Role of physiology in forest tree improvement

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Introduction

The forests of the world will play an important role in the future welfare of the human species, just as they always have. To this end the responsibility of foresters is great, for they will play a major role in the management of forests. The breeding of hardwood and coniferous tree cultivars that efficiently produce a particular wood product or amenity will be an increasingly important aspect of forest management. The breeding or engineering of high-yielding trees for wood production stands out as being especially important, as the landbase for wood production is shrinking due to competing and often exclusive uses of forest land.

Does the physiologist have a role to play in the process of tree improvement? I would say emphatically — yes! The mandate of physiology is to understand how plants work. Such understanding must be the underpinning of the practice of silviculture. In 1950 Frederick S. Baker prefaced his now classic book *Principles of Silviculture* with this statement:

> "A large part of this book is devoted to plant physiology of forest trees in the belief that a sufficiently wise and flexible silvicultural art can be developed on the ground only by practitioners who understand the forest as a biological entity."

Because it encompasses silviculture, this statement includes tree improvement as well. In fact, the processes that the physiologist tries to measure and understand are those which the applied geneticist tries to change (Richardson 1960). Breeders who do not understand the biology of the tree they are working with cannot expect to progress very far. Their tree becomes a "black box" which receives inputs and produces outputs in a mysterious way; the action of the genes regulating the functioning of the tree remains hidden.

Fortunately, most breeders recognize their need for a greater understanding of the gene-controlled physiological processes which produce growth and commercial yield. In fact, this need was expressed throughout the IUFRO joint working group meeting entitled "Biological Systems in Tree Breeding" which is the subject of this proceedings, and especially in the contribution by Eriksson (1991). What physiologists can provide to breeders and genetic engineers, in a general sense, is the opportunity to move their work from an empirical level towards a more theoretical level; i.e. towards a situation where breeding becomes both more predictable and more precise in its objectives. The success of future tree breeding efforts will depend rather strongly on movement in this direction, as the strictly empirical approach to tree improvement is strongly subject to the law of diminishing returns.

Modern agriculture represents the successful application of a physiologically based approach to crop improvement. The rather impressive gains in yield of cereal and other crops, such as soybean, have occurred, in part, because physiologists were working alongside geneticists and breeders. Much of the biology of agricultural crop plants has been elucidated, so breeders have had a clearer path to pursue, i.e. their objectives have been clearly defined. As agricultural crop improvement becomes more firmly based on the unraveling of the genome itself by molecular geneticists, the linkage between physiologists and now, genetic engineers, will strengthen.

In actuality, physiology is just one of several disciplines that comprise tree improvement (Fig. 1); each of them has something to contribute and their interaction is very synergistic. Breeders and engineers, of course, occupy a pivotal position because they are directly responsible for the output of tree improvement: new genotypes for plantation management. But the other disciplines in Fig. 1, in particular physiology, provide important inputs along the way.

What follows is a discussion of some of the ways in which plant physiology research can contribute to tree improvement. This discussion is not meant to be inclusive of every potential physiological input to tree improvement, but rather highlights those areas that show special promise for the future.

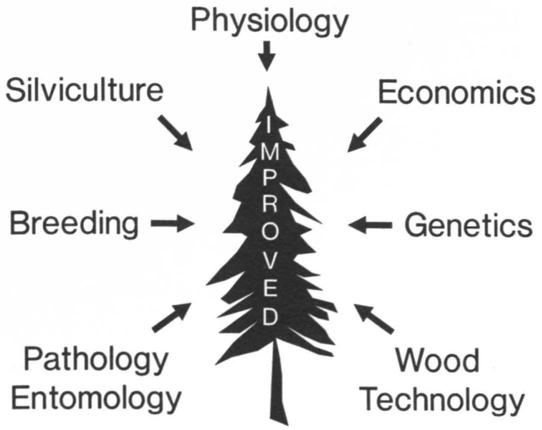

Fig. 1. The improvement of forest trees in the future will require input from various scientific disciplines, including physiology.

Biotechnology

The current cutting edge of forest genetics research surely lies in the area of cellular or molecular biology and *in vitro* culture. In addition to basic genetic studies of gene action and regulation, this area offers many opportunities to the applied geneticist. An ever increasing effort is being expended in micropropagation, culture of various organs and tissues, resistance screening, genetic transformation, and somaclonal selection, all to the end of increasing forest productivity under intensive culture. In fact, it seems as though these "biotechnology" efforts often proceed at the expense of conventional tree improvement methods. However, future gains in forest productivity will occur only if biotechnology and conventional breeding work in concert.

A close alliance of geneticists and physiologists becomes a necessity in the area of molecular and cellular biology. In fact, when working this close to the genome the distinction between a cellular physiologist and a molecular geneticist often fades; genes encode enzymes which regulate physiological processes. In fact, the application of biotechnology is constrained by the availability of background knowledge, not only genetic, but biochemical and physiological as well (Riemenschneider et al. 1988).

The synergism already derived or potentially possible from application of genetic and physiological methods of biotechnology to tree improvement can be demonstrated using two examples, one partially realized, one largely potential. There are others that could be cited, but these two perhaps offer the largest and most immediate payoffs: genetic transformation and micropropagation.

In cases where desirable genes cannot easily be transferred via sexual recombination, genetic transformation offers an increasingly viable crop improvement alternative (Gasser and Fraley 1989). But such transformations are predicated on knowledge of both the physiological and genetic bases of desirable traits (Dickmann and Keathley 1986). For example, the development of a glyphosate-tolerant *Populus* clone (Fillatti et al. 1987) was only possible because physiologists had determined that the mode-of-action of this herbicide was through inhibition of the enzyme 5-enolpyruvylshikimate (EPSP) synthase. Geneticists, in turn, discovered and identified the aroA gene locus in *Salmonella typhimurium* that encoded EPSP synthase. A mutant of this gene was then produced that encoded an enzyme with a reduced affinity for glyphosate. By using an *Agrobacterium tumefaciens* vector, this mutant gene was inserted into poplar leaf explants. Young trees regenerated from these transformed explants showed significant tolerance to glyphosate. This example demonstrates in dramatic fashion how genetic engineering can exploit the results of a physiology-genetic collaboration.

Another area where the potential for a beneficial physiology-genetic collaboration looms large is the micropropagation of conifers and determinate-growth angiosperms. Vegetative propagation is a powerful tool of tree improvement because it allows for the immediate capture of both additive and nonadditive genetic variance. Unfortunately, some of the most important commercial tree species are notoriously hard to vegetatively propagate by any means (Berlyn et al. 1986). A top research priority should be the unraveling of the genetic and physiological basis for asexual regeneration or nonregeneration and their controlling factors. With such knowledge in hand, physiologists and geneticists could devise micropropagation protocols to circumvent the systems responsible for vegetative nonregeneration in certain species or genetically engineer plants that will be vegetatively fecund.

Flowering

The benefits of a close collaboration between breeders and physiologists is very apparent in the area of flower induction and stimulation. Many forest tree species are notorious for their long period of juvenility, during which time reproductive structures are not initiated (Hackett 1985). Even after maturation or phase change, production of fruit and seed may be sparse or episodic. These tendencies impede progress in conventional tree breeding and limit seed production in orchards. Fortunately, breeders and physiologists have been actively studying phase change and reproductive mechanisms in forest trees for many years, and the results of these studies have paid dividends in tree improvement programs.

Ross and Pharis (1985) identified the basic treatments that have been shown to promote flowering in forest trees: water stress, root pruning, girdling, high temperatures, nitrogen fertilization, and application of growth regulators. Of the latter, exogenously applied gibberellins are effective promoters of precocious flowering in conifers and some woody angiosperms. Certain growth inhibitors also have been effective in woody angiosperms. It is important to note that these treatments do not cause stable changes in maturation state; young plants treated to induce flowering revert to the nonflowering, immature state after treatments cease (Hackett 1985). Such treatments are viewed by many as the major route to operational flower induction and stimulation. Although phase change and flower production are under strong genetic control (Longman 1985), breeding for a short juvenile period or high reproductive capacity may not be desirable because of negative genetic correlations with growth (e.g. Huhtinen 1976).

Although much progress has been made in our knowledge of flowering and phase change in forest trees, we are far from a complete understanding of the physiology of these processes. The controlling role of roots, for example, is poorly understood (Ross and Pharis 1985). And certain conifers, like *Picea abies*, still show a great reluctance to flower, especially in seed orchards. Thus, there is much still to be done in this area by basic and applied physiologists working in conjunction with tree breeding programs.

Selection criteria

A breeding program may generate millions of progeny each year, each with its own phenotypic characteristics. An efficient and expedient means of initially screening these progeny for further testing, commercial propagation, or production outplanting is essential. Physiologists have been asked to provide early selection criteria that are more reliable than the standard height and diameter. This need becomes even more critical as the cost-benefit ratio of tree improvement programs comes under closer scrutiny or as the costly progeny from genetic engineering efforts are evaluated.

Early selection criteria must be highly correlated with economic yield. In forest genetics tree height has been a common selection criterion in early screening. However, it is often difficult to equate seedling height (or other traditionally measured characters of young trees) and final yield (Zobel and Talbert 1984); i.e. age-age correlations are poor (Lambeth 1980). Many breeders view this problem as one of the central impediments to successful tree improvement in the future.

Conventional breeders, however, often accuse physiologists of being too caught up in precision (Fig. 2); their yield-predicting traits are very narrowly defined and measurements of them are unwieldy, time-consuming, and require expensive instrumentation. Physiologists, on the other hand, view these breeders as concentrating more on form than substance; they try to do too much and in the process sacrifice biological understanding (Fig. 2). This "gap" needs to be narrowed if we are going to advance the methodology of selecting genetically superior trees. Physiologists must become more practical and define traits that are broadly applicable to final yield and that are easily and quickly measured. Breeders, on the other hand, must get further into the plants they have created and be willing to spend the time and effort necessary to fully characterize them. Fortunately, in the area of biotechnology this gap narrows considerably.

Two traits illustrate the direction that we should be heading, both of them physiologically based. In *Populus*, leaf size — an easily-measured trait — may be a better indicator of potential stem volume than seedling height (Ridge et al. 1986). This trait is an indicator of photosynthetic potential, a primary determinate of final yield. When considering northern conifers, harvest index — the proportion of total dry matter of the crop that comprises the economic product — has been shown to be more closely correlated with yield per ha than stem volume *per se* (Pulkkinen et al. 1989). To a physiologist familiar with the literature on partitioning of dry matter within plants, this finding comes as no surprise. In agriculture the major gain in crop yield has been accomplished through genetic alteration of dry matter partitioning between the economic and noneconomic parts of the plant (Evans 1980).

Because of rapid advances in molecular genetics, the future may hold the possibility for increasing the correlation between genotype and phenotype, aiding early selection (Riemenschneider et al. 1988). Desirable alleles are becoming increasingly detectable at the molecular level, e.g. through restriction fragment length polymorphism mapping, allowing them to be directly associated with the phenotypic characteristics that they encode. Selection could then be based on the presence of markers that identify the desired genes. Another fruitful avenue of collaboration between applied geneticists and physiologists!

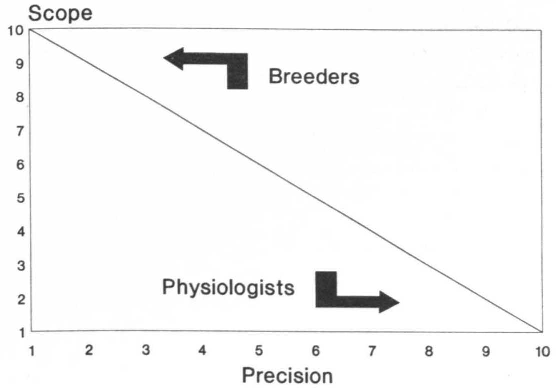

Fig. 2. The relationship between the scope of scientific research and its precision (units are arbitrary). The work of conventional tree breeders tends to be wide in scope and low in precision, whereas the opposite applies to physiologists. The resulting "gap" must be narrowed. (D.E. Riemenschneider, personal communication).

Adaptability

A major goal of most tree improvement programs is to produce cultivars or clones that are broadly adaptable across a wide range of sites; i.e. genotypes that show high phenotypic plasticity (Harper 1977, p. 649). Unplastic genotypes are less fit, in a silvicultural sense, because they will perform poorly on soil-sites that are less than optimum or during periods of adverse environmental conditions. Breeders are well aware of the importance of testing new progeny over a variety of sites, not only so that genotype × environment interactions can be assessed, but also to determine the relative plasticity in the performance of individual genotypes. For example, the two *Populus* × *euramericana* clones in Fig. 3 show contrasting adaptabilities; NE 359 performs well over a range of sites and is relatively plastic, whereas Eugenei not only grows slower but shows less phenotypic plasticity.

A tree that is successful must adapt to a multitude of interacting site factors whose individual effects may be more than additive. Adaptability to the vagaries of weather is particularly important in forestry. Sites can be carefully chosen to manifest the genetic potential of planting stock, but weather is uncontrollable. An exceptionally cold winter or severe drought can lay a carefully conceived and executed tree improvement plan to waste. As the human species continues to foul its residential planet, adaptability to the pollutants that infect the air, water, and soil must also be considered by breeders. Obviously, a comprehensive characterization of each planting site and the complexities of its associated environment is of critical importance. Physiologists can play an important role here.

Another way in which physiologist can contribute is in the understanding of the biological basis for adaptability. What are the traits that confer upon a genotype adaptation to a particular site limitation? How do genotypes compensate for multiple site limitations? As these questions are answered geneticists, working in concert with physiologists, can elucidate the genetic control of adaptive traits.

Great progress has been made in understanding adaptative physiological responses to certain limiting factors; e.g. water stress (Chaves 1991, Davies et al. 1990, Schulze et al. 1987), nitrogen deficiency (Chapin et al. 1987, Evans 1989), or cold (Guy 1990, Levitt 1980). We are less successful in understanding plant responses

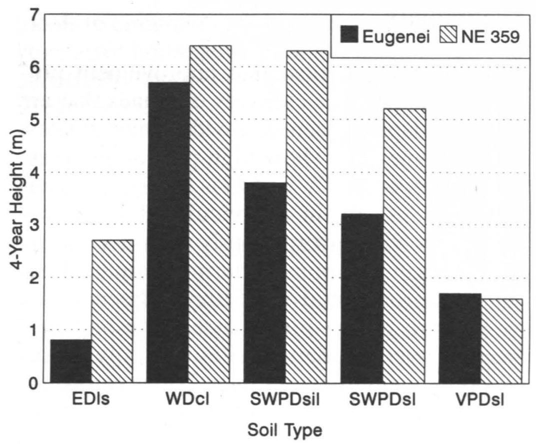

Fig. 3. The relationship of height of *Populus* × *euramericana* clones 'Eugenei' and 'NE 359' to soil type after four-years growth in the Lower Peninsula of Michigan USA. Soil drainage classes are: ED = excessively drained; WD = well drained; SWPD = somewhat poorly drained; VPD = very poorly drained. Soil texture classes are: ls = loamy sand; sl = sandy loam; sil = silty loam; cl = clay loam.

to multiple co-limitations. Chapin et al. (1987) have put forward the attractive hypothesis that adaptable genotypes have the capacity to deal with multiple resource limitations through compensatory responses, whereas a less adapted genotype cannot. The latter often may be limited by a single resource while having excess capacity for acquiring nonlimiting resources; i.e. their adaptive responses are less plastic. This certainly is a fertile area for future research.

As the traits confering adaptability are identified and characterized, selection criteria must be developed to aid the breeder. Ideally, breeding ideotypes would be constructed that included characters that confer wide adaptability. These objectives should be the ultimate goal of the applied physiologist working on site adaptability. The breeder or genetic engineer then will have a clear pathway to follow to further tree improvement.

Application of ideotypes

Another area in which physiologists and breeders can work together constructively is in the formulation of ideotypes. The concept of the ideotype was first proposed by Donald (1968), a cereal breeder, and he has since elaborated the concept extensively (Donald and Hamblin 1976, Donald 1979, Donald and Hamblin 1983). Donald defined a crop ideotype as "a plant model which is expected to yield a greater quantity or quality of ... useful product when developed as a cultivar." Donald's conception was nothing more than an extension of the approach of breeding for multiple traits, but he cast it in a holistic way: instead of looking at just a few traits, why not take the whole plant into account? Dickmann (1985) and Dickmann et al. (1992) further elaborated the ideotype concept as it applied to forest tree improvement. Although the application of the ideotype concept to tree improvement programs seems logical, few published ideotypes for forest trees exist.

The creation of useful ideotypes is built upon detailed knowledge of the structure and physiology of the plant. It follows, then, that an ideotype will be no better than the scientific foundation upon which it rests. The physiological basis of yield is admittedly complex because it is governed by numerous polygenic, organismic, and community traits that have enormous plasticity as the crop develops with multiple colimiting factors — both metabolic and environmental (Gifford et al. 1984). Therefore, some breeders prefer not to adopt the ideotype strategy because it presupposes the type of plant that will produce the highest yield (Coyne 1980). While this may be true, it should not prevent the proposing of testable hypotheses about yield enhancement, which is part of the ideotype concept.

The most fruitful application of an ideotype can occur only if it distills state-of-the-art knowledge of the attributes of the target crop plant; this is where physiologists can make a real contribution. A vague or incomplete conception of the target plant in the mind of the breeder is not enough, especially during advanced generation breeding. Not only should ideotypes be as complete as possible, but they should be published so other scientists can use the ideotype as a basis for further research into plant form and function. A cycle of formulation–application–research–reformulation, and so on, then develops, leading to advances in genetic improvement as well as understanding of the biological basis of tree growth.

Important disadvantages to ideotype breeding may hinder its application in perennial woody plants. Long generation times, the bane of tree improvement, especially with late-successional forest trees, can scuttle attempts to produce a plant that conforms to the ideotype. And although certain traits, especially those relating to tree form, are highly heritable, most are complex and polygenic and would require many cycles of breeding to build into new genotypes.

However, Way et al. (1983) caution that any single-minded breeding approach to yield improvement is unlikely to be successful, especially in advance-generation breeding. Nonetheless, it is a dictum of plant breeding that, for a given selection intensity, the efficiency of improvement of any one trait declines as additional characters are added. Therefore, it would be impossible to assemble all the yield-enhancing traits specified in an ideotype into single genotypes through recurrent, multiple-trait selection. Another approach, however, may be possible. An ideotype can be viewed as a *single quantitative trait,* and selections made based on the degree of fit to the ideotype as a whole (D.E. Keathley, personal communication). In fact, an ideotype is like any other quantitative trait (e.g., tree height or stem volume), albeit more complicated: an expression of many gene loci, all working in concert to produce a continuum of phenotypes. It may be argued that heritabilities will be low if this approach is used, but this limitation is not insurmountable. A major pragmatic problem in viewing an ideotype as a quantitative trait will be the assigning of weights to each component of the overall ideotype; i.e., formulating a scoring system to be used during selection.

Regardless of how ideotypes are employed, the practical limitations of breeding set a limit on the number of characters that can be included in an ideotype, even though from the standpoint of understanding tree growth as many yield-related characters as possible should be included. Therefore, I propose that at the outset the breeder must select a limited subset of traits from a comprehensive ideotype that offer the most promise of producing the desired genetic gain, or whose economic values are greatest, creating a practical "working" ideotype. At a minimum a working ideotype might be comprised of only two or three key traits selected from the complete ideotype. This very limited working ideotype might be particularly useful in mass selection within a large progeny test. Again, the simple working ideotype could be used as a single quantitative trait.

Obviously, there is no one ideotype for a particular crop (Simmonds 1985), nor should an existing ideotype be viewed as a final end point. Ideotype formulation is a dynamic, expanding process. Several models may be proposed for a given crop or for a particular crop-culture combination. For example, well-developed drought avoidance characteristics may be unnecessary ideotype traits when trees are irrigated, but they become important when trees are grown on sites where natural rainfall is a major limitation to growth. As physiological knowledge increases and tree improvement programs become more sophisticated, existing ideotypes will be modified and new ones proposed. It is likely, though, that all ideotypes for a particular crop, regardless of species, will have some common characteristics (Donald and Hamblin 1983).

Promoting interaction

The creative and synergistic interaction between tree breeders and physiologists — what Prof. Reinhard Stettler (University of Washington, Seattle, USA) calls a "constellation of people" — usually will not occur without effort or premeditation. Certainly there are examples of serendipity, where researchers come together, almost in a random way, only to find that they have common objectives and interests in tree biology and improvement. But we cannot count on this happening very often. There are ways, however, that the forming of constellations can be actively promoted.

Administrators of forest research programs must realize that future progress in forest science will be realized predominately through interdisciplinary interaction. Problems in the modern world are more complex than ever, and their solutions require inputs from experts with varied training and experience. Tree breeding or genetic engineering programs can no longer consist just of scientists trained in these areas; inclusion of physiologists and other experts (Fig. 1) in these programs will greatly enhance progress. Administrators and organizations must be aware of this need and 1) establish interdisciplinary tree improvement teams that are highly goal oriented, 2) facilitate the interaction of team members, and 3) provide a stimulating work environment and adequate resources.

On the other hand, scientists with an interest in tree improvement cannot be too parochial. They must be willing to look outward, rather than inward, and work cooperatively with other scientists in different disciplines. The individual, say nothing of the collective, rewards will be great. Obviously, personalities must be compatible, and like graft unions between scions and rootstocks in seed orchards, such compatibilities are difficult to predict. To some extent, though, shared interests can surmount certain incompatibilities. Again, administrators have to be aware of this problem and make shifts in personnel assignments when necessary.

Scientists are fond of meeting together at conferences and workshops, preferably in a stimulating and interesting location. While these meetings often are organized along disciplinary lines, and necessarily so, too few interdisciplinary meetings, such as the IUFRO joint working group meeting "Biological Systems in Tree Breeding" that is the subject of this proceedings, are organized. Tree breeders tend to talk to tree breeders and physiologists talk to physiologists. What is needed is for concerned workers to structure meetings in a way that is more problem or subject oriented rather than strictly disciplinary. Attendees could then be invited from many different disciplines, creating a real opportunity for "cross-fertilization." A tightly structured paper format should give way to a more informal workshop structure which allows ample time for discussion.

Interaction among applied geneticists and physiologists must have a foundation in the education process. Graduate students in genetics or physiology should be counseled to expand their view by taking courses in other disciplines. A geneticist with some training in physiology or a physiologist with a minor in genetics will be best able to respond to the future challenges of tree breeding in an interdisciplinary way. In these days of information overload it is tempting to become very narrowly focused during the years of university training. Whereas indepth training in a specialty area is essential, particularly at the Ph.D. level, view-broadening training should not be overlooked. The payoffs in productive cooperative research, say nothing of the personal rewards derived from a broad education, certainly will reward such efforts.

The greatest synergistic gain from cooperative research between geneticists, breeders, and physiologists will come from work on relatively few model species or genera. Worldwide there are many forest tree species that are the subject of genetic improvement efforts, but comprehensive, interdisciplinary research programs are not possible on all of them; there just aren't enough scientists to support such efforts, to say nothing of the lack of available funding. And furthermore, many species lack a sufficient commercial application. But certain trees — e.g. *Pinus sylvestris*, *P. taeda* and *P. radiata*, *Pseudotsuga menziesii*, *Picea sitchensis* and *P. abies*, *Eucalyptus* spp., *Salix* spp., *Populus* spp., *Betula pendula*, *Tectona grandis* — could be established as model species which would be the subjects of concentrated interdisciplinary research and improvement. To some extent this already occurs, but all to often these efforts are not efficient due to lack of close communication among scientists and the absence of an administrative framework to coordinate the work.

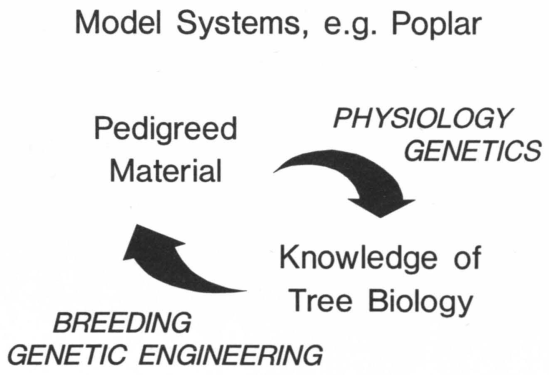

Fig. 4. Using model taxa, e.g. *Populus*, a feed-forward cycle develops where breeders and genetic engineers produce pedigreed material, which, in turn, is investigated by geneticists and physiologists. The resultant increase in biological knowledge aids the breeders and engineers in developing new genotypes, and the cycle continues.

In an ideal situation, work with a model species can result in the development of a synergistic, feed-forward cycle (Fig. 4). To a practically minded physiologist or breeder, this prospect certainly must be exciting. Improvement programs produce new genotypes through selection and breeding. Physiologists then use this pedigreed material for basic investigations on yield-related traits. This work, in turn, can be used by breeders for developing better selection criteria and in the formulation of ideotypes. The new genotypes that result can then be the subjects of further physiological research, and the cycle continues. The cycle can be even tighter when linkages are made between molecular geneticists, genetic engineers, and physiologists. In this case, the likelihood of identifying the genes or DNA fragments that encode the enzymes that regulate specific physiological processes is very real.

Conclusions

Tree physiologists certainly cannot promise the impossible; they will not pull rabbits out of a hat. However, their niche is the advancement of understanding of the structure and function of trees, from the organelle to the ecosystem level. The extent to which they successfully fulfill this mandate will determine their value to tree improvement.

Just as a breeder cannot productively improve a plant of which he/she has no understanding, so physiologists must at all times be aware that it is the genome that ultimately controls plant growth and functioning. So the link between physiologists, geneticists, and breeders is quite naturally forged. That the link exists does not mean it is always exploited. In this paper I have attempted to present reasons why the future of tree improvement must be more closely entwined with tree physiology. In the end it will take a commitment on the part of forest scientists, educators, and administrators to make it happen.

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