BREEDING PEST-RESISTANT FOREST TREES: DEVELOPMENTS AND TRENDS

Ronald J. Dinus 1/

A decade ago breeding for resistance was considered only a promising means of reducing losses to forest insects and diseases. Convincing examples have since demonstrated its practicality. These accomplishments have awakened regional, national, and international interest in resistance breeding. A review of contemporary efforts indicates that 35 breeding programs are well underway and that another 29 have been initiated recently (Gerhold 1970). Several older programs have released resistant planting stock and over half of those underway expect to do so within 10 years. A number of programs in the Southeast are in the latter category.

Unlike alternative methods of control, planting genetically resistant material can offer both economy and long-term effectiveness. These advantages plus widespread and increasing concern over the quality of our environment make it imperative that resistance breeding and research efforts be intensified.

This brief review describes some recent developments in pest resistance research and discusses their implications. Fusiform rust, caused by *Cronartium fusiforme* Hedgc. & Hunt ex Cumm., seriously threatens efficient management of loblolly (*Pinus taeda* L.) and slash pines (P. *elliottii* Engelm. var. *elliottii*). Since this disease is the concern of most papers in this session of the Eleventh Southern Conference on Forest Tree Improvement, much of this review will deal with resistance to fusiform rust.

SOURCES OF RESISTANCE

Inherent resistance to a variety of pests has been found in a number of forest tree species. Comprehensive reviews are available (Beck 1965; Bingham 1969; Ewing and Manning 1967; Gerhold 1970; Hare 1966; Toole 1966). Reference to and descriptions of specific programs may also be found in the published proceedings of two recent symposia (Bingham et al. 1971; Gerhold et ale 1966).

1/ The author is Plant Geneticist at the Institute of Forest Genetics, Southern Forest Experiment Station, USDA Forest Service, Gulfport, Mississippi.

Developments and problems relevant to the Southeast are best illustrated by several examples. Information concerning the extent and usefulness of resistance to fusiform rust and brown-spot needle blight, caused by *Scirrhia acicola* (Dearn.) Siggers, has accumulated rapidly. Reports by Wells (1969) confirm earlier indications (Wells and Wakeley 1966) that losses to rust in loblolly pine can be reduced by reforesting with seed from an appropriate provenance. Damage to longleaf pine (P. *palustris* Mill.) by S. *acicola* can be diminished by the same means (Henry and Wells 1967). Though the degree of protection ultimately desired may not be achieved, the usefulness of geographic variation as an interim step should not be overlooked. Moreover, some resistance can be obtained without sacrificing other qualities. Further evidence of geographic variation in resistance to these diseases is provided in contributions to this meeting by Derr, and Wells and Switzer.

This approach holds little promise for improving the resistance of slash pine to C. *fusiforme* (Gansel et al. 1971). This does not imply, however, that useful levels of resistance are unavailable in this species. When geographic variation in resistance is not readily apparent, variation among individual trees can be sought and exploited. For example, resistance to C. *ribicola* Fischer has been found in western white pine (P. *monticola* Dougl.) by selecting disease-free phenotypes in heavily damaged stands (Bingham et al. 1969). Subsequent progeny tests under conditions favorable for disease development have yielded a usable number of parents with high general combining abilities.

Levels of resistance obtained by the selection of loblolly and slash plus-trees free of fusiform rust have not been impressive (Goddard and. Strickland 1970; LaFarge and Kraus 1967; North Carolina State University 1970). At best, only moderate gain seems possible (Kinloch and Stonecypher 1969). Some of the uncertainty associated with phenotypic selection may be minimized by restricting the practice to young, heavily damaged. plantations. In another contribution to this conference, the author has observed useful amounts of resistance in progenies of rust-free slash pines. The parents were chosen at age 13 from a 94-percent infected plantation and individual tree histories were known. Existing provenance and progeny test plantings in hazardous areas are therefore logical places to seek new sources of resistance. The survey of rust incidence recently begun by the State and Private

Forestry Branch of the USDA Forest Service and recent studies of rust epidemiology (Snow et al. 1968) should provide much needed information on the location and. distribution of such sites. Both types of information should also contribute to the more efficient location and design of future test plantings.

The usefulness, if not necessity, of progeny testing for detecting resistance to fusiform rust has been demonstrated. (Kinloch and Stonecypher 1969). Maximum increases in resistance are expected only after existing clonal orchards are rogued or new specialty orchards are established on the basis of progeny tests. Predicted and realized gains are compared by Blair and Zobel in a contribution to this meeting. Derr and Melder (1970) found substantial variation in resistance to brown-spot needle blight among individual longleaf pines. Their results and those of Snyder and Derr indicate, however, that progeny testing is required to identify useful parents with certainty. Approximately 10 percent of the 500 selections whose progenies have been examined at several locations may be suitable for eventual release.

When variation in resistance is lacking or minimal within species, resistance genes may be available in related species. Interspecific hybridization, backcrossing, and similar breeding methods can then be employed to transfer resistance into the susceptible species. Interspecific hybridization has resulted in increased resistance to C. *ribicola, Ceratocystis ulmi* (Buism.) C. Moreau, and *Keithia thujina* Durand (Wood 1966). Attempts to produce usable hybrids of *Castanea* species resistant to *Endothia parasitica* (Murr.) A. and A. are described in a contribution by Nichols and his associates.

The disease resistance of southern pine hybrids has also been studied extensively. Derr (1966) reported that longleaf x slash pine hybrids are less susceptible than their parents to brown-spot needle blight and fusiform rust, respectively. The long-term effectiveness of rust resistance in these hybrids has been questioned, however. Though among the more resistant entries in a south Mississippi planting after 5 years, the hybrids were as susceptible as slash pines at 10 years 2/. Interspecific hybrids of slash or loblolly and shortleaf pines (P. *echinata* Mill.) have considerable resistance to fusiform rust (Schmitt 1968), but the usefulness of individual shortleaf parents can vary (Jewell 1966). The apparent necessity to select suitable parents in both species introduces a significant complication.

2/ Schmitt, D. M. Personal communication.

The considerable expense presently associated with mass-producing hybrid and backcross seed also limits the efficiency of this approach. Nevertheless, such hybrids could find practical use in the future and will continue to be valuable for studying the genetics and mechanisms of resistance.

METHODS OF EVALUATING RESISTANCE

Concern over the efficiency and reliability of progeny testing for resistance to plant pathogens in the field is widespread. The uncertainties associated with the year of planting, the amount and distribution of inoculum, and the effects of site and cultural conditions have been discussed frequently. The length of time required to obtain a satisfactory incidence of infection also represents a major shortcoming. Moreover, plantings which reliably test for resistance may prove of limited utility for evaluating other traits. A paper contributed by Schmidt and Goddard suggests that consistency of family performance is obtained only when the overall incidence of rust is moderate to high.

Artificial inoculation methods have often been adopted as alternatives or supplements to field testing. Successful procedures for evaluating resistance to a substantial number of major fungal diseases have been devised. The objectives, methodology, and advantages of these were discussed at two recent symposia (Gerhold et al. 1966; Bingham et al. 1971).

Several artificial inoculation methods are often available for investigating a particular host/pathogen combination. Some attempt to simulate natural conditions. Others are performed in the field, but modify conditions to enhance the probability of infection. Still others utilize tents, sheds, greenhouses, or specialized chambers. In most successful methods, large numbers of young trees (30 days to 4 years old) are exposed to heavy, uniform concentrations of inoculum under conditions favorable to disease development. Provision for replication in time and space are routine.. Schmidt (1971) has reviewed procedures for evaluating resistance to fusiform rust.

Several resistance-breeding agencies employ a series of artificial inoculations (Patton and Riker 1966; Heybroek 1969). That is, seedlings remaining disease-free after the first exposure are tested again in one or more subsequent seasons. Repeated exposure minimizes the frequency of escapes, thereby providing a reservoir of useful plant material. In addition, the accuracy of calculations concerning genetic ratios or the extent of additive genetic variation is increased. Unfortunately, personnel concerned with resistance to fusiform rust have not attempted reinoculation on a large scale, but provisions for both repeated inoculations and preservation of rust-free material have been made recently at the University of Florida and the Southern Station. Results from two successive inoculations of slash pine with C. *fusiforme* are described in a paper contributed by Goddard and Schmidt.

Most techniques currently used for mass screening provide only for heavy and uniform exposure to composite collections of local inoculum. Experience with crop plants shows, however, that interactions between host genotypes and inoculum densities or sources can affect the performance of individual varieties or cultivars. It may be misleading, therefore, to consider two pine selections equally useful when progeny from one are 25 percent galled. after light exposure while progeny from the other are similarly infected following a massive dose. Several agencies active in fusiform rust research have recognized this problem. Work in progress suggests that differences in the amount of rust among open-pollinated progenies of slash pine decrease with increasing inoculum densities (Snow and. Dinus, unpublished data). A report contributed by Powers et al., however, indicates that differences among open-pollinated progenies of loblolly pine can be distinguished at a number of different inoculum levels. Both studies noted a strong positive correlation between rust incidence and inoculum density.

The inoculation techniques employed in these studies of inoculum density represent major advances. Each has been described in detail at a recent symposium (Dwinell 1971; Snow and. Kais 1971). Both can be adapted to study the interaction between inoculum source and host genotype. Such investigations have been initiated by Snow and Kais (1970). Progenies from susceptible slash and loblolly selections were uniformly infected by inoculum from five geographic sources. Slash pine progenies normally resistant to Mississippi inoculum were moderately resistant to three sources, but susceptible to the others. Since some degree of pathogenic variability was evident, progeny testing with mixed collections of inoculum from the particular area to be reforested was advised. Further studies of the extent and nature of this variability are underway.

Though successful inoculations are now routine for a variety of forest diseases, knowledge of the infection process remains incomplete in many instances. Bingham (1969) emphasized the need for further information on the penetration and establishment of rusts on hard pines. At present, it is assumed that fusiform rust galls develop after penetration of the stem or of succulent tissues near the stem. Since resistance mechanisms may be operative in one or more of these places, the relative importance of each as a natural infection court must be clarified. A technique developed within the last year (Miller 1971) permits control not only of inoculum density and source, but also of the point of application. As a result, much-needed information on the mode of penetration of C. *fusiforme* and infection courts may now be within reach.

Another advance of interest to tree improvement personnel in the Southeast is that toward successful inoculation of longleaf pines with spores of S. *acicola.* As illustrated in a contribution by Derr, much valuable information on the extent of heritable variation in resistance to brown-spot needle blight has been derived from conventional or modified field tests. The technique for controlled inoculation being developed by Kais at the Southern Station, however, should hasten and increase the efficiency of testing.

Not all inoculation techniques will make practical contributions to tree improvement. The more specialized. types should provide greater insight into resistance mechanisms. The impact of those designed for mass screening, however, will be minimal unless their results accurately predict field performance. The blister rust program in Idaho has been based since its inception on the assumption that family rankings after nursery inoculation will be similar to those in forest plantations. Recent surveys tend to support this assumption. After exposure for 11 and 15 years in hazardous areas, progenies of parents selected for high general combining ability outperformed both control and wild seedlings (Steinhoff, manuscript in preparation).

To date, only three reports have been published concerning the relationship between artificial and field tests for fusiform rust (Dinus 1969; Gansel et al. 1971; Kinloch 1968). Further data will be given at this conference by Goddard and. Schmidt. Though agreement was considered. reasonable in two instances, the available methods do not seem to predict field performance with the desired degree of accuracy.

Both the failure to identify resistant selections and the identification of a susceptible selection as resistant can have serious consequences (Schmidt 1971). With rotation lengths commonly approaching or exceeding 25 years, the effects of the latter are perhaps more severe. Incorrect classification of useful parents may be less serious in that breeders could obtain sufficient usable parents by screening progenies from large numbers of selections. On the other hand, exposing young seedlings to heavy inoculum loads may be eliminating selections whose progeny express resistance only when older or in the field (Dinus 1969). Hence, breeders might be biased toward relying on a single form of resistance, possibly a form more easily overcome by the pathogen.

These problems demand immediate attention. Future mass screening studies should be designed to parallel existing or proposed field trials. Should current systems need refinement, provisions should be made for standardization of conditions, especially inoculum viability, density, and dispersal. Optimum densities, that is, densities which permit genetic differences to be expressed but minimize the frequency of escapes, must be found. Results might also be more realistic if slightly older seedlings were used. Moreover, new methods of quantifying host response deserve further investigation.

The techniques of Dwinell and Snow could prove useful for large-scale screening. Since both provide considerable control over the more troublesome variables, modifications of them are being considered for use at a central testing facility to be operated by the State and. Private Forestry Branch of the USDA Forest Service. Though much work remains undone, this facility, located at Asheville, North Carolina, is preparing to begin preliminary testing. When it is fully operational, standardized testing services will be available on a regional basis.

Evaluating resistance to insect attack is also difficult, but increased demand for resistant material in recent years has quickened the pace of research. The resultant fund of knowledge has been summarized by Gerhold (1966). The enormous and perplexing variations in the location, frequency, and severity of natural attacks make field identification and evaluation of resistance difficult, if not impossible. Callahan (1966) has discussed the problems associated with field testing and emphasized the need for perfecting reliable cage tests, attractants, and bioassays. Such methods have succeeded in several instances (Gerhold 1970).

Methods for forcing attacks by *Dendroctonus* species on western yellow pines have been developed by Smith (1969). Both the quality and quantity of resin were related to the levels of resistance possessed by individual host trees. Bioassays suggested that certain components of the resin confer resistance by the lethal effects of their vapors. Two monoterpenes, limonene and 3-carene, have been implicated. Similar approaches are being employed in studies of resistance to a number of related insects, including the southern pine beetle (*Dendroctonus frontalis* Zimm.).

Screening caged white pine (P. *strobus* L.) seedlings for resistance to white pine weevils (*Pissodes strobi* (Peck)) has also proven feasible (Soles et al. 1969). The technique has been used to distinguish among resistant and susceptible species, provenances, and individual host trees. The information accumulated is considered sufficient to justify the start of a practical program of selection and breeding.

The anticipated development of controlled testing procedures, however, should not prevent the thorough observation of natural infestations. Observations made during attacks in progeny tests, provenance plantings, and seed orchards are especially valuable. For the present, such opportunities may be the only means of determining if and to what extent inherent resistance to some insects exists. Much to the advantage of all concerned, several reports of variation in susceptibility under such circumstances will be given at this meeting.

LONG-TERM EFFECTIVENESS

Tree improvement workers continue to express the concern that pests may eventually overcome resistance. The risk associated with existing pathogenic variability or that produced in response to the planting of resistant material is not easily determined. Bingham (1969) has emphasized the pressing need for increased attention to this problem.

Until recently, most resistance research programs have concentrated on calculating heritabilities and estimating gains. Though sufficient variation in host resistance and-reasonable potential for gain have often been found, little is known about the number and nature of the underlying genes. Will collecting these genes into improved progeny result in long-term control of pests currently possessing or capable of producting pathogenic variability?

The experience of crop breeders, particularly those concerned with improving resistance in wheat and potatoes, could easily lead to pessimistic predictions. On the average, wheat varieties resistant to specific races of the wheat rust pathogen remain useful for only a few growing seasons (Borlaug 1965). The differential resistance used in these instances is based on only one or a few genes with large effects (van der Plank 1969). On the other hand, maize breeders have developed less spectacular, but longer-lasting resistance (Hooker 1967) by seeking uniform rather than differential resistance. This approach provides protection against a spectrum of pathogenic races. Apparently, large numbers of genes with small, additive effects are involved (van der Plank 1969). In view of the rotation lengths common in forestry, the consequences of intentionally or unintentionally developing differential resistance could be severe. Trees might not be harvestable, as wheat and potatoes sometimes are, before an induced change in pathogenicity assumes significance.

If resistant progeny are to be planted with confidence, the genetics of both resistance and pathogenicity must be understood. The reactions comprising the overall levels of resistance usually observed must be characterized and the responsible gene or genes identified. For example, a number of genes controlling resistance to blister rust have been found in western white pine (Hoff and McDonald 1971). Two genes control reactions in secondary needles, another controls needle lesion frequency, a fourth controls the premature shedding of infected needles, and a fifth controls a fungicidal reaction in the short shoot. The existence of others governing reactions in both foliage and bark has been postulated. Resistance apparently controlled by a single dominant gene has also been observed in P. lambertiana Dougl. (Kinloch et al. 1970). The nature of the reaction, however, has not been determined. The classification of genes in this manner and continued exposure of plants containing them should clarify the contribution of each to long-lasting resistance.

Knowledge of host genetics, however intimate, is not sufficient. Existing and potential variation in pathogenicity must also be defined. The mechanisms providing for genetic change in many important fungal parasites of forest trees are not clearly understood. Evidence for variation in characteristics other than pathogenicity is extensive (Wood 1966). Reports of pathogenic variation are fewer, but information is accumulating (Wood 1966; Bingham 1969). Recently, evidence was found for the existence of two pathogenic races of C. _ribicola_ with corresponding differential resistance genes in P. _monticola_ (Hoff and McDonald 1971). Moreover, clear indications of pathogenic variability have been found in C. _fusiforme_ (Snow and Kais 1970).

Most tree species are more heterozygous than the crops in which problems with differential resistance have arisen. Moreover, uniform resistance seems more prevalent in crops which have been subjected to lesser degrees of artificial selection (Graham and Hodgson 1965). Hence, problems such as those experienced with wheat may not, or need not, befall tree breeders. Until adequate information becomes available, however, an intensified search for uniform resistance seems the safest course. Bingham (1969) suggested that criteria such as fewer galls per tree (LaFarge and Kraus 1967) and slower gall development (Kinloch and Kelman 1965) may prove helpful in programs concerned with fusiform rust.

COMMUNICATION AND COOPERATION

Increased interest in pest-resistant forest trees has intensified the need for effective communication and cooperation among geneticists, pathologists, entomologists, and physiologists. The benefits resulting from a freer exchange of information, sharing of biological materials, and instigation of cooperative studies seem obvious. Various organizations have recognized these and resolved to facilitate communication and cooperation.

Several specialized workshops and symposia have been held in response to past resolutions. An Advanced Study Institute of Genetic Improvement for Disease and Insect Resistance of Forest Trees was held in 1964 at the Pennsylvania State University and a similar symposium, the Advanced Study Institute on Biology and International Aspects of Rust Resistance in Forest Trees, was held in 1969 at Moscow, Idaho. A session of the Second World Consultation on Forest Tree Breeding in 1969 at Washington, D.C.,also provided for contact among resistance breeders. In addition, committees concerned with resistance to conifer rusts have been formed within the framework of the IUFRO Working Group on Genetic Resistance to Forest Insects and. Disease.

The combined efforts of interested parties resulted in an informal workshop on fusiform rust in 1970 at Bainbridge, Georgia. Informal as it was, this conference provided an effective forum for reviewing progress, identifying the most pressing problems, and discussing new approaches. Considerable concern was expressed over the availability of standard inoculum sources and seed from proven resistant and susceptible selections. As a result, depositories providing for the storage and exchange of aeciospores and seed have been established at North Carolina State University and. Macon, Georgia, respectively. In addition, initial steps were taken toward obtaining support for the creation of a central rust resistance testing facility. Though loosely organized at present, the original attendees and other interested individuals could easily become a more vital force. The necessary machinery could perhaps be furnished by the IUFRO Working Group with its White Pine Blister Rust Resistance Committee serving as model. This latter group organized the highly effective Advanced Study Institute in 1969.

If existing and prospective means of communication and cooperation are to be effective, increased financial and administrative support is essential. The training value of a particular meeting might be the most meaningful criterion for attendance. Research administrators should not only be made aware of relevant professional and working meetings, but also of any realized as well as potential benefits of attendance. The merits of individual visits and additional education cannot be overemphasized. Unfortunately, funds and approval for such activities are especially difficult to obtain. Research administrators should periodically review and endeavor to fulfill these needs.

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