Biotechnology of Forest Yield

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Summary. Silvicultural and genetic manipulation of Douglas fir and loblolly pine plantations have increased their productivity 70 and 300 percent, respectively, over natural forests on the same sites. Yet these intensively managed plantations are achieving less than 50 percent of their potential productivity. Future increases in yield will result from optimization of nutritional treatments, control of noncrop vegetation, and advances in tree breeding and tissue culture techniques.

In this article we review historical levels of productivity in natural forest stands, increases in yield that have resulted from plantation management, and potential productivity from future technologies, in particular genetic manipulation. The estimates of productivity are based on research plot measurements and operational experience (*1*). The discussion is focused on two commercially important temperate coniferous forests: Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] in Washington State and loblolly pine (*Pinus taeda* L.) in North Carolina.

There is no single generally accepted measure of forest productivity. In this article yield is defined as the live standing phytomass at any point in time. Mean annual yield is yield divided by crop age. Net primary productivity is the total phytomass produced in a given year. Phytomass is the total biomass of the trees in a stand. Productivity is expressed as dry mass per hectare per year for all phytomass produced under stated management practices. Dry mass is expressed in megagrams and is determined by oven drying to a constant weight. Estimates of productivity are made by using growth and yield models along with biomass distribution equations. A range of ±25 percent is indicated for estimated productivity in coniferous forests (*2*). This is a reasonable estimate of uncertainty for the values reported here.

The climatic characteristics for a site of average productivity in the Puget Sound lowlands of Washington State are given in Table 1. Maximum mean annual yield for a natural stand of Douglas fir at this site is about 6 megagrams per hectare per year (*3, 4*).

The loblolly pine site selected for analysis is a pocosin on North Carolina's lower coastal plain. Pocosins are upland areas with poor natural drainage due to flat topography and impermeable subsoils. Because of the soil conditions and frequent fires, natural pine stands on pocosins are generally understocked, with resultant low levels of productivity. Forests consist of mixed pine stands with dense, shrubby undergrowth and may occupy only 30 percent of the area (*5*). Data on phytomass productivity for these sites are difficult to obtain, but an estimate of peak mean annual yield for a well-stocked loblolly stand is about 4 Mg/ha per year (*6, 7*). Typical climatic characteristics for this site are given in Table 1.

As both natural stands and plantations develop, annual net primary productivity is low at first, increases to a broad plateau, and then slowly declines (Fig. 1). The low values for young stands are due to incomplete site occupancy (crowns and roots do not fully utilize the growing space), while declines in vigor and increases in respiration are probably responsible for the lower values at older ages. The best values for comparison are the maximum values of mean annual yield.

Potential Productivity

Potential net primary productivity was estimated with a modification (*8*) of the model by Loomis and Williams (*9*). The basic assumption in this model is that solar radiation ultimately limits phytomass productivity. Allowances are made to reduce incident radiation by the amount that is not photosynthetically active, the amount that is reflected, and the amount that is absorbed by the nonphotosynthetic parts of the stand.

Potential gross productivity (in moles of CH_2O) is calculated by multiplying the absorbed, photosynthetically active radiation by an assumed quantum efficiency. Allowance is then made for respiration requirements to maintain life processes in the standing crop and to produce new material through growth. The rates of both are adjusted for temperature effects. Gross productivity minus respiration gives the maximum net productivity of carbohydrate. This must be adjusted for inorganic uptake to estimate the maximum net productivity of phytomass. This estimate includes material lost to mortality, to shedding (as of needles and cones), and to consumption by insects and other animals. The coefficients used in the model of potential productivity are given in Table 2. The high values are estimates of the best obtainable from ordinary biological processes, while the standard values are representative of observations in productive stands.

Predicted maximum net productivities for Douglas fir and loblolly pine are given in Table 3. Productivity for loblolly pine is higher than for Douglas fir because of greater annual solar radiation, but the higher temperatures in North Carolina reduce the difference somewhat by increasing respiration. The large range between the high and standard estimates reflects the uncertainties of this kind of analysis.

It should be emphasized that the values predicted by this model are for maximum net primary productivity, whereas the values cited for existing stands are for mean annual yield. Mean annual yield is lower because of poor site occupancy at young ages and because it excludes material lost to mortality, shedding, and so forth. Maximum net primary productivity is about 2.5 times higher than maximum mean annual yield (*10, 11*).

Loomis and Williams' estimate (*9*), if converted to a yearly value, is similar to the maximum reported here. Using a different theoretical approach, Monteith (*12*) estimated potential net primary productivity at about 55 Mg/ha per year. Maximum productivity for a temperate coniferous forest has been estimated to be at least 45 Mg/ha per year on the basis of a survey of world literature (*2*).

It appears that 50 Mg/ha per year is a reasonable target for net primary pro-

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ductivity in Douglas fir stands. This value is within the range reported by Gordon *et al.* (*8*), close to Monteith's estimate, and near the observed maximum. In Douglas fir plantations the ratio of maximum net primary productivity to maximum mean annual yield is about 2.5. Future technologies should reduce this ratio to about 2. Therefore, the target for maximum mean annual yield is 25 Mg/ha per year. In view of the greater solar radiation in North Carolina, the target for loblolly pine is taken to be 30 Mg/ha per year. The gap between observed mean annual yields in natural Douglas fir and loblolly pine stands (6 and 4 Mg/ha per year, respectively) and these goals is large. Natural production rates at the selected sites are only 23 and 12 percent of the target values.

A sensitivity analysis involving the modified model (*8*) revealed that changes in quantum efficiency and the intrinsic relative growth rate of tissue per unit mass of live material have the largest impact on productivity, and there is a significant interaction between relative growth rate and the maintenance respiration coefficient. With high relative growth rates only small amounts of live phytomass are required to fully utilize available radiation. In this case total maintenance respiration costs are small even if the maintenance coefficient is large. On the other hand, with low relative growth rates large amounts of live phytomass are required to fully utilize the radiation. In this case total maintenance respiration costs (and therefore potential productivity) are sensitive to the maintenance coefficient. Inactive absorption and albedo reduce absorbed radiation and potential productivity proportionally.

The yield gap can be closed in several ways (Fig. 1): (i) by increasing site occupancy, the number of years of low productivity at young ages can be reduced; (ii) some phytomass lost to mortality may be captured by thinning; (iii) cultural practices, such as fertilization and control of water, may mitigate factors that limit growth; and (iv) certain biological processes may be made more efficient through genetic manipulation.

Table 1. Climatic conditions for the selected sites in Washington and North Carolina. Adapted from Gordon *et al.* (*8*).

Variable	Puget Sound lowlands, Washington	Lower coastal plain, North Carolina
Number of frost-free days	200 to 240	240
Temperature (°C)		
Yearly mean	11	15
January mean	4	5
July mean	18	25
Precipitation (mm)		
Yearly mean	1000	1100
Growing season mean	420	770
Yearly mean radiation (cal/cm^2 day)	290	350

Progress from Cultural Practices

Douglas fir. Increases in the productivity of Douglas fir since about 1960 have been achieved largely through plantation establishment and nitrogen fertilization. Typical silvicultural practices to establish Douglas fir plantations involve clear-cutting, nursery production of 1- to 3-year-old seedlings, site preparation (by fire, mechanical, or chemical means), planting, and tending of the young stand (*13*). This system offers many opportunities to improve on natural regeneration processes and increase yields. Harvesting and site preparation techniques can be used to control competing vegetation, animal pressure, and the microclimate of the planted seedling. Through nursery practices the physiological vigor and morphological characteristics of the seedlings can be managed. Through proper lifting, packing, and cold-storage techniques, planting can be timed to match the physiological condition of the plant to the climate of the site. Finally, through the planting process itself, uniform stocking in reasonable soil conditions can be achieved. Maximum mean annual yields of phytomass for untreated Douglas fir plantations are about 7 Mg/ha per year (Table 4) (*14*). Thus harvesting and regeneration practices increase Douglas fir productivity about 30 percent.

Although forest soils in the Douglas fir region often contain large amounts of total nitrogen, low mineralization rates due to low average soil temperatures limit its availability to trees (*15*). Extensive trials in the region have helped to quantify the response of Douglas fir to single applications of urea (*16*). Responses to repeated applications are the subject of current research. Maximum mean annual yield may increase 20 percent as a result of applying 200 kilograms of nitrogen per hectare every 5 years starting at age 30. Peak mean annual yield in fertilized plantations would thus be about 9 Mg/ha per year, or 50 percent greater

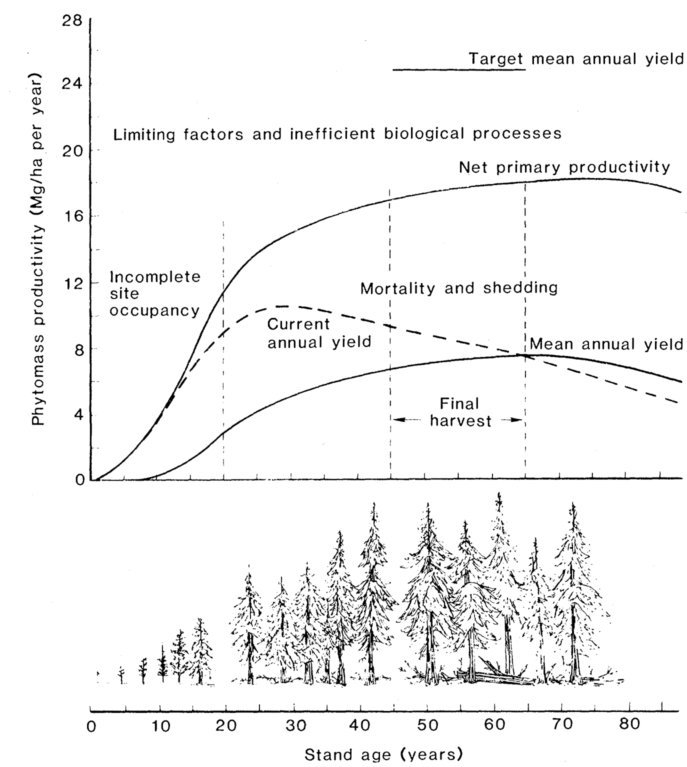

Fig. 1. Components of phytomass production versus age for a plantation of Douglas fir having 1000 trees per hectare at age 17. Mean annual yield falls below the target level because the stand fails to fully utilize the site at young ages, because production is lost to mortality, shedding, and insects, because the soil and climate fail to provide the optimum growing conditions, and because biological processes in the stand are not optimized for growth. Current annual productivity, the change in live standing phytomass during a given year, is equal to net primary productivity minus phytomass lost. Productivity is lower in natural stands because full site occupancy is delayed and because mortality is a greater proportion of yield. Net primary productivity peaks earlier in natural stands, which undergo significant mortality at younger ages. Mortality is delayed in plantations by the uniform size and spacing of the trees. Harvest at the culmination of mean annual yield maximizes the phytomass yield from the forest, although earlier harvests are often economically desirable. Data are derived from a simulation by Curtis *et al.* (*10*) and from biomass distribution equations by Gholz *et al.* (*3*). The shedding component was estimated as a fixed fraction of foliar biomass by using data from Keyes and Grier (*38*).

Table 2. Critical biological coefficients used to calculate potential phytomass productivity as a function of climatic conditions. High values are estimates of the best attainable, while standard values are representative of observations in productive stands. Adapted from Gordon *et al.* (8).

Variable	Value	
	High	Standard
Albedo (fraction)	0.05	0.10
Inactive absorption (fraction)	0.05	0.15
Quantum efficiency (mole/E)	0.10	0.05
Maintenance respiration (g/g day)	0.006	0.016
Growth respiration (g/g)	0.25	0.35
Inorganic uptake (g/g)	0.10	0.05
Relative growth rate (g/g day)	0.33	0.0033

than in unfertilized natural stands (Table 4) (*17*).

Thinning in Douglas fir stands is primarily regarded as a tool to increase their value (by concentrating the wood produced on fewer but larger stems) rather than their productivity. The situation is by no means simple, however, as the effects of thinning on productivity are related to utilization standards, the timing of the thinnings, and the manner in which removal is carried out (*18*). Small increases in productivity may result from early thinnings that leave only well-spaced stems on the best microsites.

Loblolly pine. Production of loblolly pine has been increased by site drainage, site preparation, and fertilization with phosphorus and nitrogen. Not only are the interactions between these silvicultural practices important in determining the yield increases, there are important operational interactions between these treatments and basic logging practices.

In undrained pocosins the water table ranges seasonally from about 1 meter below the ground surface to 30 centimeters above. It may be at or above the soil surface during the winter, late spring, and early summer (*5*). Loblolly pine grows best at a water table depth of 60 to 75 cm (*19, 20*). With higher water tables both soil aeration and root growth are reduced. In addition, high water tables, particularly when associated with heavier soils, can severely limit mechanical operations on a site. Logging and site preparation may cause significant soil degradation if performed under wet conditions (*21, 22*).

Early attempts to increase southern pine production by drainage can be traced to the 1930's (*19*). Current drainage practices include establishing ditches at 200-m intervals before logging and 100-m intervals before planting (*22*). This practice may lower the water table 30 to 60 cm, although winter rains will still cause the soil to be saturated (*5*).

Various investigators have estimated the increases in yield that result from drainage. Terry and Hughes (*23*) gave examples for planted southern pines that range from 133 to 1300 percent. Klawitter (*19*) indicated that the height of the dominant trees at age 50 will increase by 5 to 8 m as a result of drainage. Maximum mean annual yield in a drained plantation is estimated to be about 7 Mg/ha per year (*24, 25*). This is an increase of 90 percent over natural levels (Table 5).

Removal of excess moisture makes intensive site preparations more effective. Site preparation is necessary to reduce logging slash, ameliorate soil compaction caused by logging, improve aeration, reduce vegetative competition, and facilitate planting. One operation that provides these benefits is bedding (the forming of ridges in the soil) (*23*). Drainage facilitates bedding in that it increases the amount of time heavy machinery can operate on the site and allows beds to be formed more easily and to last longer because the soil is not saturated (*22, 23*).

As stated above, even after drainage pocosin soils are saturated in the winter. Thus, by creating ridges, bedding further increases the effective depth of the water table. Shoulders and Terry (*21*) reported that 7-year-old loblolly pines were 15 cm taller for every additional 2.5 cm of water table depth in January. Survival of planted seedlings is also likely to increase. Finally, by improving soil aeration and increasing microbial activity, bedding may improve nutrient availability. Estimated maximum mean annual yield in a drained and bedded plantation is about 9 Mg/ha per year (Table 5) (*26*).

Application of phosphorus before planting interacts with drainage and bedding in several ways. Repeated and prolonged flooding causes anaerobic soil conditions and tends to make phosphorus less available in the soil. Roots subjected to flooding may be less able to absorb phosphorus (*27*). Application of the fertilizer to the soil to correct this deficiency is facilitated by draining and may be done most effectively in the same operational process as bedding. Finally, significant positive interactions between bedding and phosphorus fertilization have been reported for the pocosin sites (*23*).

Table 3. Theoretical maximum net productivity in a single year for Douglas fir and loblolly pine. High and standard values refer to the settings of the biological coefficients which are input to the model. Values are megagrams per hectare per year. Adapted from Gordon *et al.* (*8*).

Item	Douglas fir	Loblolly pine
High values		
Entire year	245	300
Growing season	216	236
Standard values		
Entire year	37	46
Growing season	33	36

The growth response of pine trees to applications of phosphorus on pocosin-like soils is both large and long-lasting (*28*). A single application before planting may suffice for an entire rotation (*29*). Maximum mean annual yield in a drained and bedded plantation with phosphorus is estimated to be 10 to 11 Mg/ha per year (Table 5) (*30*).

Once drainage has removed excess moisture from the site, bedding has helped further with aeration, and phosphorus fertilization has removed the deficiency for that element, then there may be a strong response to nitrogen fertilization. A well-stocked stand that has been drained and fertilized with phosphorus should grow about 20 percent more in volume as a result of nitrogen fertilization (*31, 32*). Estimated maximum mean annual yield in a drained, unthinned plantation receiving phosphorus before planting and nitrogen fertilizer at 5-year intervals starting at age 10 is about 12 Mg/ha per year (Table 5) (*33*).

The effect of thinning on loblolly pine productivity is similar to that on Douglas fir. Overall productivity is not changed substantially (*34*). Two exceptions should be noted: the growth response to nitrogen fertilizer may be greater in thinned stands (*35*), and unthinned stands, it not harvested at the right time, will undergo such severe mortality that yield will decline (*24*).

The discussion of these practices has stressed their interactions on an operational and biological level. One further interaction has to do with increases in value resulting from increases in productivity. The value per unit yield of a tree is proportional to its size. Larger trees are more valuable because they yield more wood and because each unit of that wood is more valuable. For the example given in Table 5, the relative value per unit of yield increased about 50 percent due to these treatments. Thus, while these cultural treatments increased mean annual yield 230 percent, they increased value about 400 percent.

A comparison of the results listed in Tables 4 and 5 to the target mean annual yields shows that, even after gains from present cultural practices, a substantial gap still exists between actual and potential phytomass production. Douglas fir is achieving about 35 percent and loblolly pine about 40 percent of the target yields.

Opportunities for Future Gains from Cultural Practices

Theoretical maximum productivity was defined under the assumption that solar radiation is the only limiting factor. To determine the extent to which controllable site factors limit growth, the exercise must be repeated under other assumptions: for instance, all available growing season water is used to satisfy photosynthesis at the highest water-use efficiencies theoretically attainable (*36*), or all available nitrogen is supplied and recycled at a rate such that its concentration in all live tissue is maintained at a theoretical minimum level consistent with enzymatic and structural requirements (*37*). For many sites, the maximum productivity defined in these terms would fall well below the radiation-limited values. The difference would define the benefits possible from treatments alleviating these, and other, deficiencies in the presence of perfectly efficient trees.

Much more needs to be learned about the effects of cultural practices on the allocation of yield between aboveground and belowground structures. Productivity gains will be overestimated by studies that are based only on aboveground measurements when significant reallocation of production from roots to tops occurs. One study of Douglas fir demonstrated that fine root turnover accounts for only 8 percent of total annual production on a good site but for 36 percent on a poor site (*38*).

The low productivities at young ages (Fig. 1) result from the delay in canopy closure and subsequent maximization of the ratio of leaf to ground area (leaf area index) in even-aged coniferous plantations (*39*). This period may be shortened by increasing the number of trees planted per unit area. Site occupancy can also be achieved sooner by increasing the rate of crown expansion of established seedlings by controlling noncrop vegetation.

Fertilization. Numerous advances remain to be made in the area of fertilization. Much research has concentrated on determining whether a growth response to a single application will occur and then estimating its size. Recent analysis of the growth of various agronomic crops (*40*) and young trees in hydroponic culture, however, suggests a more dynamic approach. Ingestad (*41*) demonstrated that relative growth rate can be maintained as trees increase in size by using micromolar amounts of nitrate, provided that the supply of nitrate is matched to the potential relative growth rate. The constant in this system is the tissue nitrogen concentration, especially in the foliage. The tree apparently has a tendency to maintain this concentration by reducing its relative growth rate when insufficient N is supplied to the roots. Thus productivity can be N-limited even though no deficiency symptoms or lower N concentrations are detectable. The value of this approach in Scots pine plantations was demonstrated in a 6-year study in Sweden (*42*). Productivity was increased 2.5 times and relatively less of it was allocated to the root system of irrigated and fertilized trees.

Future research must concentrate on defining the optimum frequency and dosage of fertilizer applications to ensure a balanced nutrient supply to tree roots with respect to known limitations at specific sites. Wider application should also be made of existing diagnostic tests for mineral deficiencies (*15, 43*). In view of the increasing cost of fertilizers and their application, improved encapsulation techniques for controlled-release fertilizers and genetically enhanced microbial sources (*44, 45*) may become prominent.

Control of competing vegetation. Fertilization and other site improvement techniques improve growing conditions for plants that compete with the species of economic interest. Many studies of Douglas fir and loblolly pine have demonstrated that control of competing vegetation during the phase of incomplete site occupancy can lead to substantially increased size and survival of the crop. In one study in which weeds were controlled for loblolly pine during the first 5 years after planting, a 70 percent gain in yield was noted at age 9 (*46*).

An important advance is the development of effective and environmentally safe chemicals to achieve control of competing vegetation. The effectiveness of plant hormone analogs such as 2,4-D and 2,4,5-T is based on their relatively greater absorption by broad-leaved foliage, whose cellular machinery they sabotage. Recent studies of plant hormones, such as that on the role of the cell wall in releasing oligosaccharide fragments with growth-inhibiting effects (*47*), may lead to the development of alternative herbicides.

Exploitation of other interactions. Interactions among cultural treatments play an important role in yield improvement efforts. Studies have been established to determine the effects of site preparation, fertilization, and weed con-

Table 4. Productivity increases attributable to intensive management of Douglas fir.

Case	Maximum mean annual yield (Mg/ha year)	Cumulative increase (percent)
Natural stands (*4*)	5.7	
Silvicultural treatments		
Plantation establishment (*14*)	7.2	30
Nitrogen fertilization (*17*)	8.8	50
First-generation genetics (*56*)	9.7	70
Target	25.0	340

Table 5. Productivity increases attributable to intensive plantation management of loblolly pine in North Carolina pocosins.

Case	Maximum mean annual yield (Mg/ha year)	Cumulative increase (percent)
Natural stands (*6, 7*)	3.6	
Silvicultural treatments		
Drain and plant (*24, 25*)	7.0	90
Bedding (*26*)	8.6	140
Preplant phosphorus (*30*)	10.5	190
Nitrogen fertilization (*33*)	11.8	230
First- and second-generation genetics (*56*)	14.3	300
Target	30.0	730

trol on loblolly pine survival, growth, and yield (*44*). More such studies are needed, particularly in the Douglas fir region. A key interaction of which there is little quantitative understanding is that between mineral nutrition and water supply. Drip irrigation may become practical in nonremote plantations managed for specific high-value products (*48*). Even in unirrigated plantations, interactions between water and mineral nutrients determine the effectiveness of fertilization and its optimum dosage and timing. These interactions must be understood and represented in models to allow extrapolation from irrigation and fertilizer trials to a wide range of sites.

Maintenance of productivity. One concern for the future deals with the maintenance of productivity over several rotations of intensive management. For example, declines in productivity have been observed in some second-rotation stands in South Australia (*49*).

Declines in productivity due to intensive plantation management could be caused by a number of factors. These include harvesting activities on wet sites, which may cause soil compaction; whole tree utilization, which may deplete nutrient supply on marginal sites; burning, which can remove litter and nutrients; and intensive site preparation, which has the potential to increase erosion.

While mismanagement certainly causes declines in productivity, there is no reason to believe that careful intensive management will do so (*50, 51*). Where productivity losses do occur, they often can be more than offset with fertilizer applications (*52*). In fact, recent results from Australia show that scientifically treated second-rotation stands may significantly outperform first-rotation crops on the same or matched sites (*50*).

Protection efforts have played a vital role in increasing forest yields. Actual yields to date have probably been increased more by protection against fire than the cultural practices discussed. For instance, fire control increased wood volume production 200 percent in one North Carolina pocosin (*5*). Certainly, if increases in productivity are to be realized, fire, insects, disease, and erosion will have to be effectively combated.

Progress from Genetics

Genetic programs for Douglas fir and loblolly pine began in the early 1950's. The programs are designed to cope with a combination of features unique to forest trees: enormous genetic diversity (*53*); a long juvenile period before flowering; an even longer period before seedling progeny can be confidently evaluated for productivity, self-fertility, and the resulting loss of vigor; and the frequent variation of genotypic expression on the great diversity of sites. Efforts are being made to learn how desired traits are controlled genetically and to tackle the practical and economic problems of working with thousands of large trees.

Growth rate is a complex trait under the control of many genes. The objective of the breeding programs for Douglas fir and loblolly pine is to increase the frequency of desirable genes in the population while maintaining a sufficiently broad genetic base for increases to continue in the future. This is achieved by cycles of selection followed by interbreeding of selects, and by the infusion at each cycle of new parent material from sources outside the breeding population. At present, improved seed is produced operationally in large production orchards relying on the airborne pollen mix. Only the female parent is known and genetic gain is lower than if pollen from selected trees were applied. This is known as half-sib technology. The design and operation of such programs have been reviewed in detail by Faulkner (*54*). The typical sequence and time scale of operations are illustrated in Fig. 2.

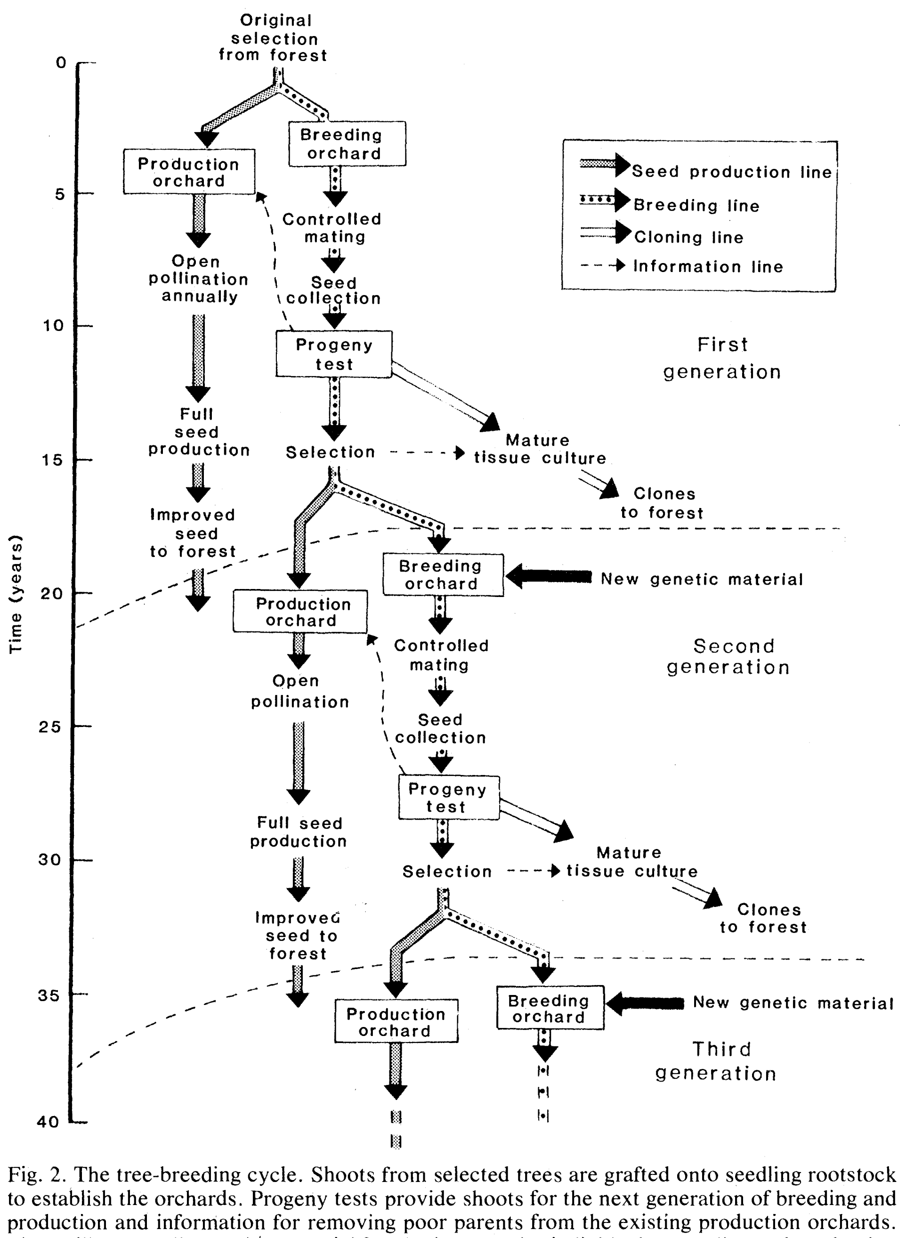

Fig. 2. The tree-breeding cycle. Shoots from selected trees are grafted onto seedling rootstock to establish the orchards. Progeny tests provide shoots for the next generation of breeding and production and information for removing poor parents from the existing production orchards. They will eventually provide material for cloning superior individuals. Breeding and production lines are separated so as to maintain a broad genetic base in the former and specialize for productivity in the latter.

Because of the 10- to 15-year breeding cycle, only recently have the first progeny tests shown stable family rankings for volume production. Current predictions of per hectare yield from them are subject to the uncertainties associated with extrapolating growth curves from individual 10-year-old trees (*55*). Many such predictions have been made (*56*). They indicate that, for Douglas fir and loblolly pine, the gain in mean annual yield will be about 12 to 15 percent per generation. Increased value and cost savings may result not only from larger size but also from stem quality characteristics, disease resistance, higher wood density, and greater product uniformity. A 12 percent gain for Douglas fir (Table 4) and a 24 percent gain for two generations of loblolly pine selects (Table 5) brings the estimates of production in intensively managed Douglas fir and loblolly pine plantations to about 10 and 14 Mg/ha per year, respectively. Thus, with current forestry technology, plantations can achieve 40 percent (Douglas fir) or 50 percent (loblolly pine) of the target mean annual yields.

Opportunities for Future Gains from Genetics

Component breeding. Combining parents that have different bases for their superiority (such as a longer growth period in one parent and a greater photosynthetic capacity in the other) will increase the chance of favorable matings over that currently achieved through "blind" selection for stem volume (*57, 58*). A synergistic gain may be seen in the offspring. To achieve this, however, an understanding of the various biological processes and their interactions is required (Fig. 3). Identifying which processes will have large general effects on growth, site-specific effects, or even mutually antagonistic effects will be aided by further development of mathematical models of growth (*59*). Many processes in the modified Loomis-Williams model show considerable genetic variation within and among forest populations. Considerable opportunity thus exists for their improvement.

Light absorption by the canopy is one of the few low-level processes consistently showing a direct relation to yield (*12, 39*). In closed-canopy coniferous forests light absorption is more efficient than in agricultural crops (*39*). Nevertheless, there is still considerable intraspecific variation in components of absorption—such as branch angle and length, leaf clustering, branching frequency, and growth habit—that are considered highly heritable (*57, 60*).

Quantum efficiency is the result of an intricate web of interacting processes, including those controlling the availability of water and mineral nutrients (Fig. 3). Consequently, although many studies have shown significant genetic variation in photosynthesis-related processes in trees (*61*), direct correlation with yield is seldom seen. Ledig (*59*) reviewed some notable exceptions.

Photosynthetic rates of single leaves in trees are only about half of those in agricultural crop species under similar conditions (*62, 63*), and appear to have been less rigorously selected for in nature. Winter photosynthesis is particularly important for annual growth in conifers (*64, 65*), exhibiting considerable genetic change along elevational and other gradients (*66–68*). Genetic variation in the stomatal response to low humidity and water stress has also been observed (*57*). Contrary to experience with agricultural crops (*63*), the prospect is good that improvements in single-leaf processes will contribute to tree crop productivity (*57*).

The rate of conversion of assimilated carbon to new structure ("biosynthesis" in Fig. 3) may limit the productivity of tree crops under field conditions more frequently than photosynthesis. Genetic variation in this conversion rate, or in the accompanying energy use ("growth respiration"), is poorly documented (*57*).

Important genetic variation occurs in the allocation of dry matter to different organs. Some families of loblolly pine, for example, grow faster by reinvesting assimilate in new leaves (*59*), while others (from drier areas) achieve superiority by investing relatively more in roots (*68*). However, allocation differences enabling an isolated tree to capture its surround-

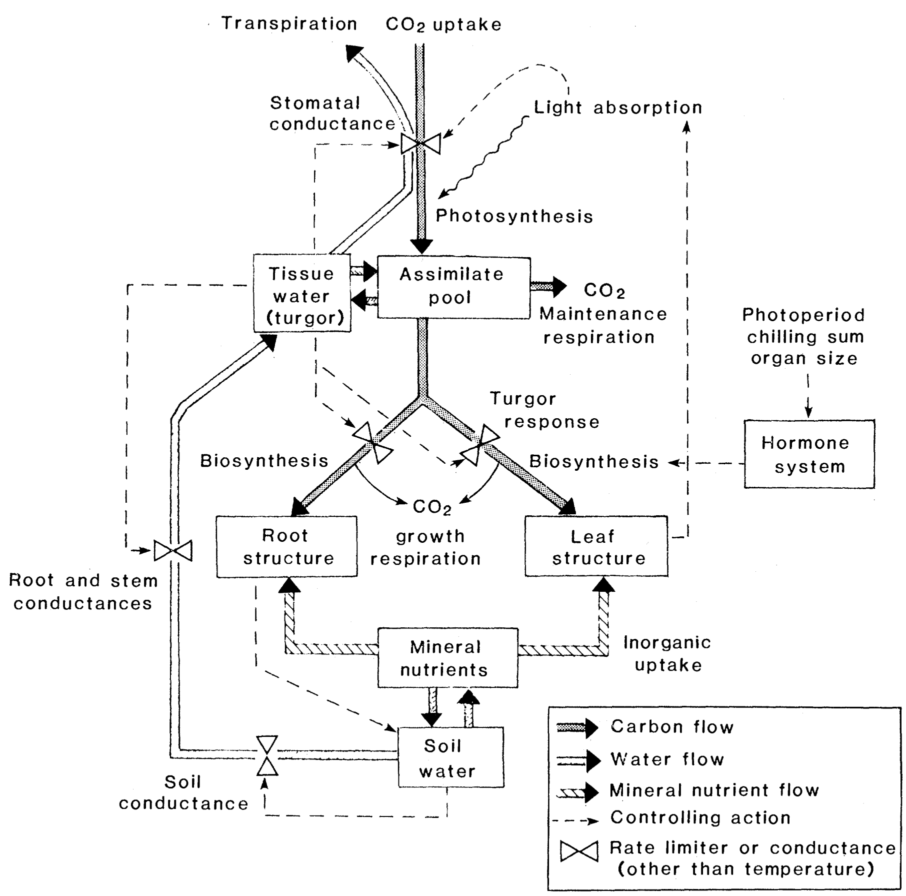

Fig. 3. Interactions among component processes of productivity. The balance between leaves and roots may be the result of competition for carbohydrate from a pool produced by photosynthesis. Competition is dependent on the activities of the respective meristems as a result of organ size or hormonal information. Conductance is the reciprocal of resistance to hydraulic flow along the soil or tissue pathway, or to vapor diffusion in the case of stomata. Water, carbon, and mineral flow processes interact at numerous points. All the indicated plant properties and processes exhibit significant genetic variation, and some contributing to mature-tree superiority can be identified in seedlings. Their separate contributions to growth in given environments must be understood through mathematical modeling for component breeding to be effective.

ings more quickly do not ensure improved productivity per hectare following full site occupancy (*55*).

The date of budbreak in spring, the number of subsequent growth flushes, and the switchover from extension of preformed shoots to building of the new apical dome and leaf primordia are all under some degree of genetic control (*57*). Some of this variation can be exploited by appropriate northward or uphill seed movement (*69*).

Avoidance of water stress by mechanisms of stomatal closure response (*57*), allocation of assimilate to roots (*68, 70*), leaf morphology, osmotic adjustment (*57*), or early dormancy (*71*) are features of genetically superior seedling families or provenances of Douglas fir and loblolly pine. Exploitable genetic differences also occur in the efficiency with which mineral nutrients are utilized (*57, 72, 73*). These and other adaptions to stress need to be emphasized wherever site limitations cannot be alleviated economically through silviculture (*74*).

Little is known of the extent of genetic variation in maintenance respiration with respect to its rate per gram of tissue, its temperature dependence, or the amount of live biomass in the crop. A line of perennial ryegrass with low maintenance respiration has, however, produced yields 12 to 20 percent higher in widely replicated field trials in Britain (*58*). This should lessen concern that low-maintenance selections might show undesirable side effects, such as early leaf senescence.

It may be possible to take further advantage of component breeding to shorten the breeding cycle. Parameters of biological processes underlying high annual yields will be identifiable much earlier than the long-term yield trends themselves and are more amenable to rapid screening. In some cases screening may be possible at a cellular level in liquid culture. Recurrent selection of natural or induced mutant cells from a single parent could then be a new source of rapid genetic gain (*75*). The correlation of fusiform rust resistance in loblolly pine callus with whole-tree resistance (*76*) and the screening of *Eucalyptus* plantlets for salt tolerance (*77*) are examples of interest.

Use of in vitro techniques. A portion of genetic variation among individual trees is due to gene interactions that are not normally transmitted intact through sexual reproduction. This "nonadditive" portion can give rise to exceptional individuals within generally superior families. It can be captured by vegetative propagation or the interbreeding of homozygous trees.

Estimates of the magnitude of nonadditive gain are scarce, varying in conifers between 10 and 30 percent (*60, 78, 79*). The accuracy and comparability of these estimates are uncertain because of the different gains already achieved in the base population, the unspecified selection intensities, and ignorance of clonal effects arising from the particular status of the parent. A clearer example is provided by *Eucalyptus grandis* in Brazil. Record mean annual yields around 60 Mg/ha per year (aboveground stem to a 5-cm top) are anticipated after repeated selection. The best clone had twice the yield of the base crop, which was already enhanced by provenance and family selection (*80*). From these observations it appears that two generations of breeding and intense clonal selection in Douglas fir and loblolly pine could improve yield nearly 100 percent over that of wild seed.

Vegetative propagation techniques in-

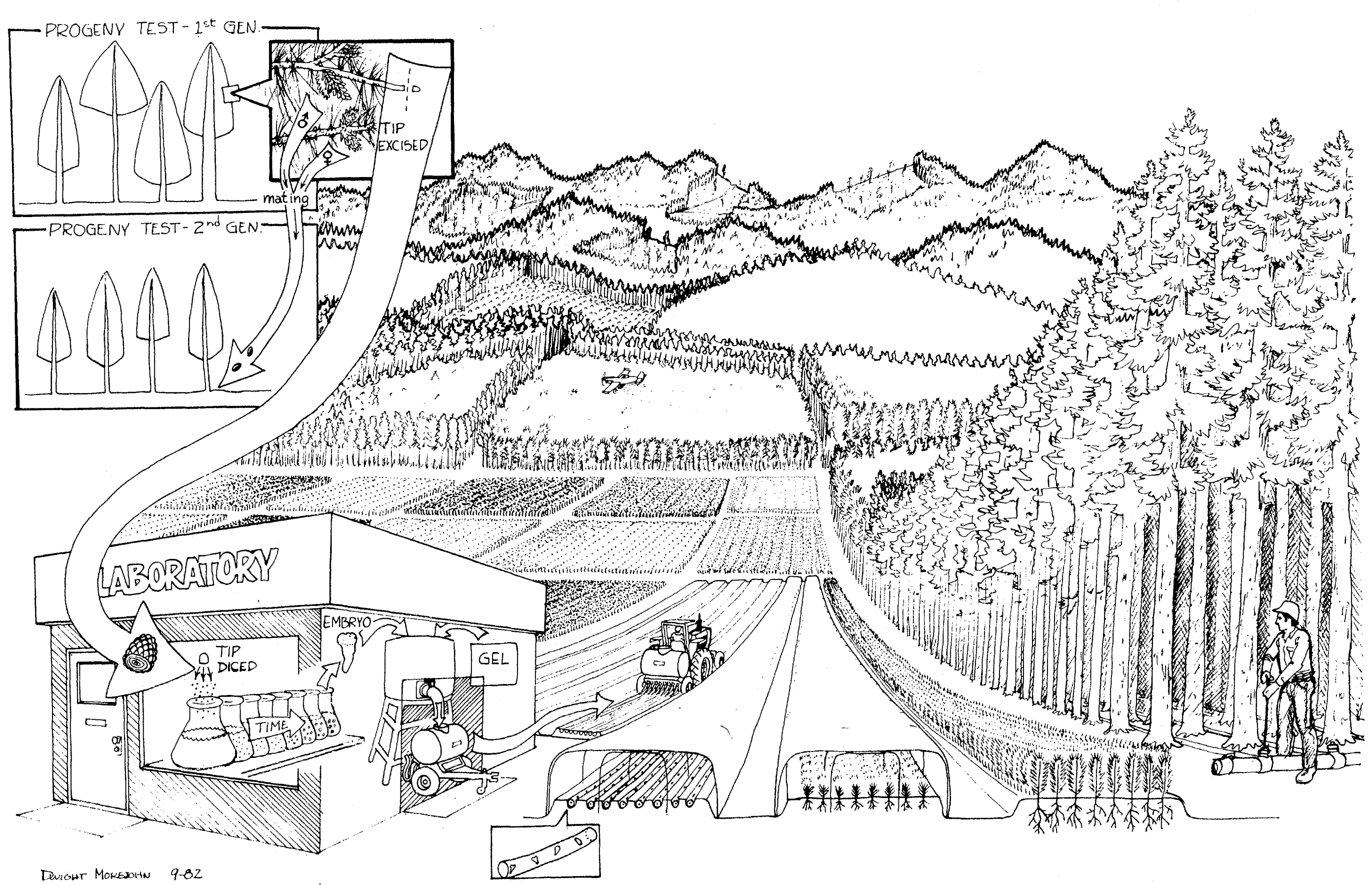

Fig. 4. Management of next century's forests? The scene illustrates the recurrent breeding cycle from first-generation flowers to second-generation progeny test (inset), the cloning of genetically superior trees from buds by embryogenesis in liquid culture, their mechanized sowing in extruded gel in protected nursery beds, intensively managed monoclonal-block plantations containing narrow-crowned, densely packed trees on which advanced fertilization and perhaps trickle irrigation are practiced, and distant mixed-genotype forests managed at lower intensity.

clude the use of cuttings and tissue culture. Cuttings are being used successfully to clone a few conifer species and have provided the genetic gain estimates above. However, they suffer from several chronic problems (*81, 82*), including difficulty of rooting, poor early growth and form, low rates of multiplication, and aging of parents. In vitro culture techniques may eliminate these problems.

Tissue culture consists of the removal of an organ or piece of tissue from the parent, its sterilization to remove surface microorganisms, and its placement in or on a suitable series of chemical media that stimulate its development into whole plants. The media provide energy as sucrose, mineral nutrients, plant hormones, and growth cofactors and are composed and sequenced so as to stimulate and sustain morphogenetic changes along one of several pathways. The current state of this art and its application to forestry have been reviewed in detail (*76, 83, 84*). As with cuttings, a major difficulty is that tissue in trees old enough to have expressed superiority (in progeny tests) is too old to be easily propagated.

The demonstrated feasibility of propagating plantlets from juvenile (cotyledon) tissue of Douglas fir and loblolly pine (*76, 84*) is being followed up by several lines of research. Foremost is the effort to make the process economical by multiplying the progeny of full-sib seed from relatively small numbers of controlled crosses in orchards. The second and more profitable step is to rejuvenate older tissue so that it will respond favorably to the juvenile process (*84*), which could then be used to clone proven individuals. Rejuvenating treatments currently under investigation include serial grafting of buds onto juvenile rootstock, severe pruning of trees to stimulate extension of latent juvenile meristems, spraying of parents with cytokinins, serial subculturing in vitro, and cytokinin-stimulated induction of adventitious buds. While some rejuvenation treatments carry a risk of genetic instability (*76, 84*), this has not yet been observed in cotyledon-derived plantlets of Douglas fir and loblolly pine. Its evaluation is the objective of extensive field trials.

A third option under study is to store juvenile tissue samples cryogenically for several years until the germ plasm is proven in a progeny test. Organized juvenile tissue of several nonhardy species, such as date palm and carnation, has been successfully recovered after 3 months of storage in liquid nitrogen (*85*). Whole conifer seedlings can be stored at $-1°C$ for up to 1 year in nonsterile conditions without cryoprotective treatment or nutrient media.

The long-term goal of forest tree tissue culture is to induce single cells or cell aggregates in a liquid medium to associate into embryo-like structures. In this process (somatic embryogenesis) the structures develop a shoot and root simultaneously (*86*). The technique is applied commercially to some horticultural plants. Feasibility has been demonstrated in a few tree species (*83*), and partially formed somatic embryos have been induced in Douglas fir (*87*). Properly controlled, somatic embryogenesis carries low risk of genetic instability, guarantees juvenile plants of normal growth habit, and is amenable to the type of process engineering that results in low production costs in large-scale application (Fig. 4).

Significant additional benefits can accrue from the use of in vitro techniques. Cloning may provide material of reduced variability to aid in the identification of properties and processes correlated with superior performance. Observations of trees flowering during or shortly after in vitro culture (*76, 86*) may provide clues to better control of the flowering process than is currently achievable (*88*). This could allow the breeding cycle to be shortened further.

A future alternative to vegetative propagation could be regeneration of haploid plantlets from female gametophytic tissue of conifers (*83*). Such plantlets offer the possibility of breeding pure lines (in which the members of any gene pair are identical) (*75*). An open-pollinated orchard containing two such lines developed from superior individuals would allow all their nonadditive genetic gain to be captured through seed.

The use of clones brings into focus the conflict between short-term and long-term objectives of tree breeding (*81, 89*). What balance should be sought in long-lived crops between specialization for economic yield and maintenance of adaptability? Highly specialized clones cannot accommodate much variation in the environment. They will thus cost more to maintain (*90*) and are more at risk from climatic extremes and disease than lower-yielding plantations with a broad genetic base. Commercial forests are thus likely to become mosaics of clonal plantations on good sites and improved-seed forests on the poorer and less accessible sites (Fig. 4). The relative proportions will be the outcome of business decisions based on economic gain and risk. Single *Eucalyptus* clones are planted in 50-ha blocks in Brazil because of their superior uniformity of growth over clonal mixtures (*80*). This contrasts with 100-clone mixes of Norway spruce in Germany (*78*).

It is essential, however, to maintain within the breeding population a broad genetic base that includes both productive and adaptive gene complexes. This is best achieved by reducing the genetic overlap among members and the frequency of deleterious genes responsible for inbreeding depression. Component breeding from widely separated parents will enhance the former. Use of pure lines may aid in identifying and eliminating the latter. For some characteristics, such as bole straightness, the genetic base in the breeding population can legitimately be narrowed (*89*).

Germplasm reserves are a necessary insurance against the loss of unrecognized beneficial genes that may befit forests for future changes in climate, atmospheric carbon dioxide concentration, disease and insect pressures, or marketable products (*53, 89*).

Conclusions

Potential productivity and target mean annual yields have been defined by using a theoretical model and observations from existing stands. Target yields for Douglas fir and loblolly pine are 25 and 30 Mg/ha per year, respectively. Even under intensive management with state-of-the-art cultural and genetic practices, both species are currently achieving less than 50 percent of these targets. Increases in yield will result from refinement of fertilizer prescriptions; control of competing vegetation; exploitation of nutrient, fertilizer, and weed control interactions; advanced tree breeding; and tissue culture techniques. In particular, the diversity of approaches to mature tree cloning and the achievements reported to date suggest that the technology will be successfully developed. Applying it along with advanced cultural techniques on good sites may be sufficient to eliminate the gap between current and target yields for plantations established by the end of the century.

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