

Discovery and utilization of QTLs for insect resistance in soybean

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Received 6 June 2003 Accepted 30 March 2004

Key words: Bt, insect resistance, linkage drag, molecular markers, QTL, soybean

Abstract

Insect resistance in soybean has been an objective in numerous breeding programs, but efforts to develop high yielding cultivars with insect resistance have been unsuccessful. Three Japanese plant introductions, PIs 171451, 227687 and 229358, have been the primary sources of insect resistance alleles, but a combination of quantitative inheritance of resistance and poor agronomic performance has hindered progress. Linkage drag caused by co-introgression of undesirable agronomic trait alleles linked to the resistance quantitative trait loci (QTLs) is a persistent problem. Molecular marker studies have helped to elucidate the numbers, effects and interactions of insect resistance QTLs in the Japanese PIs, and markers are now being used in breeding programs to facilitate transfer of resistance alleles while minimizing linkage drag. Molecular markers also make it possible to evaluate QTLs independently and together in different genetic backgrounds, and in combination with transgenes from *Bacillus thuringiensis*.

Abbreviations: Bt – *Bacillus thuringiensis*; IRQTL – insect resistance QTL; LG – linkage group; PI – plant introduction; QTL – quantitative trait locus; RFLP – restriction fragment length polymorphism; SSR – simple sequence repeat.

Introduction

Modern agriculture is characterized by monocultural cropping, often over vast areas of land. This practice results in agroecosystems in which crop plants are highly vulnerable to pathogens and insect pests, which can spread easily from one field to another. Although many insect pests can be effectively controlled through cultural practices and/or the application of pesticides, environmental and economical concerns, along with the appearance of pesticide-resistant insect populations have made a heavy reliance on pesticides undesirable. Integrated pest management (IPM) is a more holistic approach to pest control. The goal of IPM is to integrate various cultural, chemical, and genetic approaches to controlling pests, and to use pesticides only when pest populations approach

economic thresholds of damage tolerance. Plant resistance to the most important pests and pathogens is viewed as an important component of IPM, and is therefore an objective in many crop breeding programs. This article reviews what is currently known about the genetics of insect resistance in some soybean [*Glycine max* (L.) Merr.] germplasm which has been studied and used in breeding programs since the late 1960s.

The cultivated soybean is a member of the Leguminosae family, and is thought to have originated in northern and central China (Probst & Judd, 1973). Soybean is one of the major crop species in North America, South America, and Eastern Asia, where it was first cultivated at least 3000 years ago. Soybean is important for human nutrition in Asia, but is grown primarily as an oil crop and source of protein-rich meal

for poultry and livestock feeds in the Western Hemisphere, where it is a major agricultural commodity in the United States, Brazil, and Argentina.

Soybean is a host for 36 insect species in North America, but only eight of these are of major importance (Lambert & Tyler, 1999). Five of the eight major pests feed exclusively on foliage, two exclusively on fruit forms, and one on both fruit forms and foliage. Damage to seeds by chewing or piercing and sucking insect pests can cause abortion or deformation of seeds, thus reducing both the weight and quality of the mature seeds. Soybean can tolerate up to 40% defoliation prior to the onset of fruiting, and 30% after fruiting with little or no yield loss (Lambert & Tyler, 1999). The effect of insect feeding damage on yield is reduced when environmental conditions (particularly soil moisture) favor foliage regrowth after insect feeding pressure subsides.

The most serious insect pests are in the orders Coleoptera, Lepidoptera, and Heteroptera (Lambert & Tyler, 1999). Major lepidopteran pests in North America include corn earworm [*Helicoverpa zea* (Boddie)], soybean looper [*Pseudoplusia includens* (Walker)], and velvetbean caterpillar [*Anticarsia gemmatilis* (Hübner)]. Larvae of all three species are foliage feeders, but corn earworm also feeds on reproductive structures and developing seeds. Soybean looper is noteworthy in that it has an unusually high tolerance to a variety of insecticides, and the ability to develop resistance to many pesticides rapidly. Velvetbean caterpillar is also a major pest in the soybean producing regions of Southern Brazil and Northern Argentina, and is a particularly voracious foliage feeder. In the United States, these insects cause the most damage in the Southeast and Delta regions because of the long growing season and their proximity to tropical regions where soybean looper and velvetbean caterpillar overwinter.

Three modalities of plant insect resistance have been described (Painter, 1951; Kogan & Ortman, 1978), and all three exist in soybean. *Antixenosis*, or non-preference, involves a morphological or biochemical trait that affects insect behavior to discourage oviposition, colonization, or feeding. *Antibiosis* involves a negative effect on insect growth, development, and/or reproduction following ingestion of plant tissue. Examples would include toxins and antinutrients such as certain

proteinase inhibitors. Phytoalexins produced by soybean and other plants can be involved in either or both types of resistance, so antibiosis and antixenosis should not be viewed as discrete modes of resistance. The third mode is *tolerance*, which refers to the ability to tolerate a moderate amount of damage without appreciable yield loss.

Insect resistance in soybean

Most of the elite cultivars grown in North America are descendents of a small group of progenitor genotypes (Gizlice, et al., 1994). These ancestors consisted of plant introductions (PIs) or early-generation progeny of PIs that exhibited desirable agronomic qualities when grown under North American environmental conditions. Although there may have been some degree of selection based on response to natural infestations by certain insects, agronomic performance and seed composition traits were the primary criteria for selection. This narrow genetic base severely limited genetic diversity, and consequently, the number of alleles conditioning resistance to various pests and pathogens within the elite breeding populations used for cultivar improvement.

Evaluations of maturity group VII and VIII PIs from the USDA Soybean Germplasm Collection in the late 1960s identified three Japanese PIs resistant to the Mexican bean beetle [*Epilachna varivestis* (Mulsant)] (Van Duyn et al., 1971, 1972). 171451 ('Kosamame') had been collected in Kanagawa, Japan, 229358 ('Soden-daizu') from an unspecified location, and 227687 ('Miyako White') from Okinawa (USDA-ARS Germplasm Resources Information Network; <http://www.ars-grin.gov/npgs/searchgrin.html>). These PIs exhibit both antixenosis and antibiosis resistance to a number of soybean insect pests, including soybean looper, velvetbean caterpillar, cabbage looper [*Trichoplusia ni* (Hübner)], corn earworm, tobacco budworm [*Heliothis virescens* (Fabricius)], bean leaf beetle [*Cerotoma trifurcata* (Forster)], and the striped blister beetle [*Epicauta vittata* (Fabricius)] (Clark et al., 1972; Hatchett et al., 1976; Kilen et al., 1977; Luedders & Dickerson, 1977; Lambert & Kilen, 1984). The PIs also show resistance to some soybean pests from Taiwan, including the lepidopterans beet armyworm [*Spodoptera exigua* (Hübner)] (Family Noctuidae), *Porthesia taiwana* (Shiraki) (Family Liparidae), and *Orgyia* sp.