Strategies and Case Studies for Incorporating Ecophysiology into Southern Pine Tree Improvement Programs

T.A. Martin, *School of Forest Resources and Conservation, University of Florida, Gainesville, FL 32611-0410;* **P.M. Dougherty,** *MeadWestvaco, Summerville, SC 29484;* **M.A. Topa,** *The Holden Arboretum, Kirtland, OH 44094; and* **S.E. McKeand,** *North Carolina State University, Raleigh, NC 27695.*

Both genetic and environmental influences on tree growth are expressed through physiological processes. This central, integrating role of physiology has made the field of forest ecophysiology a major area of biological research for the past several decades. Specifically, forest ecophysiology is the study of how plants interact with their abiotic and biotic environment to acquire the resources (sunlight, CO_2, water, and nutrients) needed to produce assimilates necessary for growth, reproduction, competition with other plants, and defense against insects and disease. Because of their commercial and ecological importance, southern pines, especially loblolly pine (*Pinus taeda* L.) have been intensively studied by ecophysiologists. Although an exhaustive review of the ecophysiological literature is not possible here, examples of the physiological and morphological determinants of growth that have been studied in southern pines include the following: leaf area development (Gresham 1982, Martin and Jokela 2004), crown and canopy structure (Kinerson et al. 1974, Gillespie et al. 1994), light interception (Dalla-Tea and Jokela 1991, Will et al. 2001), carbon fixation (Bormann 1956, Teskey et al. 1987, Ellsworth 2000, Yang et al. 2002), respiration (Brix 1962, Kinerson et al. 1977, Maier et al. 1998), carbon allocation (Kuhns and Gjerstad 1988, Retzlaff et al. 2001b), tree water relations and stand water balance (Knauf and Bilan 1974, Seiler and Johnson 1985, Fites and Teskey 1988, Phillips and Oren 2001), root structure and function (Sword et al. 1996, Topa and Sisak 1997, Wu et al. 2000), and nutrient uptake and utilization dynamics (Switzer et al. 1966, Birk and Vitousek 1986, Dalla-Tea and Jokela 1994, Barron-Gafford et al. 2003). Important areas of emphasis have included genetic variation in physiology and morphology (Thames 1963, Ledig and Perry 1967, Bilan et al. 1977, Bongarten et al. 1987, McGarvey et al. 2004), physiological responses to silvicultural treatments (Johnson 1990, Murthy et al. 1997, Samuelson et al. 2001), and the potential effects of pollution and climate change on physiology (Sasek et al. 1991, Tissue et al. 1993, Teskey 1997, Oren et al. 2001). Taken together, the broad and deep coverage of ecophysiological investigations with southern pines (in particular, loblolly pine) have enabled a level of biological understanding that is rivaled in only a few other forest tree species, such as Douglas-fir (*Pseudotsuga menziesii*), Scots pine (*Pinus sylvestris*), and radiata pine (*Pinus radiata*).

Our detailed physiological knowledge of important commercial tree species has laid the groundwork for our modern approach to forest management. Most university forest management curriculums require a formal course in forest ecophysiology, and imparting a mental model of how the various biotic and abiotic components of a forest community interact is the composite goal of all university forestry programs. This goal is established on the realization that to anticipate the long-term consequences of forest management decisions, land managers must understand the mechanisms by which trees interact with their environment. The discipline of ecophysiology is expected to play an even bigger role in forest management in the near future because of the rapid changes that are occurring in our environment (carbon dioxide, ozone, atmospheric nitrogen inputs, temperature, and rainfall); in the forest genetic base being applied to managed forest systems; and in forest composition due to the application of increasingly intensive forest management practices. These rapid changes in forest environments and movement toward management scenarios that differ greatly from the past somewhat lessen the utility of empirical growth and yield models and make it imperative that we develop process-driven growth models capable of simulating forest growth under diverse situations (Landsberg 2003).

Over the past two decades, considerable progress has been made in bringing the fruits of forest ecophysiological research to bear on applied forest management problems.

NOTE: T. A. Martin can be reached at (352) 846-0866; Fax: (352) 846-1277; tamartin@ufl.edu. Manuscript received August 23, 2003, accepted April 28, 2004. Copyright © 2005 by the Society of American Foresters.

One avenue for this application has been through the development of process-based models with potential utility for forest managers. The nutrient models NUTREM (Ducey and Allen 2001) and SSAND (N. Comerford, University of Florida, unpublished data) have incorporated our understanding of stand nutrient demand, soil nutrient supply, and tree nutrient uptake into a framework that provides information useful for estimating fertilizer requirements of southern pine plantations. The voluminous southern pine ecophysiological research underpinned the development of a number of process-based models that are being used to enhance yield predictions for southern pines under different environmental conditions. Such models include Pipestem (Valentine et al. 1997), PTAEDA-Maestro (Baldwin et al. 1998), 3-PG (Landsberg et al. 2001), TREGRO (Weinstein et al. 1991), PNET (McNulty et al. 1998), and BIOMASS (Sampson and Allen 1999). The utility of these process-based models is that they can simulate forest productivity under environmental or management scenarios that have not occurred in the recent past. For example, Pipestem (Valentine et al. 1998) and PTAEDA-Maestro (Baldwin et al. 1998) have provided our first estimates of the effects of changing atmospheric carbon dioxide concentrations on the loblolly pine site index. Pipestem also has the ability to predict stem taper, branch size, and branch distribution (Makela 2002). Sampson and Allen's (1999) loblolly pine version of BIOMASS (McMurtrie and Landsberg 1992) is a powerful tool for evaluating how climatic variations across the range of loblolly pine affect potential productivity. Such evaluations can influence decisions ranging from fertilizer prescriptions to genetic deployment strategies to timberland acquisitions.

While ecophysiology has made numerous contributions to forest management, it is more difficult to find examples of direct contributions to southern pine tree improvement (TI) programs. The possibility of shortening selection time by using instantaneous measures of physiological processes and inferring long-term productivity potential from these measures has been considered for several decades (Cannell 1979, Burdon 1982, Dickmann 1991). Reducing the time required to evaluate progeny or clones would be of great benefit, especially for southern pine clone programs where tissue maturation makes it difficult to vegetatively propagate any particular genotype for more than a few years. Thus, if rapid, early ecophysiology measures could be identified to facilitate selection of winners or elimination of losers this would be of great value. In this article, we will (1) identify possible obstacles to the development of productive linkages between ecophysiology and TI programs; (2) describe some ongoing ecophysiological research efforts in three areas (family selection, clone selection, and identifying root system genetic differences) that are attempting to gain information to improve TI programs; and (3) suggest ecophysiological research approaches that have promise for assisting TI programs in selecting desirable genotypes. This discussion will center on ecophysiology and breeding in southern pines, especially loblolly pine.

Potential Obstacles to Ecophysiological Contributions to Tree Improvement Programs

Historically, TI programs have selected and bred trees on the basis of growth rate, stem straightness, stem form, disease resistance, and branch characteristics (e.g., White et al. 1993, Li et al. 2000). In contrast, screening for genetic differences in ecophysiological traits such as net photosynthesis rates (Ledig and Perry 1969, Boltz et al. 1986), respiration rates (Ledig and Perry 1967, Anekonda et al. 1994), and nutritional attributes (Xiao et al. 2003) have been attempted but never successfully integrated into conventional TI programs. In general, measurement of individual physiological processes or morphological traits has not been helpful in identifying high performing taxa. However, the lack of success in this area may be attributable to the following problems: selecting the wrong physiological parameters for screening, making physiological measurements at inappropriate spatial and temporal scales, and attempting to use seedlings to predict field performance of older trees. Growth is a function of many integrated physiological processes. These processes change with plant development and acclimate in response to an environment that changes dramatically over a rotation as stands develop and stand stature changes with age. Consequently, traditional ecophysiological approaches, which use instantaneous measurements of physiological processes at a single point in time on a small amount of tissue, may be expected to be poor predictors of long-term yield potential (Hinckley et al. 1998, McGarvey et al. 2004). Fortunately, new measurement technologies have been developed that enable ecophysiological measurements to integrate morphology and physiology over time, and that can be applied to larger trees. In addition, integrating physiological measurements with physiologically based models may be an important screening tool for identifying potential ecophysiological traits that significantly alter production (Martin et al. 2001). Coupling the more integrated measurement technology that can be applied to larger trees with emerging process models gives us hope that useful ecophysiological measures can be made and scaled to assess variation in southern pine genotype growth potential. This article will provide a number of examples of the utilization of this new generation of ecophysiological measurement tools and challenges that we face in assessing above- and below-ground structure and function.

Moving Forward: Assessing Variation in Belowground Ecophysiology and Morphology

Ecophysiological investigations in southern pines suggest that the rate of tree growth from out-planting to crown closure is highly dependent on the amount and quality of the soil environment that is created or modified through site preparation (Colbert et al. 1990, Will et al. 2002). Many soils in the southeastern United States that are used for southern pine production are highly eroded and depleted of their original organic matter and nutrient content (Richter et al. 2000). With increased demands for shorter rotations and

faster growing trees, proactive land management is necessary to ensure continued and possibly increased production and revenue through the management and recovery of the soil resource (Johnston and Crossley 2002). In particular, a greater emphasis on topsoil recovery would not only increase soil fertility over time but would also minimize disturbance of beneficial soil microorganisms. Rhizosphere microorganisms such as mycorrhizas, *Rhizobium*, rhizobacteria (Nehl et al. 1996), and mycorrhizal helper bacteria (Garbaye 1994) can stimulate tree growth through enhanced mineralization and nutrient acquisition, biological control of pathogens, lengthening of fine root lifespan, and production of plant growth regulators (Marks and Kozlowski 1973, Enebak et al. 1998, King et al. 2002, Topa et al. in review). Although soil N often greatly exceeds plant N, many southern forested ecosystems are N limited because only a small fraction of total N is available to plants. Ectomycorrhizas allow woody plants to compete with soil microorganisms for both nitrogen and phosphorus (Marschner and Dell 1994, Chalot and Brun 1998). Because nitrogen, phosphorus, and water are the major limiting factors to stand productivity throughout a rotation, it should be expected that acquisition and uptake of these soil resources are paramount to maintain high productivity throughout a rotation. If so, improving the uptake efficiency of southern pine root systems (roots + associated biota) should provide good returns in terms of yield increases. Yet, we know little about genetic variation in root uptake efficiencies in populations of field-grown trees. Since much of the natural range of southern pines includes soils that are nitrogen and/or phosphorous deficient, southern pines have coevolved a high dependency on ectomycorrhizal associations for acquiring nitrogen and phosphorous from the soil (Marks and Kozlowski 1973, Marx et al. 1977). A recent study with several loblolly pine families from Texas and the Atlantic Coastal Plain suggests that the mycorrhizal network may play a critical role in maintaining water uptake during the dry summer months (Retzlaff et al. 2001a). Clearly, because the factors that limit productivity are soil borne resources (nutrients and water) that must be taken up through the root system, this component deserves more research effort than has been applied in the past.

Because of the technological difficulty in monitoring root system growth and function in the field on large trees, much of our understanding of tree root function is based on seedling greenhouse studies (Kozlowski and Pallardy 1997). Unfortunately, juvenile-mature correlations for root traits affecting uptake efficiency are most likely weak because of inherent differences in root system development, architecture, mycorrhizal community, physiological transport characteristics, soil environmental conditions, whole-tree nutrient dynamics, and whole-tree carbon dynamics. Consequently, the biggest challenge facing tree root biologists is to find new technologies that will allow us to examine in situ root system growth, development, and function in trees of variable size in the field. In situ measurements of fine root demography (root growth and turnover) and function, and how rhizosphere microbes may alter function, will allow tree root biologists to better ascertain what root traits are most closely associated with enhanced aboveground growth under different soil environments (Table 1).

One of the most promising technologies for assessing genotypic differences in root system function is stable isotope technology, utilizing both natural abundance and enrichment studies. For example, Retzlaff et al. (2001a) used stable hydrogen composition of soil water, rain, and plant tissues to determine whether loblolly pine families from drought-hardy Texas and Atlantic Coastal Plain sources obtained water from different soil horizons (i.e., deep versus surface soil water) throughout the growing season. Interestingly, all families planted on this North Carolina sandhill site obtained water from the upper soil horizons during the dry summer months, whereas family differences were most pronounced during the wetter winter months. The results suggest that the mycorrhizal network may play a critical role in maintaining tree water relations in dry sandy soils of the Atlantic Coastal Plain. Carbon isotopic analysis of foliage is a powerful tool for providing time-integrated estimates of water use efficiency (WUE, the ratio of carbon fixed to water lost), integrating shoot and root morphological traits and physiological processes over an entire growing season (Farquhar et al. 1989). Some recent studies with conifers, including loblolly pine, show a stronger correlation between WUE and growth than between more instantaneous measurements of photosynthesis and growth (Major and Johnsen 1996, Johnsen et al. 1999, Yang et al. 2002). This suggests that carbon isotopic analysis of foliage could be a convenient screening tool for field assessments of genotype x environmental effects on productivity. ^{15}N enrichment studies are being used more frequently in the field to obtain better estimates of uptake efficiencies of root systems (Gebauer and Ehleringer 2000, Persson et al. 2003), whereas natural abundance studies may provide information on nitrogen sources of uptake in the soil and contributions of mycorrhizas to the uptake process in roots (Hobbie et al. 2001). Preliminary results of a ^{15}N enrichment study with fast- and slow-growing families of loblolly pine indicate that uptake rates are correlated with growth, but that proportional N distribution among the various tissues is similar (M.A. Topa, unpublished data).

Since fine root production and maintenance costs in conifer forests have been estimated to be 30% to 77% of net primary productivity, it is not unreasonable to postulate that

Table 1. List of root and rhizosphere traits that need to be better understood and the potential technology for assessing these traits.

Root/rhizosphere trait	Potential technology
Physiological transport characteristics	Stable carbon and hydrogen isotope analysis
Mycorrhizal and rhizosphere microbe community structure	DNA fingerprinting/molecular tools
Fine root production/turnover	Stable carbon isotope analysis/ minirhizotron
Fine root architecture/deployment	Ground-penetrating radar

genetic variation in aboveground production is associated with genetic variation in belowground carbon demands (Harris et al. 1977, Agren et al. 1980, Fogel 1983, Gholz et al. 1986, Gower et al. 1994). Fast-growing trees may have more efficient root systems, and ultimately, allocate proportionally less carbon belowground than slow-growing trees. There is a critical need for better estimates of belowground carbon costs associated with fine root production, root turnover, and mycorrhizal associations, and how these costs may change with stand age and soil environment. A combination of stable isotope, minirhizotron, and ground-penetrating radar technologies provides great hope for making better estimates of annual costs for fine root production and maintenance (see Hendrick and Pregitzer 1992, King et al. 2002, Butnor et al. 2003 for examples). In a recent study utilizing some of these improved technologies, Topa et al. (unpublished data) found family and family x environment differences in fine root production and turnover in fast- and slow-growing families of loblolly pine; some families exhibited significant reductions in root production and longer lifespans with fertilization than other families. Consequently, annual carbon costs for fine root production would be expected to be less in these families, and more carbon would be available for aboveground (bole) production.

Another area of below-ground ecophysiology research that has been neglected in southern pines is the cost/benefit of mycorrhizas and their role in enhancing production. Southern pines have evolved a dependency on ectomycorrhizal associations that not only enhances nutrient acquisition from nutrient-poor sites but also offers protection against soil pathogens (Marx 1973). A limited number of studies in forests suggest that mycorrhizal species diversity is relatively high (Perry et al. 1989, Allen et al. 1995, Hagerman et al. 1999), but also that community structure is dynamic, changing with age of stand, season, and aspects of site history including harvesting, site preparation, and fertilizer application (Hagerman et al. 1999, Johnston and Crossley 2002, Jones et al. 2003). After intensive site preparation, diversity may be low and most likely consists of opportunistic fungal species that may be less beneficial to the trees than on a site with less soil disturbance, although research is still lacking to test this hypothesis. Future research needs to be conducted to determine whether mycorrhizal community structure affects the carbon cost of root function, and ultimately, aboveground production, i.e., are some mycorrhizal species more beneficial than others? If so, can site preparation methods be altered to encourage colonization by more beneficial communities? Loblolly pine is colonized by a wide range of fungal species, and some are known to have growth-promoting effects at the seedling stage (Marx and Bryan 1971, Marx et al. 1977, Marx et al. 1991). However, whether this growth promoting effect occurs beyond the seedling stage in the field is unknown. Unfortunately, little field information is available on belowground mycorrhizal diversity, and how it may change as a stand ages. Whether fast growth in southern pines may be associated with different mycorrhizal communities in the field has not been examined.

Moving Forward: Assessing Variation in Southern Pine Ecophysiology and Morphology Using Family Block Studies

Most genetics and physiological genetics investigations focus on particular taxa (families or clones) growing in single-tree plots or in row plots of 5 to 10 trees. In this situation, a tree's nearest competitors may or may not belong to the same taxa. In contrast, operational deployment generally involves planting taxa in large, homogeneous blocks in which all inter-tree competition is between closely related genotypes (or the same genotype, in the case of clones). The upshot of this situation is that the competitive relationships, and resulting structural and functional responses of the taxa of interest, observed in traditional progeny-test type studies may or may not be representative of those that will take place when the taxa are deployed operationally (Martin et al. 2001). One solution to this dilemma is to study taxa of interest in situations similar to which they will be deployed: in blocks. The vast majority of plantations on industry lands (80%) are established using family blocks (McKeand et al. 2003). By investigating structure, physiology, stand dynamics, and growth of half- or full-sib families or clones growing in blocks, direct inferences can be made regarding how these taxa will perform when deployed operationally.

The great expense involved with block plot studies means that careful consideration must be given to which taxa are chosen for testing. Candidate taxa for block plot studies can be selected in a number of ways. One is simply to choose the best performing taxa from single-tree or row plot studies. Another potentially complementary approach is to use the results from ecophysiological and modeling studies performed on single-tree or row plot experiments to hypothesize which taxa exhibit the characteristics of a crop ideotype. Crop ideotypes are imaginary or model trees that have characteristics enabling them to grow well in intensively managed, tightly spaced plantings, without competing aggressively with their neighbors (Donald and Hamblin 1976, Cannell 1978). It is possible that trees with crop ideotype characteristics may not perform well in progeny test environments, where they are out competed by more aggressive neighbors from other taxa, but could perform quite well when mixed with other, less aggressively competitive neighbors from their own taxa (Martin et al. 2001). In addition to planting taxa that are expected to perform well in large blocks, it is usually helpful to also test one or more taxa that are poor or average performers. The presence of these "dog" taxa provides a useful contrast to the high performers, providing the opportunity to determine what mechanisms or characteristics set winning and losing taxa apart.

A research study by McCrady and Jokela (1996, 1998) provides an excellent example of the use of family block plots to understand the biological bases of performance differences. This study examined five open-pollinated loblolly pine families growing in family block plots at two relatively tight spacings (0.92 and 1.83 m). The researchers

quantified a number of canopy structural and functional characteristics, including leaf area index, vertical leaf area distribution, duration of leaf area display, radiation interception, and radiation use efficiency (biomass production/radiation interception), all of which were related to the genetic growth differences exhibited by the different families. This study underlined the overwhelming importance of canopy structure for determining growth performance of southern pines. A number of other experiments in the region have used half- and full-sib family block plots to study stand-level growth and canopy dynamics. The study described by McKeand et al. (2000) contrasts five half-sib families within each of two loblolly pine provenances (East Texas "Lost Pines" and Atlantic Coastal Plain), with control and high fertility levels of fertilization. This experiment provides the opportunity to determine what mechanisms are responsible for the dramatic provenance growth differences observed in these two seed sources and to determine whether these differences are consistent across widely varying soil nutrient availability (e.g., to determine whether there is a genotype x environment interaction). Within-provenance family variation can also be examined with this experimental design.

More recently, a series of eight studies has been installed from southeastern Georgia, across the Gulf Coastal plain to western Louisiana and East Texas (Roth et al. 2002). This experimental series is designed to quantify and determine the mechanisms underlying variation in growth performance of different full-sib families growing under factorial combinations of wide (2.8 × 2.8 m) and narrow (1.4 × 2.8 m) planting spacing and high and low silvicultural intensity (composed of contrasting levels of weed control and fertilization). A comprehensive set of baseline measurements are collected at each location, including annual above and belowground biomass increment and nutrient concentration, leaf area index from litterfall, and understory vegetation quantity and nutrient content. Detailed site meteorological and soil water data are also collected continuously with automated dataloggers. This suite of measurements is intended to facilitate the design and testing of family-specific process models across the range of soil and climate conditions represented by the experiment. This research philosophy will undoubtedly become more common and more powerful as the fields of ecophysiology, production ecology, and process modeling continue their current trend of increasing collaboration (Martin et al. 2001).

Moving Forward: Assessing Variation in Southern Pine Ecophysiology and Morphology Using Clonal Studies

Studies on half- or full-sib families contribute valuable information regarding both the basic ecophysiology and morphology of specific genotypes, as well as applied issues relating to deployment of genetic material. However, the changing face of both basic biological research and operational genetic deployment dictates that research on clonal material moves to the forefront. There are a number of characteristics of clones that confer considerable advantages for both applied and ecophysiological research. First, because clonal material is generated from a single genotype, there is no genetic variation from plant to plant. This has huge implications for ecophysiological research, because the environmental and genetic effects on any process (e.g., growth, photosynthesis rate, nutrient uptake) can be completely separated experimentally, allowing direct inferences to be made about the relative role of each in any particular situation. Consequently, a stronger correlation may be found between growth and specific ecophysiological processes. Operationally, the elimination of genetic variation in desired traits (such as stem form, wood properties, or even tree size) will allow the streamlining of forest operations from propagation through harvest and secondary processing. The lack of genetic variation also allows breeders to select the very best performing clones from the best families. Clonal selection can potentially produce realized gains in stem volume as high as 50%, compared with 30% for controlled cross selections and 10% per generation for open pollinated selection (D.A. Huber, personal communication). It should be noted that the desire to deploy clones is not only because of the possibility for increased volume production, but also because clonal selection may enable great improvement in stem properties such as specific gravity, lignin content or stem straightness that result in raw material with higher value.

Second, vegetative reproduction of trees, in combination with genetic transformation (the introduction of genes from one individual into another) allows the rapid production of genotypes that would be difficult or impossible to produce with traditional tree improvement approaches. Biological researchers take advantage of this attribute by using custom-made genotypes to better understand how genetic changes impact ecophysiological processes or tree structure. Applications from transformation are potentially large, and may include development of clones with any of a number of desirable attributes, such as wood quality characteristics, growth rate, disease resistance, nutrient use efficiency or others, alone or in combination within a single plant. A number of research programs in the Southeastern United States are currently carrying out experiments to better understand both the biological and applied attributes of clones.

The clone screening program at MeadWestvaco (MWV) is an example of an industry-based effort to use ecophysiological and morphological measurements to identify traits or genotypes with potential commercial value. This program is designed to (1) identify unique ideotypes with respect to physiology and morphology; (2) gain insight into how to deploy and culture the selected clones; (3) identify processes or traits that if altered through biotechnology would likely increase productivity or stem value; and (4) identify genotypes that may be useful in a trait-based breeding program. Several traits (Table 2) were examined in MWV's first clonal screening trial and were found to be associated with variation in growth rate. Some of the trait groups that proved informative in this trial included crown structure, resource use efficiency, and long-term integrated carbon gain.

Table 2. Example of traits examined in a MeadWestvaco loblolly pine clone screening trial. A "NO" indicates no relationship found between clone stem wood production and a trait, and "YES" shows that the measured trait did correlate with stem wood production.

Ecophysiological traits	
Leaf-level net photosynthesis rate	NO
Annual whole tree carbon gain	YES
Phenology	NO
Foliage nutrient concentration	YES
Biomass allocation (root vs. shoot)	YES
Growth efficiency	
Biomass/crown plan area	YES
Biomass/leaf area	YES
Biomass/canopy N content	YES
Morphological traits	
Crown plan area	YES
Branch size and frequency	YES
Internode length	YES
Below ground traits	
No direct work done	
Nutrient accumulation after fertilization—(ongoing)	

Crown architecture or structure is a potentially important trait that has bearing on an individual tree's potential to capture light but also on how well groups of trees perform together as a stand. These concepts are considered explicitly in the design of tree ideotypes, in which trees with wide, spreading crowns that aggressively compete with neighboring trees are characterized as "isolation ideotypes" or "competition ideotypes," whereas "crop ideotypes" generally have more compact crowns which effectively intercept light without interfering with neighboring trees (Cannell 1978). Crop ideotypes are generally considered desirable for growth in closely spaced, intensively managed forest stands. The 120 clones included in MWV's first clonal screening trial demonstrated a wide range of crown sizes. Trees with narrow crowns often had small branches as well. Several clones were identified that had both narrow crowns and high growth rates; these clones probably meet the definition of a crop ideotype, and may be highly efficient and suitable both for high-density pulpwood plantings and high quality sawtimber trees. Several clones had wide crowns associated with rapid growth rate, a trait combination that might be desirable for accelerating crown closure and reducing the need to apply extended vegetation management treatments.

Ratios of biomass or biomass production relative to crown size are sometimes good indicators of the efficiency of resource capture and conversion. This trial examined several indices of growth efficiency, including stemwood volume per unit crown projected area and stemwood volume per unit leaf area. The latter index successfully predicted clonal rankings for growth. An index of the amount of stemwood produced annually relative to the amount of nitrogen stored in crown foliage at the beginning of the year was also closely correlated to clone performance.

Although long-term integrated measures such as growth efficiency or morphological properties such as crown width, leaf area, and crown nutrient content were very useful, measurements of net photosynthesis of foliage showed no difference between slowly and rapidly growing clones. When leaf-level photosynthetic rates were combined with a knowledge of leaf area amount and distribution and scaled across the year to the whole tree level using a process model, Maestro (Wang and Jarvis, 1990), the resulting index of annual carbon gain was much more closely correlated with growth.

The results from MWV's first screening trial indicate that morphology (inferred allocation) is more important than physiological differences (net photosynthesis) in developing indices of clone growth potential. This initial work has also indicated that integrated measures or derived indices of clone performance such as annual whole tree carbon gain are useful for identifying promising clones. In addition to identifying high- performing clones, ecophysiological measures have also provided insight into how clones might need to be deployed. For example, for clone #93 that does not develop a broad crown but has rapid height growth, mixing broad-crowned "competition ideotype" clones with narrow-crowned "crop ideotype" clones would not likely be desirable. The range of nutrient utilization efficiency levels identified in this trial may have implications for the nutrient regimes (dose and frequency of fertilizer) that would be required for pure stands of high performing clones with high or low nutrient use efficiency. The initial results of this screening trial have generated considerable excitement about the role that ecophysiological screening can play in identifying useful ideotypes, developing deployment guidelines, and guiding trait based breeding or biotech programs designed to enhance select wood or timber properties. Designing better test environments to facilitate ecophysiological screening, using integrated measures of tree functioning and morphology and combining these measures in a process model format should permit even more useful results from ecophysiological screening to be derived.

Researchers at the University of Florida are also beginning to conduct ecophysiology screening of clones. They have two clonal research experiments in place that are designed to increase understanding of the genetic structure and biology of southern pine clones. The first study investigates the biology of 300 clones from five different full-sib loblolly and slash pine families. This study utilizes measurements that integrate biological information over space or time. For example, detailed crown structural information for each clone is used to parameterize the process model MAESTRA, which can then be used to estimate the total amount of radiation intercepted by each clone over large spans of time (months – seasons). Additional measurements in this study include whole-tree sap flow (integrates leaf physiology over the tree crown over long periods of time, see Martin 2000) and leaf carbon isotope discrimination (integrates leaf physiology over long periods of time, see Mortazavi and Chanton 2002). This research approach is based on the proposition that biological measurements that match the spatial and temporal scales at which growth is observed (e.g., whole trees over seasons to years) are more likely to be informative than measurements made over temporal and spatial scales much smaller than growth observations (Hinckley et al. 1998, Martin et al. 2001). This

proposition appears to be paying off in this study, where integrated whole-crown radiation interception explains over 70% of the variation in single-tree growth in some families, compared with leaf area alone, which only accounts for about 50% of the variation in growth (V.I. Emhart and T.A. Martin, unpublished data).

The second UF clonal study is installed on 13 sites across the Atlantic and Gulf Coastal Plains (Forest Biology Research Cooperative 2000). Each study site contains 900 loblolly or slash pine clones (derived from 60 full-sib crosses between elite parents) planted in single-tree plots under both high- and low-intensity silvicultural treatments. The design of this study, similar to traditional progeny tests used by tree breeders, is intended to enable the quantitative investigation of the genetic mechanisms controlling tree-level growth strategies, pest resistance, wood quality, and other characteristics. Recurring measurements planned for the study include the following: artificial inoculation screening of all loblolly and slash pine clones for both pitch canker and fusiform rust; annual field inventory of height, diameter and crown characteristics; field measurement of water relations parameters including predawn water potential, leaf relative water content, and leaf stable carbon isotope discrimination; and growth, morphology, phenology, and wood characteristics.

As industrial and University researchers gain experience with clonal material, experimental approaches are likely to become more sophisticated, which will lead to the ability to answer more sophisticated questions. For example, incorporating transgenic approaches into biological research with southern pines could eventually reap huge benefits. Although genetic transformation of conifers has been achieved (Walter et al. 1998, Wenck et al. 1999), routine transformation of southern pines remains problematic. Once this hurdle is cleared, however, substantial and rapid progress in understanding the molecular genetic basis of many physiological and biological processes is likely, considering the strides in understanding that have been achieved with more easily transformed species (Somerville and Somerville, 1999). Without this level of understanding, the production of field-ready, "custom-made" tree genotypes will remain theoretical.

Moving Forward: Strategies for Ecophysiological Screening

Ecophysiology screening in the future can be made more efficient by designing test environments in which soil resources can be easily and rapidly manipulated. Under such controlled test conditions, genotypic response to the quantity or timing of soil resource availability could be used to make inferences about root system distribution, root system functioning, and internal carbon assimilation limitations relative to nutrient uptake limitations. This approach will be very useful if ecophysiology measurements and measurements of gene activation that occur in response to rapid changes in a particular site resource can be coupled.

Future screening efforts will need to take full advantage of integrated measurements such as sap flow or isotope discrimination. Equipment and integrated measurements like sap flow systems will need to be developed and deployed in a manner that allows rapid measurements of greater numbers of individuals, whereas stable isotope technology allows more integrated measures of water use efficiency. The close linkage between carbon uptake and water use implies that estimates of water loss derived from sap flow measurements should reflect canopy carbon gain, and therefore productivity potential. Sap flow measurements also have the potential for making rapid estimates of leaf area in individual trees. Under conditions where stomatal conductance is expected to be fairly uniform among trees (high soil water content, low vapor pressure deficits), differences in water loss rates between trees should be directly proportional to differences in leaf area. Exploitation of this or similarly rapid methods for estimating individual tree (clone) leaf area would open the avenue for calculation of other indices to help identify unique ideotypes and potential high producers. For example, once leaf area is known, then simple measures of nutrient concentration and annual growth measurements make it possible to estimate nutrient use efficiency and growth efficiency on a leaf area basis.

It may be advantageous for future screening systems to couple continuous measurements of controlled and manipulated environmental conditions, integrated and point measurement of tree function, and measures of tree form into process models to fully probe and calculate each clone's ecophysiological attributes. Table 3 outlines a potential roadmap for combining these elements into a coherent ecophysiological research strategy that can contribute to tree improvement and forest management.

Potential Applications of Current Ecophysiological Research to Tree Improvement Programs

A number of applied benefits are likely to arise from ecophysiological research on southern pine families and clones. Family-level studies have revealed and will continue

Table 3. Strategies for future ecophysiological clone screening programs (A), potential outputs (B), and potential implications of these types of programs (C).

A. Strategies
Increased focus on ecophysiological measurements in clonal studies
Grow clones in test fields that permit resource manipulation
Utilize integrated ecophysiological measurements to identify clonal differences in structure and function associated with growth
Apply process models to develop integrated indices of clone structure and function
Assess gene expression to help inform molecular biology work
B. Potential outputs
Estimates of clonal growth efficiency, fertilizer uptake efficiency, nutrient use efficiency, annual carbon gain, biomass allocation patterns, growth and yield, economic value
C. Potential implications
Provide a basis for assessing growth and yield impacts, timber value improvements
Provide insight into taxon-specific silvicultural requirements and growth regimes
Identify clones for trait-based breeding

to reveal family-specific patterns of canopy development and stand dynamics, which will enhance our ability to select families that produce well at the stand level, as compared with performance in single-tree progeny test plots. For clonal experiments, the first and most direct application is likely to be the identification of useful clones. Due to the sheer numbers of genotypes that are observed and measured in single-tree clonal studies, there will emerge a number of clones with desirable growth, wood quality, and disease resistance characteristics. In the future, the applied benefits of transformation, and the ability to create "designer" trees with desired growth, wood quality, or disease resistance characteristics may overshadow all of the other benefits listed here. Finally, all of these research approaches will contribute to the development of more mechanistic growth and yield models. These models, likely to take the form of "hybrids" between biological process models and traditional growth and yield models (e.g., Baldwin et al. 1998), will have the ability to predict forest productivity under unique management or environmental scenarios, areas of weakness for traditional growth and yield models, which are based on past growth of forest stands. When these models are parameterized with information for specific taxa (families or clones), the development of both site- and genotype-specific silvicultural prescriptions will become a reality, an advance that will truly move forestry into the 21st century.

Summary

There is still much work to be done in using ecophysiological processes as screening tools rather than just tools for characterizing tree responses to changes in environmental conditions. There is no doubt that ecophysiological research will continue to provide useful information for clone selection, clone deployment strategies, and identification of specific processes that could be targeted for up- or down-regulation.

Although we have broadened the role of ecophysiology in identifying individual clone attributes that are beneficial to increasing production rates or stem value, we must not stop there. Ecophysiological researchers need to take leadership roles in guiding managers and biotechnologist in manipulating the entire managed community, not just the crop tree component. For example, we know through ecophysiology studies that a net immobilization of nitrogen occurs in loblolly pine forest floors over the entire rotation (Richter et al. 2000). Identifying or altering genotypes to have foliage chemistry that would permit rapid turnover and cycling of the large nitrogen pool that now accumulates over the rotation could be a better avenue for increasing stand productivity than using biotechnology to directly enhance biochemical or physiological processes of the crop tree itself. Another indirect manipulation that may be important is to develop clones that are better hosts for developing more efficient mycorrhizal networks. This could be more important than attempting to develop trees with larger root systems.

Almost twenty years ago, the eminent tree physiologist Paul Kramer stated that there was a "... need for better cooperation among forest geneticists, silviculturists, and physiologists in identifying physiological limitations to growth and in finding remedies for them" (Kramer 1986). Although ecophysiologists so far have struggled to live up to this mandate and contribute to tree improvement programs, there is no doubt that they can and must play an integral role in bringing to bear the power of ecophysiological research, biotechnology, and clonal forestry to help move tree improvement into the 21st century.

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