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BREEDING FOR QUANTITATIVE RESISTANCE TO LEAF BLIGHTS OF CORN: A CONTINUING SUCCESS STORY

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The development of high yielding, disease resistant hybrids is the goal of most public and private corn breeding programs. These programs have largely been successful in reducing the incidence and severity of foliar diseases of corn in the U.S. Significant, damaging levels of leaf diseases are considered the exception throughout most of the corn belt, and a healthy corn crop the norm. This highly desirable situation did not arise by chance or good fortune, but rather is the result of dedicated efforts of corn breeders and pathologists over the decades. Unlike most other crops, corn breeders have been able to successfully integrate quantitative resistance into their elite germplasm and select for it during the breeding process. Single, race-specific genes have been used in corn to a limited extent, but their use has largely been abandoned due to the well documented ability of pathogens to overcome this type of resistance and the conservative nature of the backcross breeding methods used to incorporate these genes into elite lines.

What is “Quantitative” Resistance?

Quantitative resistance to plant diseases is has been reported in most crop species, although it has not been as well studied as resistance controlled by single, race-specific genes. Quantitative resistance is called so named because it is commonly expressed in a quantitative manner as a reduction in disease development. Therefore it is sometimes referred to as ‘partial’ or ‘incomplete’ resistance. Also because it is often considered to be effective against all strains or races of the pathogen, it is sometimes called general resistance or race non-specific resistance. Quantitative resistance is usually controlled by multiple genes and is considered a polygenic trait and is therefore sometimes referred to as ‘polygenic’ resistance. While it is often convenient to use all these terms synonymously, bear in mind that exceptions to these generalizations exist. There are forms of polygenically inherited resistance that produce a qualitatively different phenotype than a susceptible genotype. There are corn hybrids with such high levels of polygenic resistance to certain foliar diseases that they appear practically immune, so their resistance could hardly be called ‘partial’. Conversely, the single race specific gene HtN confers a quantitative form of resistance to northern leaf blight of corn.

Disease resistance is usually considered quantitative if there is continuous variation for disease resistance in genetically segregating populations with no apparent means to classify individuals into discrete categories. This continuous variation is assumed to be the result of the action of many genes acting together, with the effect of any one gene too small to be readily detected.

Why Quantitative Resistance to Leaf Blights has been Successful in Corn

The apparent success with which quantitative resistance to leaf blights has been exploited in corn may be attributed to a number of factors: the large amount of genetic variation for resistance, present even in adapted maize germplasm; the high heritability of quantitative resistance; the small numbers of genes involved in quantitative resistance; the lack of a negative correlation between quantitative resistance and agronomic performance; the ease with which corn can be manipulated with a variety of plant breeding methods; and ability to increase quantitative resistance by selection for individual components of
resistance. Corn is probably unique among crop species in having all these factors at work for the breeder interested in exploiting quantitative resistance.

**Genetic Variation for Quantitative Resistance:** One of the first prerequisites in breeding for disease resistance is to find a suitable source of resistance. An ideal source of resistance in corn should be adapted in terms of maturity, plant height, etc., and preferably have at least acceptable agronomic combining ability. The less adapted and elite the source of resistance used in the breeding program, the more difficult it becomes to find an acceptable combination of resistance and improved agronomic performance. For most of the more common foliar pathogens of corn, acceptable useful levels of resistance may be found among the elite inbred lines that constitute the main germplasm base in the breeding program. Selection of parental lines to form a breeding cross or population involves finding elite lines in the same heterotic group that have the proper complement of resistances and combining ability.

**Heritability of Quantitative Resistance:** Another related determinant of the chances of successfully selecting for quantitative resistance is the amount of variation for resistance that is under genetic control. Heritability is simply the proportion or percentage of the observable (phenotypic) variation in disease resistance that is genetically controlled and can be ‘fixed’ in an inbred line of corn. The higher the heritability of the trait, the more rapid and effective the selection process will be. Although published estimates of heritability for quantitative resistance to foliar diseases of corn vary widely, most are considered to be in the medium to high range (>50%). The development of effective artificial inoculation methods, reliable and repeatable disease ratings scales, and the use of replicated, multi-location disease testing all increase heritability. Often significant progress can be made by simple phenotypic selection of individual plants.

**Numbers of Genes Governing Quantitative Resistance:** The continuous variation seen with quantitative resistance is assumed to be the result of the action of many genes acting together, with the effect of any one gene too small to be readily detected. Generally, the fewer the number of genes involved, the easier it is to select and transfer a trait. While quantitative resistance is amenable to classical quantitative genetic analysis, in almost all cases, so-called polygenic disease resistance appears to be controlled by a relatively small number of loci, usually acting in an additive manner. Estimates of the numbers of loci controlling quantitative resistance are commonly less than four or five, and seldom more than ten. This is in contrast to traits traditionally thought of as being polygenic, such as grain yield, seed weight, grain quality, etc., where the number of loci is thought to be much greater. Furthermore, the actual numbers of quantitative trait loci (QTLs) needed to confer an adequate level of resistance may be substantially less than the maximum number detected in a given genetic study. The use of molecular marker assisted selection to speed the process of transferring QTLs for quantitative resistance is now being practiced by several groups. QTL mapping of quantitative resistance also offers the promise of increasing our knowledge of the effects of individual QTLs on disease development through the use of marker assisted backcrossing to develop near-isogenic lines of corn, and marker assisted breeding to identify and pyramid or combine QTLs from different sources of resistance into a single inbred line.

**Correlation of Quantitative Resistance with Agronomic Performance:** Selection for more than one trait (such as yield and disease resistance) can be complicated if those traits are negatively (unfavorably) correlated; that is, if resistance were associated with poor agronomic performance. There are two lines of evidence that this is not the case with quantitative resistance to foliar diseases of corn. First, there is the empirical evidence of high yielding, disease resistant hybrids that already exist and have been successfully marketed throughout much of the cornbelt. While it is usually possible find an example of a popular, high yielding hybrid that is especially susceptible to a particular disease, there are almost always
alternative hybrids with improved resistance and nearly equal agronomic performance. However, although high levels of resistance to the important foliar diseases may be found among commercial hybrids, rarely is a hybrid highly resistant to all diseases. As the number of traits (yield, stalk strength, resistance to several foliar diseases, insect resistance, grain quality, etc.) selected increases, the selection process becomes increasingly complicated. However, this complication is more likely due to the sheer numbers of traits under consideration rather than any unfavorable correlation between them. The limited studies where the genetic correlation between quantitative resistance to corn leaf blights and yield have been estimated suggest that there is either no correlation between yield and resistance or the correlation is favorable.

**Breeding Methods Available to Corn Breeders:** Corn breeders are fortunate in that they are working with a plant that is highly amenable to a wide array of breeding methods and approaches. The plant is easily self or cross pollinated, with hundreds of seeds being produced from a single pollination. Furthermore, a single unskilled breeder can make hundreds of artificial pollinations in a single day. It is the common experience of corn breeders that it is easy to generate much more genetic material than it is humanly possible to thoroughly evaluate.

The pedigree method (or some variant thereof) is used in a typical commercial inbred line development program. The usual approach is to make a single cross of two elite lines of the same heterotic group and whose traits are complementary, followed by several generations of self pollination and selection. At some point (usually the S2 or S3 level of inbreeding), lines are testcrossed to a tester inbred of the opposite heterotic group and the resulting testcrosses evaluated in yield trials at several locations. Lines that display superior combining ability in this early test are then advanced with several more generations of selfing, followed by more testcrossing to more testers and more extensive yield trials. Resistance to foliar diseases can be selected throughout the line development process. Often the selection for resistance is more a process of eliminating the most susceptible individuals or lines than it is a conscientious selection for the absolute highest levels of resistance. It is very common for breeders to use a mixture of inoculum of various foliar diseases in their nurseries and simply select plants with the most “stay green”. Modified backcrossing is another approach to incorporating quantitative resistance into elite inbred lines. By alternating generations of backcrossing with either selfing or sib mating of the more resistant plants, it is possible to develop inbred lines that have the combining ability and phenotype of the recurrent elite inbred line with enhanced quantitative disease resistance. Population improvement methods such as mass selection and the various forms of recurrent selection are useful ways to develop breeding populations with adequate levels of resistance and combining ability. Usually, only 3 or 4 generations of selection are needed to dramatically improve the level of resistance to a particular foliar disease. Selection for genotypes that yield well under high disease pressure has been a different approach to improving corn breeding populations for grain yield and disease resistance simultaneously.

**Selection for Components of Quantitative Resistance:** Because quantitative resistance to leaf diseases of corn is often expressed as a reduction in the rate of disease development, it is sometimes useful to know how individual steps or components in the disease process are affected in a resistant plant. Reduced foliar disease development in a quantitatively resistant corn plant may be the result of any or all of the following epidemic components: a reduced infection efficiency (# of lesions produced/ spore landing on the plant), an increased latent or incubation period (the time between initial infection and the appearance of a sporulation lesion), reduced lesion size, and reduced intensity of sporulation in the lesions. If resistance of adult plants in the field (measured as a reduced % leaf area blighted) is well correlated with one of these components measured on seedling plants, then it is possible to use this information to increase the efficiency of selection for resistance. Resistance to southern corn leaf blight
and anthracnose leaf blight are highly correlated with lesion size on seedling plants; resistance to northern leaf blight has been shown to be well correlated with increased latent period.

### Potential Problems Ahead and the Need for Vigilance

Because of the efforts of plant pathologists and plant breeders in the public and private sectors, widespread significant damage to the U.S. corn crop from foliar diseases is the exception rather than the rule. However, changing cultural practices, the constantly changing genetic base of corn hybrids, and evolving pathogen populations mean the corn disease picture is also constantly changing, requiring constant vigilance. There are several examples in recent times of corn diseases that were formerly considered ‘minor’ but now are a major concern to the seed industry. Gray leaf spot, Eyespot, Anthracnose, are all examples of corn leaf diseases that were considered of negligible importance to the U.S. cornbelt but are now well established potential problems over wide areas of the country due largely to the widespread adoption or reduced or no-till production practices and perhaps the susceptibility of the genetic base of popular hybrids. Although good resistance to most leaf diseases of corn is available in adapted, elite germplasm, adequate levels of resistance to Gray leaf spot is not yet available in all hybrid maturities, although the progress is being made. The risk of becoming complacent, the problem of genetic uniformity in U.S. corn hybrids, and the possible introduction of new pathogens remain.

**The Problem of Complacency:** The current successful use of quantitative resistance to corn leaf diseases may lead to future problems. There is some evidence that, at least in the case of northern corn leaf blight, that the periodic epidemics may be attributed to a new “disease cycle” where a significant epidemic is followed by a flurry of research to find and deploy resistant hybrids followed by a period where the incidence and severity of the disease dramatically declines leading to reduced emphasis on resistance by breeders (the disease is no longer considered ‘important’) which leads to the widespread use of susceptible germplasm, which sets the stage for the next epidemic. It must always be kept in mind that the reason why many diseases are no longer important is due to the success of the breeding process. If particularly susceptible hybrids are widely grown, it is only logical that it is only a matter of time before their weaknesses will be exposed.

**The Problem of Genetic Uniformity:** Following the devastating southern corn leaf blight epidemic of 1970, the problem of the genetic uniformity of our crops was brought to the attention of the scientific community and the public. Despite the experience of the 1970 epidemic (and other historic plant disease epidemics) and the many warnings by experts, the genetic diversity of U.S. corn hybrids remains low. Most hybrids still represent the same narrow heterotic pattern (Iowa Stiff Stalk Synthetic X Lancaster Surecrop) used since the early days of hybrid corn. Little use has been made of the wealth of genetic resources represented by corn germplasm banks in U.S. and Latin America. The many problems inherent in breeding exotic corn and adapting it to cornbelt conditions have traditionally discouraged corn breeders who are under pressure to produce short-term results. The LAMP (Latin America Maize Project) and now the U.S. GEM (Germplasm Enhancement of Maize) projects are examples of how a public-private partnership can be used to address the problem of genetic uniformity in U.S. crops.

**The Problem of ‘New’ Diseases:** Many corn diseases now considered important were considered ‘new’ at some point in time. As mentioned above, many of these so-called minor diseases later became major problems for the reasons cited above. There several foliar diseases of corn in other parts of the world or of very limited distribution in the U.S. that are today’s ‘minor’ diseases but could be tomorrow’s major problems. Phaeosphaeria leaf spot has only been reported to occur in a limited area in south Florida, but its potential to spread into important corn production areas such as the cornbelt is unknown. This disease is the new emerging disease in other parts of the world including Brazil and South Africa.
There is also the problem of the demonstrated ability of plant pathogens to arise that are adapted to resistant hosts. This has historically been a problem when single dominant genes for disease resistance are used. In corn, the gene *Ht 1* was widely used for control of northern leaf blight during the seventies, but by 1980, virulence to this gene was widely distributed throughout the central and eastern cornbelt. It is often assumed that pathogens are unable to overcome polygenically controlled, quantitative resistance. Although there is no clear evidence that this type of resistance has ever been overcome in nature, laboratory selection experiments have demonstrated that *Bipolaris maydis*, cause of southern leaf blight, can at least partially adapt to corn inbred lines with quantitative resistance. Therefore, it becomes even more important to continually search for and identify new genes for quantitative resistance to leaf blights and incorporate them into elite germplasm.

**References**


