-sense heritability may be around 0.8. One should note that latewood percentage is related to other factors such as fertilization and it also affects the average cross-sectional tracheid dimensions which are very important for pulp and papermaking. On the average, latewood cells are slightly longer than earlywood cells.

Cell Dimensions

Tracheid length is moderately to strongly heritable, but information is somewhat limited, particularly in hardwoods. Most of the work in hardwoods has been with eucalypts and poplars. Estimated heritabilities ranged from 0.36 to 0.86. It has also emerged that polyploidy has a major effect on fiber length in both natural and artificially produced polyploids, increasing fiber length by 21% to 26%. Reported narrow-sense heritabilities in conifers range from 0.28 to 0.9 and broad-sense heritabilities from 0.56 to 0.86. In some species such as Scots pine (*Pinus sylvestris*), lodgepole pine (*P. contorta*), and shortleaf pine (*P. echinata*) differences among provenances have been reported.

Tracheid diameter and wall thickness are in general fairly strongly inherited, but information is quite limited. In loblolly pine (*Pinus taeda*) heritabilities up to 0.8 were reported. Inheritance in *Eucalyptus viminalis* was equally strong.

Spiral Grain

Spiral grain is probably related to wind resistance, but is difficult to measure accurately. If severe it can be a problem for solid-wood products, but generally it is not economically important. It has been intensively studied in *P. radiata* where it can cause problems. Heritability is strong enough to make genetic improvement feasible. There are also some data for eucalypts and beech indicating the same situation. Some species, such as sweetgum (*Liquidambar styraciflua*), have interlocking grain, which can be very troublesome but is also amenable to genetic improvement.

Chemical Properties

Genetic control of wood chemistry is topical, for two reasons. Much work is going on with control, at the molecular level, of lignin synthesis, and new techniques have been developed to analyze small wood samples in large numbers.

Traditionally the lignin, cellulose, and extractives content have been studied most extensively. Lignin content is very strongly inherited but its range of variation is small, indicating that it is very important and natural selection maintains it in a very narrow range. It can be determined extremely accurately. Cellulose cannot be measured as accurately; this lowers the heritability and makes genetic improvement more difficult. In eucalypts, however, considerable progress has been made in increasing cellulose content in clonally propagated trees.

Oleoresin components are quite often under the control of individual genes of large effect, and could be manipulated readily. There has been limited interest, with the exception of overall resin yield in pines, and the presence of limonene, which conveys insect resistance. In the decade 1970–80 some terpenes were used as a form of early genetic marker in studies of forest tree populations.

Other Wood Properties

Compression wood is rather strongly inherited both in loblolly pine and radiata pine. Surprisingly the relationship with form is rather weak, so factors other than straightness must play a major role. Another important property is heartwood formation, but its heritability is rather low.

A trait that is currently of major interest is microfibril angle. It is inherited rather strongly and is related to the strength of individual fibers as well as solid-wood stiffness. Bark percentage is rather variable in loblolly pine, being very important in young trees, where it can occupy as much as 50% of their volume. It is much less so in mature trees and it has a strong geographic component.

Finally, in eucalypts it has been found that collapse during drying, a rather common defect, is highly heritable.

Interrelationships among Traits

Interrelationships among traits are of great importance to the breeder. To select for one trait, but accidentally cause an adverse change in another, may be fruitless. For instance, if wood specific gravity and volume growth were negatively correlated, then selection just for wood specific gravity would decrease growth. This could be good or bad. Selection for low wood specific gravity could result in increased volume and wood that is more suitable for newsprint. On the other hand, selection for increased growth could result in wood less suitable for sack paper. In principle, one copes with this by using a selection index. Knowing the economic value of the traits under selection and their genetic and phenotypic relationships, one can assign a weight to each trait, to give a best estimate of the overall genetic value. A way to show the interrelationships among traits is by use of the so-called coefficient of genetic prediction. This shows the purely incidental change in trait 2 from a change of one standard deviation in trait 1. An example is given in **Table 1**.

Specific Gravity and Growth Traits

In general, there tends to be a weak negative correlation between specific gravity and height and diameter growth. Since in general the correlations between specific gravity and growth are not strong, it is usually not difficult to find individuals with desirable combinations for both traits. Specific gravity and date of bud break have a noteworthy correlation based on research done in Norway spruce. Early flushing is associated with less latewood, lower wood specific gravity, and greater ring width.

Wood Specific Gravity and its Components

Because of the totally different anatomy of the wood of conifers and hardwoods, they will be discussed separately. In loblolly pine latewood percentage, latewood specific gravity, earlywood specific gravity, and latewood tangential tracheid width showed the strongest genetic relationships to overall wood specific gravity. The first three factors have a positive association, while the tangential tracheid width has a negative relationship to overall wood specific gravity. Compression wood has a strong positive relationship with specific gravity.

In hardwoods little is known about the genetic relationships among the proportions of different cell types, but the important cell types are tracheids, libriform fibers, vessel elements, and medullary ray parenchyma.

Relationships among Other Wood Properties

In a few conifers tracheid length has a negative genetic correlation with wood specific gravity and growth rate and positive correlations with other

Table 1 Coefficients of genetic prediction (CGP). Selecting a population of parents one standard deviation above or below the average for a trait listed in one of the columns, will change the genotypic values of the progeny traits by the CGP times one standard deviation (based on data from the Western Gulf Forest Tree Improvement Program). The CGP is calculated as the phenotypic covariance of trait 1 and trait 2 divided by the product of their genetic standard deviations

	25-year height	*25-year DBH*	*25-year volume*	*Juvenile SG*	*Mature SG*	*Average SG*
25-year height	0.22	0.16	0.18	−0.06	−0.06	−0.08
25-year DBH		0.25	0.26	−0.12	−0.11	−0.14
25-year volume			0.26	−0.12	−0.11	−0.13
Juvenile SG				0.19	0.16	0.21
Mature SG					0.36	0.30
Average SG						0.30

DBH, diameter at breast height; SG, specific gravity.

fiber dimensions such as lumen diameter, tangential and radial width, and wall thickness in the latewood.

In loblolly pine the microfibril angle in the earlywood is greater than in the latewood. It is fairly constant in the earlywood, but decreases from the pith to the cambium in the latewood.

In loblolly pine and eucalypts moisture content is negatively correlated with wood specific gravity. Hence, while wood specific gravity increases, the green weight stays relatively constant, since water is replaced with wood substance.

Controlling Wood Properties by Breeding

First one should consider the breeding objectives in terms of the end product. Since the trees will be harvested 50 to 75 years after the selections are made, it seems advisable to breed for properties that are generally desirable, because future wood technology is so uncertain. Increased specific gravity would be particularly suitable, since the use of thinnings and shorter rotations associated with plantation management depresses wood specific gravity (along with other components of wood quality), and it will be important to compensate for this, especially in corewood, which will make up a larger portion of the wood harvested. Another useful strategy is to try to reduce wastage and/or processing costs, e.g., by reducing lignin or by modifying lignin so it can be more easily removed by pulping. Significant reductions in lignin content probably cannot be achieved without major modifications in the system of growing, harvesting, and processing the trees. Wood uniformity within and between trees is also of great importance to the users of wood.

When designing a long-term breeding program for wood quality two key decisions must be made: (1) how to cope with the correlations among traits and (2) how to deal with the selection and progeny test phases. Index selection is, in principle, the best way to deal with adversely correlated traits. In order to cope with the negative correlations between specific gravity and growth, a multiple-population breeding strategy may be considered as an alternative to simultaneous improvement within a single population. Differentiated 'breeds' may be used for different end products or even for different categories of site.

Progeny testing is actually not necessary for traits as highly inherited as wood properties. Just selecting the individuals with the most desirable wood properties would suffice. Since selection for wood properties is generally combined with selection for other properties, such as growth rate, form, and disease resistance, progeny tests will be available anyway, and thus one only has to evaluate the best individuals already selected for other reasons. The age of testing is another major consideration. Since juvenile and mature wood properties are highly correlated, early selection is desirable. Another possibility is to use selection for wood properties in a stepwise screening program, where trees are evaluated first for the traits that can be measured easily and cheaply and are subsequently tested for properties that are progressively more expensive to determine.

Breeding for Wood Specific Gravity

A main consideration when breeding for wood specific gravity is whether wood specific gravity is a main objective or a secondary trait. Most breeding programs opt for the second alternative. One needs to consider, however, that it has a high economic worth, and the fact that an increase in quality generally means higher economic returns than increases in yield. Specific gravity should therefore be a high priority. An additional attractive feature of high wood specific gravity is that in the production of pulp and paper it allows a better combination of tensile strength and tear factor, which is desirable for some products such as multiwall sack paper. The economic effect of perhectare fiber yield can vary according to the ownership. Since the weight of the green wood is not affected by wood specific gravity and pulpwood is often sold by weight, there is little incentive for a small private landowner to increase wood specific gravity. On the other hand, a company that grows wood on its own holdings has several incentives: increased dry matter production, increased quality, and reduced transportation cost.

Breeding for Other Wood Properties

This is not often done, because they are more expensive to evaluate and often less important. Tracheid length and microfibril angle are the two traits sometimes considered. However, owing to recently developed methods for high-throughput analysis of wood properties the situation is rapidly changing. There is an increased interest in microfibril angle, because of its effect on wood stiffness and pulp properties. Many chemical properties can be determined by the same methods as well.

Chemical properties can also be modified indirectly through improvement in stem straightness and branch size. This results in a reduction in reaction wood, which in conifers reduces lignin content and microfibril angle.

How Are Genetic Gains Obtained Operationally?

There are two major approaches: the seed orchard approach and clonal forestry. The seed orchard approach involves selecting the best individuals, grafting them in seed orchards, progeny testing the orchard to remove the less desirable clones and providing a new generation to select in. Operational plantations are generated from the seed produced by the orchards.

Clonal forestry depends on the availability of efficient vegetative propagation methods, usually rooted cuttings, sometimes tissue culture. A few highly selected individuals can than be propagated to reforest substantial acreages. Because of the cost involved this is most economical on the best sites, located close to manufacturing facilities. Because the time to deployment is shortened this method lends itself to tailor-making trees for specific products. For example the Aracruz company in Brazil has achieved rotations of 6 to 7 years with eucalypts. With *Gmelina arborea* 4 year rotations are possible. With blocks of well characterized clones, it is possible to fine-tune processing to the individual clones.

See also: **Genetics and Genetic Resources**: Molecular Biology of Forest Trees. **Papermaking**: Overview; World Paper Industry Overview. **Pulping**: Chemical Pulping; Mechanical Pulping. **Tree Breeding, Practices**: Biological Improvement of Wood Properties. **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement; Conifer Breeding Principles and Processes; Forest Genetics and Tree Breeding; Current and Future Signposts. **Wood Formation and Properties**: Formation and Structure of Wood.

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Breeding for Disease and Insect Resistance

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Introduction

Pest resistance historically has been the single most important trait in crop breeding, reflecting the vast number of biotic agents that challenge domesticated plants. The number of diseases and insects that afflict forest trees may be even greater than their agricultural counterparts, but no comparable investment to combat them has been made, in spite of the fact that some forest trees have been victims of some of the most spectacular and disastrous epidemics known. Virtual elimination of American chestnut to chestnut blight and extirpation of large populations of American and European species of elm to Dutch elm disease, and white pines to white pine blister rust are textbook examples, as are the depredations of gypsy moth on North American hardwoods. Other important epidemics that started in the last century, some recently, include dogwood anthracnose, butternut canker, Port-Orford cedar root rot, pitch canker of pines, sudden oak death in North America, and the pinewood nematode in Japan. Almost all, of course, are the result of introduced pests. More will undoubtedly follow.

Exotic pests have caused immense economic and ecological damage, and, with few exceptions, are the only ones that merit serious attention. A few pathosystems that exhibit properties of both endemic and exotic diseases are often disturbed, or 'degenerate,' as a result of human intervention (for example, offsite planting, narrow genetic base, dysgenic selection). The same applies to insect pests. The far greater number of endemic forest pests has been regulated by natural selection over epochs of mutual adaptation through coevolution with their hosts.

While much basic understanding of pest resistance and breeding strategies have come from agronomic crops, distinctive properties of tree populations make the former incomplete models. The most important of these properties is the extension of trees in space and time. This has several important biological and practical consequences, especially for disease resistance. Great size projects a tree's parts into different microenvironments above and below ground, providing diversity of niches and habitats,