Ideotype Development in Southern Pines: Rationale and Strategies for Overcoming Scale-Related Obstacles

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ABSTRACT. Indirect genetic selection for early growth and disease resistance of southern pines has proven remarkably successful over the past several decades. However, several benefits could be derived for southern pine breeding programs by incorporating ideotypes, conceptual models which explicitly describe plant phenotypic characteristics that are hypothesized to produce greater yield. The potential benefits of using ideotypes include improvement in trait heritabilities and genetic correlations, higher genetic gain in diverse silvicultural environments, guidance for developing mating designs, and provision of a framework for synthesis of tree production physiology knowledge. There are numerous obstacles to the development of ideotypes for southern pines, most of them related to the difficulty of linking traits and processes that operate at small spatial and temporal scales (e.g., tree crown morphological traits or leaf net photosynthesis) with outputs that occur at large spatial and temporal scales (e.g., stand-level, rotation-age stem biomass yield). Fortunately, as we enter the 21st century, several relevant advances are converging that bode well for overcoming these obstacles. These advances relate to improvements and developments of process modeling, advances in technologies that permit measures of component processes at relevant scales, the likely future importance of intensive clonal forestry, and the movement toward large-scale genetic block plot experiments. For. Sci. 47(1):21–28.

Key Words: Process models, tree improvement, scaling, intensive management, clonal forestry.

Forest tree improvement is one of the greatest applied biology success stories in forestry. The impact of this biological research for the practice of forestry in the southeastern United States is especially remarkable. Genetically improved southern pines currently being planted yield 20 to 40% more wood volume at rotation age (White et al. 1993, McKeand and Svensson 1997, McKeand and Bridgwater 1998) and are considerably more disease resistant than their unimproved predecessors (Schmidt et al. 1996, Pye et al. 1997). Considering that most land reforested with southern pine is planted with genetically improved seedlings, this genetic gain alone has substantially increased growth and reduced rotation lengths of southern timberlands.

Most tree improvement programs begin with selection of promising phenotypes from natural populations. Subsequent crossing and selection in breeding programs are based on information obtained from progeny tests (e.g., White et al. 1993, McKeand and Bridgwater 1998). Characteristics used for selecting promising phenotypes from progeny tests are generally direct measurements of growth such as height or volume at 25% to 50% of rotation age, as well as visual scores of disease incidence. This selection for early growth is clearly

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a pragmatic and logical approach, considering that increased growth is the primary goal of most tree breeding programs. However, an alternative approach, which holds promise for increasing rotation-age yield and quality, is the ideotype approach.

An ideotype, formally introduced by Donald (1968), is "a plant model which is expected to yield a greater quantity or quality of grain or other useful product when developed as a cultivar." In other words, an ideotype is a conceptual model that explicitly describes the phenotypic characteristics of a plant that are hypothesized to lead to greater yield. Donald also pointed out that management conditions under which the plant is grown must be specified in any ideotype, since these conditions have direct bearing on phenotypic performance.

In his paper introducing the ideotype concept, Donald (1968) outlined an ideotype for wheat grown in dense spacing in fertile soil. The ideotype specified a short, strong stem, single culm, a small number of small, erect leaves, an erect and large ear, and the presence of awns. Brothers and Kelly (1993) described an ideotype for pinto beans that specified an upright growth habit, steep branch angles, "medium" seed weight, and a low number of seeds per pod and pods per plant. These examples and most published ideotypes are based only on morphological characteristics, since most breeding programs require easily measured characteristics to screen thousands of progeny for phenological characters. However, in concept, an ideotype can also specify biochemical, physiological, or other attributes of desirable phenotypes.

The *Populus* ideotype published by Dickmann (1985) and Dickmann and Keathley (1996) is an example of an ideotype that contains much nonmorphological information. The intended silvicultural environment for the *Populus* ideotype is a high-density, nonirrigated plantation grown for energy or wood fiber. This ideotype, one of the few developed for forest trees, includes a long list of desirable traits in several different categories, including growth and physiology, ecological characteristics, morphology, stem, and wood properties, and root characteristics (Table 1). The generalized Scandinavian conifer ideotype presented by Kärki and Tigerstadt (1985) shares many features in common with the *Populus* ideotype, but with less emphasis on physiological characteristics (Table 1). The few other ideotypes developed for trees are discussed by Dickmann et al. (1994).

In this article, we will discuss the ideotype concept as it relates to tree improvement and biological research in general, with specific references to intensively cultured southern pine. Our objectives are to: (1) review previous work on tree ideotypes and describe the rationale for their development; (2) highlight the problems of spatial and temporal scale that hinder the development of tree ideotypes; (3) suggest several strategies for overcoming these scale-related obstacles; and (4) emphasize current trends that favor the development and application of ideotypes to intensively managed southern pine systems.

Why Develop Ideotypes for Trees?

Traditional selection for early growth and disease resistance has worked well for southern pines, producing disease-resistant trees that grow faster than unimproved trees; however, Dickmann (1985) outlined several reasons to consider developing ideotypes for forest tree breeding programs. Ideotypes specify explicitly the morphological or other traits that tree breeders should be seeking in their selections. If the ideotype is based on good biological information, these traits could potentially be better linked to rotation-age yield than

Table 1. Examples of tree ideotypes.

	Populus[a]	Scandinavian Conifer[b]
Specified growth conditions	High-density, nonirrigated, intensive silvicultural system	Specify that silviculture should be developed specifically for the ideotype
Growth and physiology	Rapid height and diameter growth High photosynthetic rate per unit leaf area or mass High ratio of photosynthesis to dark respiration Leaves, cambium and fine roots that osmotically adjust to dehydration	Rapid height and diameter growth
Ecological characteristics	Weak competitor Tolerant of winter minimum temperatures Unpalatable to animals	Wind-firm Tolerant of snow loads
Morphology	Sylleptic branching Rapid natural pruning of dead branches Large, vertically oriented leaves in upper crown Long seasonal leaf retention High ratio of indeterminate to determinate shoots in the upper crown	Slow-growing, small branches 90° branch angles Large leaf area per unit branch weight Long, narrow crown Few flowers
Stem and wood properties	Straight, low-taper stem Thin bark resistant to winter sunscald High density wood that is low in gelatinous fibers	Straight, low-taper stem Thin bark "Good quality" timber
Roots	Strongly rooting cuttings High degree of branching throughout the soil profile Low rate of fine root turnover	Not specified

[a] Dickmann 1985, Dickmann and Keathley 1996.
[b] Kärki and Tigerstedt 1985.

traditionally measured parameters such as growth in genetic tests that are typically measured at one-fourth to one-half rotation age (Dickmann and Keathley 1996). In particular, most genetic tests are designed such that each family or clone occupies a very small plot with only one to a few trees (e.g., Loo-Dinkins and Tauer 1987, White and Hodge 1992), and selections are often based on juvenile growth (e.g., Lambeth et al. 1983, McKeand 1988, Burdon 1989). This means that nearly all selections currently practiced in tree improvement programs are a form of indirect selection (Falconer and Mckay 1996), because the selection criterion (juvenile growth in small plots) is distinct from the target trait (rotation-age yield in pure plantations of selected material). Genetic gain from indirect selection depends in part on the heritability of the traits in the selection criteria and their genetic correlation with the target trait (Falconer and McKay 1996). It is conceivable that current selection practices lead to selection of trees that are less than ideally suited for rotation-age stand growth and yield in intensively managed, genetically homogeneous plantations.

This is best illustrated by considering the three main categories of ideotypes described by Donald and Hamblin (1976) and Cannell (1978). The isolation ideotype grows well in the absence of competition (i.e., open-grown conditions), and tends to have a large, long crown and a spreading root system. The competition ideotype is similar to the isolation ideotype, except that it rapidly exploits site resources, aggressively expanding its crown and root structure to the detriment of neighboring genotypes; in other words, it is a strong competitor. The crop ideotype efficiently exploits locally available resources, while not competing strongly with neighboring trees. Presumably the crop ideotype model will produce the greatest yield per unit ground area in intensively managed monocultures (Cannell 1978).

The typical selection process in most tree breeding programs could have three disadvantages when considering the range of ideotypes and their implications for stand-level yield: (1) selection for growth in young progeny tests that have not yet reached canopy closure probably biases in favor of isolation ideotypes; (2) selection for growth in the same progeny tests after canopy closure and the start of intertree competition may bias selections toward competition ideotypes; and (3) weak competitors (crop ideotypes) which may perform best in intensively managed monoculture plantations are perhaps overlooked. The upshot is that a tree ideally suited for rapid growth in an intensively managed, monocultural plantation might be at a competitive disadvantage in a progeny test environment (Cannell 1979, Dickmann 1985, Marshall 1991).

An ideotype-based approach could help overcome these selection biases by providing breeders with an explicit description of the characteristics of a southern pine crop ideotype based on harvest-aged yield and better guide breeders to selection of promising phenotypes which may not necessarily be the largest or best performing trees in wild populations or in progeny test environments. In particular, definition of a detailed southern pine crop ideotype based on underlying biochemical, physiological, or morphological traits could have several specific advantages: (1) underlying traits could have higher heritabilities than growth traits currently used, if they are closer to genome level and less influenced by environmental noise; (2) underlying traits could have a higher genetic correlation with the target trait (the rotation-age crop ideotype) if they are less influenced by the selection age or test design than current traits; (3) basing selection on underlying traits composing the crop ideotype could allow more predictability and therefore more genetic gain if selections are planted in silvicultural conditions different from those in genetic tests; (4) mating designs for breeding could be enhanced above the blind breeding now practiced by allowing breeders to form complimentary crosses (such as a cross between one selection that maximizes leaf-level photosynthetic rates and another that tends to maximize leaf area development) and (5) ideotypes can serve as a basis for understanding tree production physiology, by formally integrating our understanding of the structural and functional components controlling growth. Much like process models, the conceptual model of the ideotype serves as a framework for synthesis. In addition, ideotypes provide opportunities for geneticists, tree breeders, and physiologists to interact, a process that should lead to more efficient application of the results from basic physiological and genetic research.

Obstacles to Tree Ideotype Development

Unfortunately, there are obstacles to the development of ideotypes that are unique to trees. Most of these problems are linked to issues of spatial and temporal scale. First, physiological research primarily focuses spatially at the organ level and below, while productivity of trees and forests is manifested at the level of the individual and the stand, respectively. Similarly, physiological research tends to focus on temporal scales of seconds to hours, while forest growth proceeds over spans of years and decades. The disconnect between the temporal and spatial scales of inquiry versus the temporal and spatial scales of application is a major obstacle to a full understanding of the structural and functional bases of growth (Hinckley et al. 1998), knowledge that is necessary for the development of ideotypes. While these problems exist to some extent for agronomic crops, they are magnified in forestry because of the greater size and longer lifespans of tree crops.

In addition to measurement-related issues of temporal scale, the longevity of trees themselves also hinders tree ideotype development; during their various developmental stages, different underlying traits are likely to differentially impact growth. In other words, the "optimal" suite of traits for growth is likely different for trees as seedlings, saplings, and mature individuals. In addition, Farnsworth and Niklas (1995) point out that since plants grow additively, current morphological traits tend to constrain future morphology. This means that later stages of morphological development probably cannot be studied in isolation, since they are derived from morphology earlier in the tree's development.

Tree canopy structure is likely to be an integral part of any tree ideotype, just as is the case with agronomic ideotypes. However, the structure of tree canopies embodies many of the

spatial and temporal scale challenges unique to tree ideotype development. Tree canopies are extensive, deep and far from the ground, all physical obstacles to their study. Tree canopies also tend to be more complex than other crop canopies: they are horizontally and vertically heterogeneous (Parker 1995), making their quantification more complex and difficult than for agronomic crops. In addition, tree canopy architecture is dynamic, moving through several morphological phases during stand development, all with varying impacts on growth (Cochrane and Ford 1978, Ford 1982).

Finally, the biology and genetics of the species of interest can stymie the realization of ideotype development. In the 1970s and 1980s, there was great interest in improving tree growth rate by breeding trees that had greater internode lengths (stem unit length) with trees that had greater number of internodes (stem unit number). The result would be an ideotype that achieved improved height growth via these two separate components. Early optimism for this approach was based on the notion that these two traits were inherited independently since stem unit initiation and elongation result from activities of different meristems [apical meristem for stem unit initiation, and the rib meristem for stem unit elongation (Romberger 1963)], the activities of which were temporally separate (Cannell et al. 1976). Close examinations of the genetic relationships of these traits in *Pinus* (Kremer and Larson 1983), and *Picea* and *Pseudotsuga* (Bongarten 1986) have revealed that the desired ideotype is a difficult one to achieve as the two traits are strongly negatively correlated, both environmentally and genetically. Although the two traits may be controlled by separate meristems, Bongarten (1986) hypothesized that the negative correlation was due to the traits both relying on the same finite pool of assimilates. He suggested that increased yield may be possible by selecting positive deviations from the stem unit number-stem unit length regression line. This case study exemplifies the interference genetic correlations among component traits can have on the practical realization of a conceptual ideotype. As will be discussed below, the use of clonal material may well make the combination of desired traits in one individual more feasible.

Potential Roles of Scaling and Process Models

Physiological process models may be a very effective tool for addressing scale-related obstacles to southern pine ideotype development. This is because process models, by definition, are built to integrate physiological and morphological information over time and space (Jarvis 1993). We will outline several broad approaches to illustrate some possible ways that process models may contribute to southern pine ideotype development.

Process models are well suited for interpreting physiological genetics data and making linkages from empirical studies to theoretical ideotype models. Most studies contrasting different genotypes identify differences in structure or function (e.g., Nali et al. 1998, Kavanagh et al. 1999). However, the spatial and temporal scale or level of observation in these studies is generally smaller than the level at which growth differences are manifested. The challenge in these cases is to identify which traits actually have potential to contribute to enhanced productivity at the desired temporal and spatial scales. Process models are an obvious tool for addressing these questions.

An example of this approach to interpreting empirical physiological genetics data is a study by Pepin and Livingston (1997), which compared stomatal responses to light in *Thuja plicata* grown from seed from "moist" and "dry" sources. Pepin and Livingston found that stomata of the dry seed source responded to light much more quickly at low air temperatures, with a time constant that was approximately 50% faster than the moist seed source at 10°C. This result demonstrates intriguing physiological differences between the sources, but in itself is not particularly informative about the relative ability of the plants to gain carbon. Pepin and Livingston took the analysis one step further, applying a simple model of stomatal dynamics and photosynthesis to evaluate the impacts of these genetic differences for carbon gain of the contrasting sources. They concluded that under some meteorological conditions, the enhanced stomatal light response at low temperature in plants from the dry seed sources conferred a biologically significant increase in carbon gain. This analysis allowed Pepin and Livingston to expand the temporal inferences of their data from the short time spans of laboratory measurements to the longer time spans in the field relevant to carbon gain and, presumably, productivity of the different sources. Similar gains in interpretive power could be attained by incorporating process modeling into the analysis or interpretation of data from most physiological, ecological, or silvicultural studies with a genetic component. In all of these applications, process models would allow researchers to more rigorously examine data from empirical genetic comparisons, and help to determine whether the traits found are good potential candidates for inclusion in ideotypes.

There may also be utility in using process models to propose optimum traits or suites of traits, and evaluate the effects of these characters for carbon gain or growth. Depending on the model structure, the optimization can be carried out analytically or iteratively, while the output that is maximized could be growth, carbon gain, or some other relevant variable. A modeling exercise by Wu (1993) is an excellent example of this approach to ideotype development. Wu used a simple canopy photosynthesis model to propose an optimum set of characteristics for a generic forest canopy. By maximizing the system equations for carbon gain, Wu concluded that N is optimally allocated when N allocation directly parallels the patterns of light interception in the canopy. By comparing instantaneous photosynthesis rates of canopies with optimum or uniform N distributions, across a range of light levels and with different canopy light extinction coefficients and leaf area indices, Wu was able to propose one "optimum" set of morphological and physiological characteristics for a tree canopy. Ford (1985) used a similar series of simulations to explore how variations in branch structure affected carbohydrate export, suggesting that such an optimization approach could potentially be used

to design branch ideotypes. Clearly, the results from exercises like these are constrained and limited by the assumptions of the model used. In addition, several authors have pointed out the potential pitfalls in defining a single optimum set of traits, the most obvious being that in any complex system there are probably many combinations of characters that would produce similar outputs (Ford 1992, Farnsworth and Niklas 1995, Dickmann and Keathley 1996). However, these examples demonstrate that given the current biological state-of-knowledge, it is possible to identify structural and functional characteristics that are likely linked to increased productivity. This type of approach should be particularly useful for identifying traits or trait combinations that are not commonly observed in breeding populations.

Process models can also aid ideotype development by integrating or scaling up information from the organ and tree level to the stand level. As discussed previously, most genetic information for tree breeding programs is derived from single-tree or row-plot progeny tests, in which each individual competes with different genotypes and often different families. In contrast, modern forestry deployment strategies will compel us to understand how elite genotypes or proposed ideotypes will grow in single-family or even clonal blocks, where competition is either between closely related individuals or identical genotypes, respectively. Genetic block experiments (e.g., McCrady and Jokela 1998) are one way to gain this information, but field studies are time-consuming and expensive, and field experiments obviously cannot address hypothetical ideotype trees. Process models provide an ideal, short-term solution for scaling up the morphological and physiological attributes of a genotype or ideotype from the single-tree to the stand level. Using process models, physiological geneticists can aggregate the physiological and morphological attributes of their proposed ideotype (or of a specific, studied phenotype) to the primary level of importance for forest production: the stand. The development of hybrid models, which combine physiological process models with more traditional growth and yield models, will be especially useful for integrating physiological processes with larger scale stand dynamics processes. Hybrid approaches will also be effective for developing ideotypes for silvicultural scenarios such as sawlog production, where stand structure is as important a consideration as per-hectare yield.

Ideotypes developed for southern pine or any other tree species can incorporate a host of morphological, physiological and other attributes, as evidenced by the Dickmann and Keathley (1996) *Populus* ideotype. While this proliferation of ideotype traits is useful for heuristic purposes, the fact remains that the successful incorporation of ideotypes into breeding programs probably depends on identification of only a few, critical traits that are closely correlated or linked with rotation-age yield. This is because as additional traits are added to a selection program, the efficiency of improvement in any one trait decreases (Cotterill and Dean 1990, Dickmann et al. 1994). While efforts have been made to develop multitrait selection indices practical for tree breeding (Bridgwater et al. 1983, Cotterill and Jackson 1985, Burdon 1989), research into ideotype development for southern pines would do well to focus on identifying the one or two traits most indicative of the "crop" ideotype. A coordinated program of empirical physiological genetics studies, supported by modeling approaches such as those described previously, should be able to identify these critical traits.

It is important to note that the necessity of empirical field trials cannot be entirely circumvented by the use of models. Process models which operate at the stand level will lessen some of the need for large-scale field experiments, especially during the early ideotype development phases, and will aid in the design of large-scale field studies. However, before proposed traits are incorporated into breeding programs, field studies which deploy blocks of genotypes or clones expressing some or all of the identified characters will likely be required to verify for breeders the validity of those traits. Experiments such as these which incorporate numerous genotypes in large blocks, preferably under variable silvicultural and soil conditions, will be large, expensive, and challenging to implement (Foster and Knowe 1995).

Promising Developments

While there remain numerous obstacles to the practical incorporation of ideotypes into southern pine tree improvement programs, there are fortunately several relevant advances that are converging as we enter the 21st century that bode well for this task. These relate to improvements and developments of process modeling, advances in technologies that permit measures of component processes at relevant scales, the likely future importance of intensive clonal forestry, and the movement toward large-scale genetic block plot experiments.

First, the field of process modeling is progressing rapidly, and its development is being accelerated by the fact that traditional growth and yield models are becoming inadequate for intensive southern pine plantation forestry (Landsberg et al., this issue). Several models are already in place which allow scaling of detailed morphological and physiological information from the organ and whole-tree level to the stand level. The model of Chen et al. (1994) utilizes fractal methods to simulate the branching structure of *Populus* trees and incorporates leaf development dynamics. By allowing aggregation of individual trees into simulated stands, this model provides a powerful framework for exploring the impacts of changes in morphology at the leaf, branch, and tree levels on light interception at the canopy level. Since the model was developed for *Populus* it would not be directly applicable to southern pine, but the approach and methods are certainly amenable.

The process model MAESTRO (Wang and Jarvis 1990) and more recent iteration MAESTRA (revised by Belinda Medlyn: http://www.ed.ac.uk/~bmedlyn/maestra/) is even more powerful, because it incorporates physiological processes such as transpiration, respiration, and photosynthesis, as well as sophisticated descriptions of crown structure. This model has already been parameterized for loblolly pine (Cropper et al. 1998), making it an ideal candidate for use as a scaling tool for southern pine ideotype development. Cropper and Gholz's Slash Pine Model (SPM, Cropper and Gholz

1993 and SPM2, Cropper 2000) is another model that has been developed specifically for southern pines and proves useful for scaling organ-level physiological processes to the stand level.

Significant progress has also been made in linking physiological processes with larger scale stand dynamics processes. A hybrid model for loblolly pine stands was recently developed by Baldwin et al. (1998) which combines the process model MAESTRO with the distance-dependent growth and yield model PTAEDA. Landsberg and Waring's (1997) model 3-PG incorporates large-scale biological phenomena such as radiation use efficiency, carbon partitioning and self-thinning, and produces outputs (such as stemwood biomass production) that are easily transferable to forest plantations. The 3-PG model was recently parameterized and tested for intensively managed loblolly pine plantations (Landsberg et al., this issue). In any application of process models to ideotype development, it is critical to consider the uncertainty inherent in model predictions. Unfortunately, it is hard to quantify the accuracy of many model predictions, simply because it is difficult or impossible to directly measure some model-predicted output parameters in "real" systems. For example, MAESTRO produces estimates of hourly carbon fixation for an individual tree, a parameter that cannot be measured with current technology. Improvements in measurement and modeling technology have started to ease this problem slightly. At the ecosystem level, eddy correlation has been used to compare modeled with measured carbon flux in a few forests (Williams et al. 1996, Cienciala et al. 1998, Clark et al. 2001). Some models such as 3-PG, SPM2, and MAESTRO-PTAEDA produce more easily measured output terms such as biomass production. In some cases, these models produce predictions that are very close to measured growth in forests. For example, simulations of sixth-year dbh by 3-PG explained over 95% of the variation in measured dbh for a fertilized loblolly pine plantation in North Carolina (Landsberg et al., this issue). Unfortunately, comparisons of model predictions with measurements in real forests remain rare and are sorely needed to provide estimates of the potential error associated with process model application.

A second promising development is that there have been major strides in technology and analytical techniques that now permit the clear identification of genotypes that possess traits to be incorporated into ideotypes. Typically, tree physiologists have relied on making inferences based on instantaneous measurements of processes such as photosynthesis and stomatal conductance. Over the past 10 yr, much effort has gone into developing and applying large-scale approaches such as whole-tree assessments of water use via sap flow measurements (Granier 1987, Martin et al. 1997, Ewers et al. 1999). Thus, measurements are now possible at a more realistic spatial scale of interest. Even instantaneous physiological measurements are improving and have been used to elucidate component traits (Johnsen and Major 1995, Major and Johnsen 1996). Another major technological advance has been in the use of stable isotopes to assess and understand processes at multiple scales (Farquhar et al. 1988, Brooks et al. 1998). Variation in stable isotopes of hydrogen have been used to quantify where different species (Flanagan et al. 1992) and even different loblolly pine families (Bill Retzlaff, pers. comm.) acquire their water from the soil profile. Variation in carbon isotope discrimination is proving a powerful tool for understanding subtle variation in water use efficiency (WUE). Carbon isotope discrimination has been used with forest trees to detect variation in WUE among provenances (Zhang et al. 1993, Cregg et al. 1999) families (Zhang et. al. 1994, Flanagan and Johnsen 1995, Pennington et al. 1999) and clones (Fan et al. 1999). A study by Johnsen et al. (1999) applied the technique in combination with sophisticated quantitative genetics analyses on a 7 × 7 black spruce diallel experiment and demonstrated carbon isotope discrimination was under high genetic control and was highly genetically correlated with growth. Recent applications of quantitative trait loci analysis to trees (Bradshaw and Stettler 1995, Wu 1998) demonstrates the powerful ability of this technique to identify the genetic bases of growth components. All these techniques are improving our ability to make component trait assessments, necessary for developing ideotypes, at relevant scales.

Third, intensive southern pine plantation forestry is developing rapidly. Management intensity is increasing via fertilization (Allen 1999), site preparation (Schultz 1997), and competition control (Zutter et al. 1999). The result is that the environment trees will be exposed to in these situations is becoming much more predictable. In these settings, clonal forestry will eventually be the norm. The application of ideotypes to clones should prove easier and more direct than with traditional breeding systems. Nonadditive, in addition to additive, genetic variation can be exploited with clones. Developments in genetic transformation technology for pines (Walter et al. 1998, Wenck et al. 1999) will make it possible to combine a particular suite of traits, overcoming negative genetic correlations, into one individual. These increases in predictability of the plantation system and the ability to manipulate plant form and function *via* genetic transformation will greatly increase the probability that modeled ideotype performance can be realized.

Finally, progress is being made toward design and implementation of the types of large-scale genetic block experiments needed to test ideotype concepts at the stand scale. Existing genetic block plot experiments have already produced valuable information regarding the relative roles of intergenotypic and intragenotypic competition on stand growth (e.g., Foster et al. 1998), and more are planned for the near future. As one example, the Forest Biology Research Cooperative at the University of Florida, in cooperation with a number of forest industry cooperators, recently installed a series of large (> 10 ha/installation) field experiments which deploy full-sib families in pure block plots under a range of soil and silvicultural (spacing, competition control, and fertilization) conditions (Forest Biology Research Cooperative 1998).

It is becoming exceedingly clear that we have the tools necessary for developing and applying ideotypes to southern pine. The successful utilization of these tools, however, will depend on combined, collaborative research efforts among physiologists, geneticists, biochemists, silviculturists, and modelers. Fortunately, the rich collaborative atmosphere that has already developed between modelers and tree physiologists during the past decade (e.g., Gholz et al. 1994, Fox and Mickler 1998) and the growing support of forest industry for basic biological research (Martin 1997) should facilitate development of the additional collaborative linkages needed to accomplish this goal.

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