

Tolerance : An Ideal Co-Survival Crop Breeding System of Pest and Host in Nature with Reference to Maize

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In nature, plant diseases, insects and parasites (hereafter called as "pest") must be co-survived. The most common expression of co-survival of a host crop to the pest can be tolerance. With tolerance, chemical uses can be minimized and it protects environment and sustains host productivity and the minimum pest survival. Tolerance can be applicable in all living organisms including crop plants, livestock and even human beings. Tolerant system controls pest about 90 to 95% (this pest control system often be called as horizontal or partial resistance), while the use of chemicals or selection of high resistance controls pest 100% (the most expression of this control system is vertical resistance or true resistance). Controlling or eliminating the pests by either chemicals or vertical resistance create new problems in nature and destroy the co-survival balance of pest and host. Controlling pests through tolerance can only permit co-survive of pests and hosts. Tolerance is durable and environmentally-friendly. Crop cultivars based on tolerance system are different from those developed by genetically modified organism (GMO) system. The former stabilizes genetic balance of a pest and a host crop in nature while the latter destabilizes the genetic balance due to 100% control. For three decades, the author has implemented the tolerance system in breeding maize cultivars against various pests in both tropical and temperate environments. Parasitic weed *Striga* species known as the greatest biological problem in agriculture has even been controlled through this system. The final effect of the tolerance can be an integrated genetic pest management (IGPM) without any chemical uses and it makes co-survival of pests in nature.

Keywords: tolerance, co-survival, horizontal resistance, environmental protection, maize, corn, resistance breeding

Responses of a host to a parasite could be grouped into three categories: high resistance, tolerance and susceptibility. Resistance of a crop to plant diseases, insects and parasitic weeds can be divided into two broad categories:

vertical resistance (or race-specific resistance) and horizontal resistance (or race-nonspecific resistance, general or tolerance). The former is controlled mostly by a single gene and inherited qualitatively with 100% resistance. It often be called as complete resistance or true resistance. Agricultural scientists often prefer to breed a crop cultivar through the vertical resistance due to the easiness of resistance gene conversion and clear cut response of the host to a pest. The most popular pest control system in recent years by the genetically modified organism such as *Bacillus thuringiensis* (BT) genes and herbicide resistance belongs to the vertical resistance. While, the latter is controlled by oligogenically or polygenically with a partial infection of the pest and its resistance is inherited quantitatively. Tolerance is defined as the ability of a plant to yield well in spite of the initial stage of infection and symptom development (Kim, 1991). The expression of tolerance is resemble to horizontal resistance. The tolerance tends to be more durable than vertical resistance and it can be also called as durable resistance.

The terms 'resistance' and 'susceptibility' are used to describe the reaction of a plant to a pest and are the results of host-parasite interaction. Both terms are relative and can be considered extremes, between which a continuum of different levels of resistance and susceptibility is possible. The degree of plant resistance is related to the relative severity of infection (Nelson, 1973).

Biotypic-specific resistance is characterized by a hypersensitive, fleck-type reaction of the host. Inheritance is commonly monogenic, with resistance mostly dominant (Brewbaker, 1983; Hooker and Saxena, 1971). Flor's work (1955) with flax rust (*Melampsora lini*) elucidated a gene-for-gene relationship between the host and pathogen. For each gene conferring resistance in the host, there was a specific and related gene in the pathogen which could overcome that resistance. Efforts are needed to achieve genetic diversity for sources of resistance in a crop. New races of the biotypes will continue to evolve and become apparent when directional selection pressure is given such as high-level resistance (vertical resistance) is used. This type of resistance has been a major tool to control diseases in the developing coun-

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tries, particularly in Asia. However, its non-durability is increasingly becoming a serious limitation for sustainability and environmental protection, also causing considerable skepticism, if not outright pessimism, regarding host plant resistance (Kim, 1993a; 1993b; Kim and Singh, 1992). Specific resistance is dramatically effective against one or more races of a pathogen and ineffective against other races, i. e., it is an all-or-nothing resistance. Specific resistance is easily recognized and readily incorporated into a susceptible line or cultivar because of its simple inheritance. Change in host response begins when current resistance has been matched by a new race of the pathogen.

Genetically durable resistance is often of a quantitative nature (Parlevliet, 1993). Parlevliet and Zadoks (1977) earlier showed that polygenic resistances operating on a gene-for-gene basis with polygenes in the pathogen could be race non-specific or horizontal in nature. Selection for durability through partial resistance seems easiest (Zadoks, 1993). Durable resistance is often used as a synonym of general resistance, horizontal resistance, tolerance (Kim, 1994a; 1994b; 1996a; 1996b; 1998a; 1998b), polygenic resistance (including oligogenic), quantitative resistance, and partial resistance. The antonym of durable resistance can be temporary resistance, specific resistance, vertical resistance, hypersensitive resistance, monogenic resistance, qualitative resistance, complete resistance and true resistance (Brewbaker, 1983; Buddenhagen, 1977; Hooker, 1979; Kim, 1976; Nelson, 1973; Parlevliet, 1993; Parlevliet and Zadoks, 1977; Van der Plank, 1968; Zadoks, 1993). The author prefers the terms 'tolerance', 'horizontal resistance' or 'durable resistance' because the final aim of resistance breeding is co-survival and durability as well as sustainability of plant protection. The use of the term 'durable resistance' must be based on demonstrated durability of resistance but experiences of the author and many others prove that durability of resistance can be predicted based on experiences and scientific knowledges accrued.

In spite of numerous deliberations on breeding for resistance to diseases and insects (Flor, 1955; Van der Plank, 1968; Nelson, 1973; Singh, 1986) understanding of tolerance and horizontal resistance is still vague (Kim, 1998a). Researchers and extensionists often debate on terminologies. Terminology is not important but the controlling of the host problems must be the key issue of scientists' concern. Terminology must be simple and generalized.

The potential vulnerability of vertical resistance has encouraged a systematic search for sources of horizontal (general) resistance adapted to the demands of severe epiphytotics (Kim and Brewbaker, 1976a). Most resistance is a cost-effective and biologically safe means of plant protection. The significance of resistance and its durability for

plant production in all countries and especially in developing countries justifies that breeding for resistance be given top priority worldwide (Hogenboom, 1993).

For sustainability and environmental protection, durability of resistance genes becomes a major concern in plant breeding and crop protection (Kim, 1993a; 1993b; 1994a; 1994b). Chemicals may still be needed as an emergency measure when specific resistance is overcome by new pathotypes. The following examples will illustrate the limited value of specific resistance.

A broad-spectrum single-gene resistance from a rice cultivar IR8 was the basis for the rice blast (*Pyricularia oryzae* Cav.) resistance breeding strategy in Asia in 1970s. The most popular rice cultivar, 'Tong-II', in South Korea with IR8 genetic background of resistance to rice blast became susceptible during the late 1970s. Before the Korean rice blast epidemic, a sign of potential vulnerability was seen in one of the southern states in Korea but researchers ignored it, having regarded it as possible genetic segregation or contamination. The author predicted the genetic vulnerability of Korean rice blast three years before the severe epidemic occurred (Kim, 1976). The prediction was based on IR8 and its related cultivars, all having the same genetic background, were grown on approximately 0.8 million hectares in Korea alone. Selection pressure of the resistance gene on the pathogen population was extremely high. Most rice scientists in Korea and international centers (Ou, 1972) did not support that prediction. They were of the view that the single gene resistance would not break down due to its broad spectrum of resistance. Kiyosawa (1972) reported the possible gene-for-gene relationship in true resistance of rice to *P. oryzae* blast. However, a reported different view was that a severe outbreak would not occur if a cultivar had a strong gene or a broad spectrum of resistance (Ou, 1972).

Epidemics are products of the interrelationships of hosts and pathogen biotypes under a given environment. With tolerance, plants can 'live with' a certain amount of disease without serious ill effects. This theory can be also applicable for human beings. When healthy people can not be ill with a cold due to their tolerance to cold virus. For durable resistance, breeders should select plants against susceptibility and complete resistance (Parlevliet, 1993). The term durable resistance was introduced by Johnson (1978) as a neutral term to designate resistance that has proved long-lasting in widely grown cultivars. In many respects 'tolerant', 'durable', and 'horizontal' are similar: certainly the intended effect of 'horizontal resistance' is durability (Buddenhagen and de Ponti, 1983).

This paper summarizes and reviews the 'author' views and theory on breeding and deploying tolerance crop cultivars that make co-survive pests in nature and sustain or

increase crop production worldwide, particularly resource-poor developing countries. Experiences of the author with maize streak virus, common rust (*Puccinia sorghi*), southern rust (*Puccinia polysora*), northern corn leaf blight (*Exserohilum turcicum*), southern corn leaf blight (*Bipolaris maydis*), downy mildew (*Peronosclerospora sorghi*), ear rot complex, *Curvularia lunata*, European corn borers, African specific stem borers, and *Sitophilus* weevils and parasitic plant *Striga* are presented here. The author illustrates the approaches of how to breed tolerance crop cultivars in an environmentally friendly way and also points out general misunderstandings on the terminologies of tolerance and resistance.

SPECIFIC EXAMPLES OF BREEDING FOR TOLERANCE

Maize streak virus

Maize streak virus (MSV), transmitted by *Cicadulina* (Naude) leafhoppers, is the most important disease of maize in sub-Saharan Africa (Efron *et al.*, 1989; Soto *et al.*, 1982). Breeding for maize streak virus resistance in maize at IITA was initiated in 1971 (Buddenhagen, 1977). Selections were made of plants with streak symptoms to avoid escaped plants. A genetic study revealed that two to three major genes control streak resistance in IB32 (Kim, *et al.*, 1989). The maize research team at the International Institute of Tropical Agriculture (IITA), in collaboration with the International Maize and Wheat Improvement Center (CIMMYT) and African national programs, developed over 100 streak-resistant (SR) maize varieties (open-pollinated and hybrids) adapted to the lowland forest, savanna, and mid-altitude ecological zones in Africa (Efron *et al.*, 1989). SR varieties are of different grain colors (white and yellow), grain texture (dent, flint, and semi-flint), and different maturity groups (early, medium, and late). The resistance sources used were a mixture of 'La Revolution' controlled by possibly a major gene and the IB32 type controlled by two to three genes (Kim *et al.*, 1989). 'La Revolution' was developed by scientists at the Centre de cooperation internationale en recherche agronomique pour le developpement (CIRAD) in France from a local collection of maize in La Union Island and 'IB32' was developed by scientists at IITA from an IITA tropical *zea* yellow (TZ-Y) resistance population, which originated from East African germplasm (Efron *et al.*, 1989; Kim *et al.*, 1989). These streak resistance genes admitted some infection at early stages with ontogenetic change to resistance towards maturity (Kim *et al.*, 1989; Soto *et al.*, 1982). Tolerant plants with mild symptoms were selected to minimize directional selection pressure on MSV. This also guaranteed the nonselection of escaped plants. Scientists at

IITA identified three different types of streak resistance: single gene resistance (A-type, no apparent streak symptoms) in inbreds TZMi 301, Pop.10; oligogenic resistance (B-type, some streak symptoms), with two to three genes involved) in IB32, TZi 1, TZi 3, TZi 10, TZi 25, TZMi 101 and minor polygene resistance (C type, lots of symptoms) in TZi 15, TZi 18 (Kim, 1998c). Temperature greatly affects maize streak symptom in lines with of B- and C-type resistance. Attempts to incorporate C type resistance into susceptible lines by the backcross method failed. Durability of A type resistance cannot be confirmed presently because this gene has not been used widely in Africa. The author also has identified B-type resistance genes in germplasm from the Philippines, Phil. DMR-6, and South Korea, a Korean waxy line. Tolerance genes would be present more commonly in unselected germplasm.

Great confusion has arisen from a misunderstanding the quantitatively inherited genes of B- and C-type streak resistance (both can be described as tolerance) that the symptoms are varied by environmental factors. While symptom expression of the A-type was consistent across test locations. The

Table 1. List of ten maize inbred lines with tolerance to major diseases.

Disease	Inbred lines*
Maize streak virus	TZi 1, TZi 3 (Tuxpeno), TZi 4, TZi 7, TZi 10, TZi 25 (B73), TZi 30 (Hi28), TZMi 102, TZMi 302, TZMi 35 (KU 1414)
<i>Puccinia sorghi</i>	Ant.2D, B73, CM105, CM111, H98, Hi32 (Oh545), IL667a, KU1418, Mo17, Pa762
<i>Puccinia polysora</i>	Hi34, ICA L219, ICA L223, ICA L224, KU1414, TZi 1, TZi 3, TZi 4, TZi 25, (B73), TZMi 102
<i>Exserohilum turcicum</i>	Fla2AT116, Hi39, ICA L 27, KU1414-SR, N3, SC, TZMi 102, TZMi 301, TZMi 407, 89223 (Cameroon)
<i>Bipolaris maydis</i>	Fla2AT115, Fla2AT 116, Fla2BT73, Fla 2BT106, Mo17, TZi 1, TZi 3, TZi 4, TZi 18, TZi 25
<i>Perenosclerospora sorghi</i>	KS6, KU1403, KU1409, KU1414, KU1418, INV 138, MIT 2, MIT 11, Narino 330, Phil. DMR6
Ear rot complex	Hi35, ICA L36, INV 302, TX601, TZi 3, TZi 4, TZi 5, TZi 18, TZMi 101, TZMi 407
<i>Curvularia lunata</i>	ICA L210, ICA L221, KU 1403, KU1409, KU1414, Narino330, TZi 4, TZi 12, TZi 25, TZi 30

*CM(India), Fla(Florida), H(Purdue), Hi(Hawaii), ICA(Colombia), IL(Illinois), INV(Texas), KS(Thailand), KU(Thailand), MIT (Philippines), Mo(Missouri), N3, SC(Zimbabwe), Narino(Thailand), Oh(Ohio), TX(Texas), TZi(IITA lowland), TZMi(IITA mid-altitude)

author confirmed the symptoms from the two distinct ecological zones, the lowland zone in Nigeria and the mid-altitude zone in Zaire under artificial infestation with MSV. Over 50 different plantings have been made during ten years and observations were consistent. In addition, the multi-locational testing of IITA's SR varieties conducted in over 20 countries in Africa for over two decades showed that B type of resistance was stable across the environments throughout Africa (Kim, 1990a). Most of the present arguments over the so-called breakdown of streak resistance in IITA varieties were caused by the misunderstanding of the expression of tolerance (Kim, 1998c).

The university of Hawaii, Ohio State University and IITA collaborate on mapping maize streak resistance genes in different maize lines through the random recombinant inbred. The team recently identified the presence of B-type of MSV resistance on Chromosome 1 (Lu *et al.*, 1999). The outstanding sources of resistant maize inbred lines to MSV are listed in Table 1.

Common rust

Common rust (*Puccinia sorghi* Schw.) is often severe on maize in the mid-altitude areas and highlands in the tropics and on sweet corn in temperate regions (Hooker, 1979; Kim, 1974; Kim and Brewbaker, 1976a; 1976b; 1977). Recently *P. sorghi* has high infection in the southern areas of U.S. Corn Belt and also in both South and North Korea (Kim, unpublished). Even though at least 24 different allelic single-gene loci with race-specific (vertical) resistance have been reported, general resistance is used to control common rust world-wide. All the reported dominant Rp (resistant to *P. sorghi*) genes have broken down, especially in Hawaii. A single recessive gene in inbred IL677rp still confers resistance (Kim and Brewbaker, 1987). Gene *Rp1-d*, located near the short arm of chromosome 10, also produces epiphytotic in the U.S. Corn Belt. The current susceptibility of previously resistant cultivars with single genes for resistance has demonstrated the lack of sustainability of specific resistance (Hooker and Saxena, 1971; Kim and Brewbaker, 1976a; 1977). Rp resistance was characterized by a typical hypersensitive reaction from the seedling stage to maturity. On the other hand, general or horizontal resistance exhibits ontogenetic changes (Kim *et al.*, 1980) and many sources were reported among tropical germplasm (Kim and Brewbaker 1976a). The outstanding sources (maize inbred lines) of general resistance to *P. sorghi* rust are listed in Table 1.

Southern rust

Southern rust (*Puccinia polysora* Underw.) is prevalent throughout the lowland tropics and the southern parts of

U.S.A. *P. polysora* was first introduced into West Africa during the early 1950s and it produced severe epidemics (Fajemisin, 1976; Rhind *et al.*, 1952). When maize from temperate regions is introduced into the tropics, *P. polysora* is one of the major pathogens attacking it (Kim *et al.*, 1988a). Severe infection occurs at later stages of plant growth than in the case of common rust and becomes apparent after flowering time. Several specific resistance genes, *Rpp* (resistant to *P. polysora*) were reported (Fajemisin, 1976; Kim *et al.*, 1987; Rhind *et al.*, 1952, Smith and White, 1988; Storey and Howland, 1967; Ullstrup, 1965), but none of them was in use extensively. Plants with the resistance showed a hypersensitive reaction throughout the crop growing season for the first 3 years, after which it was overcome by virulent strains. Breeding for single-gene (race-specific) resistance was, therefore, stopped. Selection has been carried out only for general resistance. The epidemics in Africa were tackled by the introduction of materials with general resistance from Latin America (Buddenhagen, 1977; Rhind *et al.*, 1952). General or horizontal resistance is the major type of resistance to *P. polysora* in the tropics and most of the maize varieties developed by CIMMYT and IITA now confer general resistance. Plants with general resistance are characterized by slower development of rust ('slow rusting') than the susceptible plants and their resistance has been durable. One interesting observation was that the *Rpp* gene, although nonfunctional, is still present in some maize inbred lines.

A total of 69 tropical open-pedigree lines were tested in four trials in Nigeria and one trial in Texas. Fifteen lines from America, five from Asia, and three from Africa showed high general resistance. Data from Nigeria were significantly correlated with the Texas evaluation ($r=0.59$) (Brewbaker *et al.*, 1989). The outstanding sources (maize inbred lines) of durable resistance to *P. polysora* are listed in Table 1.

Northern corn leaf blight

Northern corn leaf blight is caused by *Exserohilum turcicum* Pass. (synonym: *Helminthosporium turcicum* Pass.). Several different genes for specific resistance, called *Ht* genes, have been reported (Hooker and Kim, 1973; Hooker and Saxena, 1971; Kim *et al.*, 1974). Only one gene, *HtN*, still confers resistance to *E. turcicum* in Hawaii (Berquist and Maisas, 1974). Almost all resistant materials from Mexico and the US Corn Belt were highly susceptible screened under heavy artificial infestation in the midaltitude ecology in Nigeria (Kim *et al.*, 1988a). Results of a genetic study revealed that additive genes play a major role in inheritance of *E. turcicum* resistance among IITA's maize inbreds (Kim, 1997). Through a collaborative project with the University

of Hohenheim in Germany, an attempt was made to determine the stability of resistance sources. The university of Hawaii formed a synthetic of maize resistant to *E. turcicum* with 14 lines selected across Hawaii, Kenya, and Nigeria (Brewbaker *et al.*, 1989). The synthetic is called 'MIRSYN 1 (*turcicum*)' or Maize Inbred Resistant Synthetic 1.

A recent observation on *E. turcicum* resistance in Hawaii showed that some exceptions might occur with 'tough' single genes underlying general resistance (J.L. Brewbaker, personal communication). The outstanding sources (maize inbred lines) of resistance to *E. turcicum* are listed in Table 1.

Southern corn leaf blight

Southern corn leaf blight caused by *Bipolaris maydis* (Nisik.) Shoemaker (synonym: *Helminthosporium maydis* Nisik.) is common in the lowland tropics as well as the southern parts of the temperate regions (Brewbaker 1983; Hooker 1979). Tolerance expression to this disease is controlled by general resistance (Hooker, 1979; Kim *et al.*, 1974; Lim, 1975). Only one specific resistance gene, *rhm* is known. Lines from Florida (Fla. 2AT and Fla. 2BT series) and from the U.S. Corn Belt (NC248 and Mo17) exhibited an adequate level of resistance in the tropics (Goodman, 1992; Kim *et al.*, 1988a). Stability of resistance to *B. maydis* across locations appears to be high. Genetic vulnerability of maize plants with Texas male sterile (*Tms*) cytoplasm by race T of *B. maydis* was another historical example of the limitation of a single gene controlled mechanism (Lim and Hooker, 1972). The outstanding sources (maize inbred lines) of resistance to *B. maydis* are listed in Table 1.

Downy mildew

Downy mildew (DM) is caused by *Peronosclerospora sorghi* (Weston & Uppal). This disease is the most important maize disease in South Asia (Frederiksen and Renfro, 1977). DM is rapidly spreading westward in Nigeria at a rate of approximately 100 km per year (K. Cardwell, unpublished). Resistant materials from Thailand and Philippines showed some variation in resistance in Nigeria, and most maize lines from Texas showed high susceptibility (Fajemisin, 1985; Kim *et al.*, 1988a). Because of the systemic infection of the DM, selection for tolerance is difficult. Ontogenetic changes of resistance towards maturity with fewer symptoms are not commonly visible. Uninfected plants are often classified as escapes. The author observed some formation of cobs in infected plants (Kim, 1998c). In general, DM infected plants do not produce any cobs. Data for both incidence and severity are being taken. Most of DM-resistant lines in Nigeria showed high infection in Thailand (Carlos de Leon, personal communication), indicating that a difference in virulence

between the Asian and African DM population. This is to be expected as DM originated in South Asia. Only high and uniform infestation can also secure the selection of durable resistance against downy mildew. Preliminary data showed that the expression of resistance in progeny from crosses with the best DM resistant lines from Thailand, inbred KU1414, varied according to inoculum dose and to the genetic background of the other parent involved (Kim *et al.*, 1994b). There appears to be more than one gene involved. The outstanding sources (maize inbred lines) of durable resistance to downy mildew are listed in Table 1.

Ear rot complex

Major ear rot fungi on maize in West Africa are *Fusarium moniliforme* (Sheld.), *Botryodiplodia theobromae* (Berk.), and *Macrophomina phaseoli* (Maubl.) (Fajemisin *et al.*, 1987). In the lowlands, *F. moniliforme* is the most prevalent, while *B. theobromae* is more prevalent in the midaltitude zone. Germplasm bred in the midaltitude zone in Cameroon showed high susceptibility to *B. theobromae* in Nigeria. In addition, response of maize lines to ear rot pathogens in the lowland forest of Nigeria is also different from that of the mid-altitude zone. Location \times pathogen \times genotype interactions are significant for disease severity (Kim, 1990a). A race-specific single gene for ear rot resistance in maize has not been reported. The selected maize inbred lines with resistance to ear rots are listed in Table 1.

Curvularia leaf spot

Curvularia leaf spot on maize caused by *C. lunata* (Wakker) is severe in the lowlands of Central and West Africa. The disease used to be considered only cosmetic and not damaging to yield significantly. However, recent observations indicate that the yield of susceptible materials could be reduced by 50% (Kim, 1997). Most widely grown lowland varieties, including the Tuxpeno population, are highly susceptible. One of the susceptible inbred lines is TZi 3, which was derived from CIMMYT Tuxpeno (Population 21) and IITA's streak resistance population, TZSR-W. The best available sources of resistance are the Thailand downy mildew-resistant materials, e.g. KU1414 (Kim *et al.*, 1988a). The resistance appears to be oligogenic. Genetic studies, both by diallel crosses and generation mean analysis, are being carried out. The sources of resistance (maize inbred lines) to *C. lunata* are listed in Table 1.

European corn borers (ECB)

European corn borer (*Ostrinia nubilalis*) with first and

Table 2. List of maize inbred lines with tolerance to major insects.

Insect	Inbred lines*
European corn borer	TZi 4, Fla2AT116, CIM.A.-6(Hi), TZi 3 CM118, SC123, ICA L36, CIM. A. 21 (Hi), SC301D, INV534.
African stem borers	TZi 4, Across 7624 S3 lines, CM116, INV575 (<i>Sesamia</i>); MP704, PRMo2C6752-1, MP496, MRMo2 x PRMPoSQB874, PRMo2C688-8, 8338-1 hybrid (<i>Eldana</i>).
Asian corn borer	Hi32, ICA L25, NC248, Hi x 4231, PAC 90038, CIM. T. 11ES, Mo5 and Hi34.
Weevils	Hi41, Hi34, ICA L29, KU1409, Hi39, ICA L221, TZi 18, TZi 15-1, 8329-15, TZSR-Y-1.

*CIM(CIMMYT), CM(India), Fla(Florida), Hi(Hawaii), ICA (Colombia), INV(Texas), KU(Thailand), TZi(IITA inbred), TZSR (IITA streak resistance population).

second generations is considered the most important insect attacking on maize in the temperate zone including U.S. Corn Belt, China and Korea (both North and South Korea). Many of commercial hybrids and their parental inbred lines are resistant to the first generation attacking during the early stage of plant growth, but susceptible to the second generation attacking from the flowering time (Klenke *et al.* 1986; Guthrie and Russell, 1988). Yield reduction of susceptible hybrids by the second generation was estimated as 40% under high infestation. Resistance sources with a moderate level have reported by Sullivan *et al.* (1974) and Kim *et al.* (1988a; 1988b) from tropical materials (Table 2). Information on genetics of the resistance lines were also reported (Kim *et al.*, 1988c). Recent work controlling ECB, however, has focused on the development of genetically modified hybrid maize controlled by Bt gene. This new biotechnology product controls the insect 100% without any room for the pest for their survival. The effectiveness of the control is considered to be too high. The author and others predicted new biotypes of ECB, a decade ago, that overcome the Bt gene with time because of its against the co-survival system in nature (S. K. Kim and W. D. Guthrie at Iowa State University, unpublished, 1987).

African stem borers

Three stem borers, *Sesamia calamistis*, *Eldana saccharina* and *Busseola fusca* occur only in Africa and all attack on maize. The first two are widespread in the lowland humid areas of almost all the countries of sub-Saharan Africa. Farmers in West and Central Africa seldom plant maize as a second season (July-November) and the main reason for this is the crop damage by the two insects. *S. calamistis* attacks maize at an early stage, resembling of the first generation

ECB, except that it often causes dead hearts as well as overall plant damage. While *E. saccharina* attacks maize at a late growing stage, in a similar manner to the second-generation ECB, damaging the stem and ears. IITA scientists initiated breeding for resistance to *S. calamistis* in the late 1970s. The identification of sources of resistance to the first two insects were achieved (Bosque-Perez *et al.*, 1988; Kim *et al.*, 1988a) and some of the lines are listed in Table 2. This success was the result of the development of uniform and efficient artificial infestation techniques. Effectiveness of resistance breeding against stem borers was also facilitated by line-hybrid development approach (Kim, 1997).

Asian corn borer

The Asian corn borer (*Ostrinia furnacalis*) is the most serious insect pest of maize in Southeast Asia and the Pacific (Brewbaker *et al.*, 1989). Out of the 120 MIR (Maize Inbred Resistance) lines tested against *O. furnacalis* in Guam and Taiwan, eight inbred lines showed moderate levels of resistance and the parentage of these lines are Cuban flint and Antiqua group of germplasm (Table 2).

Weevils (*Sitophilus* spp.)

Sitophilus weevils damage maize grain worldwide. Infestations with weevils are higher in tropical zone where the problem begins in the field and continues through the storage period. Tightness of husk cover and many husks are considered to be major morphological traits that minimize field infestation of the insects that damage grain in storage (Dicke, 1977; Kim, 1974; Brewbaker and Kim, 1979). Selection for increased yield and fast dry down of maize often results in poor husk cover. Maize plants of tropical germplasm have an average of 12 husk leaves compared to seven for temperate inbreds (Kim, 1974; Brewbaker and Kim, 1979). Grain texture appears to have some correlation with weevil damage. Popular maize populations with dent grain texture such as Tuxpeno and its related La Posta (two best maize populations developed by CIMMYT) are highly susceptible (Kim, 1997). Resistance to weevil attack of some MIR and other inbred lines has been observed in Nigeria and Hawaii. Significant genetic variation for tolerance to weevil damage was observed among tropical inbred lines and hybrids (Bosque-Perez *et al.*, 1988; Kim and Kossou, 2000; Kim *et al.*, 1988a). Among the MIR inbreds, three Hawaiian inbred lines with Antigua background (Hi41, Hi34, Hi39), two Colombian inbred lines (ICA L29, ICA L221), one Thailand line (KU1409) and several IITA lines (TZi 18, TZi 15-1 lines, 8329-15 hybrid and TZSR-Y-1 open-pollinated) showed tolerance and resistance (Table 2).

Parasitic weeds

Striga species are considered to be the greatest biological constraint for cereal crop (maize, sorghum, millet) production in sub-Saharan Africa (Kim, 1991; Sauerbourn, 1991). In Africa alone, 21 million ha are infested and an additional 23 million ha are potentially endangered (Saubourn, 1991). The parasitic weeds are a serious threat to crop production in 17 countries and a moderate threat in 25 countries in Africa (Lagoke *et al.*, 1991; Mboob, 1986). The three most important *Striga* species which attack the food crops in Africa are *S. hermonthica* (Del) Benth, *S. asiatica* (L.) Kuntze and *S. gesnerioides* (Willd.) Vatke. The first two infect cereal crops while the third infects cowpea (*Vigna unguiculata* L. Walpers). Research on *Striga* resistance has been carried out for about a century based on *Striga* emergence (Kim, 1991). However, host plant damage by *Striga* appears to be the most important criterion for selection of tolerance. Selection of host plants based on emergence of *Striga* plants might reduce the chances of selecting polygene controlled tolerance which has poor correlation with *Striga* emergence counts (Kim, 1994a; Kim and Adetimirin, 1995). The hypersensitive reaction affects initial haustorium attachment and is highly correlated with low emergence of *Striga*. In contrast, tolerance plants allow attachment of the parasite and reduce selection pressure on the parasite population. The important aspect is that breeders must select tolerant crop plants with moderate *Striga* emergence.

Approximately 80% of *Striga* species originated in Africa, mostly West and Central Africa (Raynal-Roques, 1991). The removal of *Striga* from Africa, the center of the origin of the parasite, would be an impossible task. We would be better to accept the presence of *Striga* species but control them at a level such that the parasites do not affect host crops significantly. *Striga* emergence counts in maize vary significantly upon plots in a same trial, different locations in the same ecology and years, and the counts show a poor correlation with host plant damage symptoms (Kim, 1994a; Kim and Adetimirin, 1997a; 1997b). In 1988, the IITA maize program developed a reliable artificial infestation method with a large quantity of *Striga* seeds (10,000 seeds with 3,000 germinable seeds for per maize plant), low nitrogen application, and ridge sowing. Approximately 50,000 maize genotypes have been screened under the uniform challenge of *Striga hermonthica* infection (Kim, 1997). The progress of IITA maize breeding for *Striga* tolerance has been achieved with emphasis on damage to the host (Kim and Winslow, 1991).

A three-year study of two tolerant and two susceptible hybrids under six levels of nitrogen (0-150 kg ha⁻¹) in Nigeria showed that *Striga hermonthica* infestation (3000 germinable seeds per maize plant) reduced grain yields of

Table 3. List of ten selected maize inbred lines for tolerance to *Striga hermonthica* and *S. asiatica*.

Striga	Inbred lines*
<i>Striga hermonthica</i> and <i>Striga asiatica</i>	B73, C15, Fla2BT54, N28, TZi 3-STR, TZi 12-STR, TZi 25-STR, TZi 30-STR, TZMi 301-STR, <i>Zea diploperennis</i>

*B(Iowa), C(Cameroon), Fla(Florida), N(Nebraska), TZi(IITA lowland), TZMi (IITA mid-altitude)

susceptible hybrids by 20-78% and of tolerant hybrids by 3-46%. The two tolerant hybrids produced on average 85% greater grain yield under low N (0-60 kg ha⁻¹) than the two susceptible hybrids (Kim *et al.*, 1997). The grain yield loss in tolerant hybrids was minimized at 90 kg N ha⁻¹, while that in susceptible hybrids was minimized at 150 kg N ha⁻¹, showing that tolerant hybrids had an additional advantage of lower nitrogen use. The effect of *Striga* on grain yield, host plant damage and plant height varied depending on inoculum dosage (Kim and Adetimirin, 1997b) and host genotype (Kim and Adetimirin, 1997a), implying the involvement of quantitatively-inherited genes.

A strain-specific resistance was reported in cowpea lines affected by *S. gesnerioides*. SUVITA 2 showed high resistance in Burkina Faso, moderate resistance in Mali and Niger and high susceptibility in Nigeria (Aggarwal, 1991). Observations with another single gene in B301 (Singh and Emechebe, 1990) in Togo showed a similar trend (N. Muleba, 1990 personal communication; G. Myers, 1991 personal communication; B. B. Singh, 1993 personal communication). Presence of strain variation of *Striga hermonthica* was confirmed with three cereal hosts (millet, sorghum and maize). This indicates the importance of horizontal resistance of a crop against different strains of the parasite (Kim *et al.*, 1994). In case of maize, the first author believes that enough sources of tolerance are available (e.g., TZi 3 STR etc.) with outstanding genetic background and combined resistance to major stresses such as maize streak virus, leaf blights (*B. maydis* and *E. turcicum*), ear rot complex (biotic stresses), drought and nitrogen deficiency (abiotic stresses). Introduction of wild maize genotypes (e.g., perennial maize) aiming to reduce *Striga* plant emergence would be a waste of research fund and time. The sources of tolerance of maize inbred lines to *S. hermonthica* and *S. asiatica* are listed in Table 3.

APPROACHES IN BREEDING FOR TOLERANCE

The value of resistance of a crop must be evaluated in an environmental protection, economic sense and sustainability based on the period over which the resistance is durable in the areas of crop cultivation. Because of the dramatic effec-

tiveness of vertical resistance and the ease of resistance breeding until a matching race occurs, little effort is made to develop varieties with 'long-lived', tolerance (horizontal resistance), which is mostly controlled by polygenes. Vertical (specific) resistance tends to be 'short-lived' and is controlled by mostly dominant single genes (Hooker, 1979; Brewbaker, 1983).

The importance of tolerance

The author has experience with single gene resistance to plant diseases, such as *Ht1-A* resistance to *E. turcicum* in South Korea, resistance to *Puccinia sorghi* in Hawaii, and resistance to *E. turcicum*, *Bipolaris maydis* and *P. sorghi* in Illinois, and to *P. polysora* and *E. turcicum* in Nigeria (Brewbaker *et al.*, 1989; Hooker and Kim, 1973; Kim, 1976; 1993a; 1993b; Kim and Brewbaker, 1976a and 1977). The most striking was the short-time resistance of the 24 different single genes to *P. sorghi* in Hawaii and Illinois. During a 5-year period, 22 resistance genes were overcome by the pathogen. The remaining two, *Rp1-d* and *Rp1-g*, were overcome within the following five years in Hawaii (Kim, 1993b). The author does not wish to underestimate the importance of vertical resistance. In some cases it may work. The important message is that durability of specific resistance cannot be guaranteed. We have seen numerous examples of the overcome of resistance by pathogens, starting from rusts in flax, wheat, maize, soybean and other foliar diseases, including late blight in potato and leaf blights in cereals (Brewbaker, 1983; Buddenhagen, 1977; Flor, 1955; Hooker and Saxena, 1971; Van der Plank, 1968). The association of vertical resistance and genetic vulnerability is common for many diseases and parasites, including another parasitic plant, *Orobanche* (Cubero, 1986), and it occurs across crop species.

Through selection, 50% gene-frequency of both horizontal and vertical resistance would be maintained in a single population. Breeders can maintain vertical resistance gene under the umbrella of horizontal resistance genes (Kim and Brewbaker, 1977)

IITA's maize research depends heavily on horizontal resistance and tolerance (Buddenhagen, 1977; Efron *et al.*, 1989; Kim *et al.*, 1989; 1997b; 1998; Soto *et al.*, 1982). When breeding for resistance in the center of origin of a crop, such as for *Striga* resistance in cereals and cowpea in Africa, it is better to depend on tolerance (Kim, 1996a and b).

Tolerance is environmentally safe, economically feasible and sustainable (durable) system

Tolerance is environmentally safe and it does not require any use of chemicals and its genetic base alone is sustain-

able and its application is feasible and economically sound. Hence, it can be called as an integrated genetic pest management (IGPM). Every living organism, including plants has an intrinsic nature to get itself succeeded in the next generation. Vertical resistance mostly with hypersensitive reaction is indeed against this nature. It completely hinders parasite organisms from being reproduced in subsequent generations; thus in ensuring survival, these organisms mutate into virulent forms, which are able to overcome vertical resistance. Hence, the vertical resistance is against sustainability. In contrast, the horizontal resistance allows room for succession of pest continuity. The genetic diversity of a crop which is grown commercially is important. Both tolerance and horizontal resistance contribute to the diversity. If a same gene confers vertical resistance against a certain pathogen in different varieties, the chance of genetic vulnerability is still high and all varieties with the same gene base can be susceptible at one time (Kim, 1993b).

Too much effort put on vertical resistance by the multi-donor international agricultural research centers (IARC) is a dangerous strategy to tackle parasite problems in the world, particularly for developing countries due to its expected unsustainability. Once the resistance is breakdown, the poor farmers lose the crop completely or find out an alternate solution, if affordable, a chemical to rescue the crop (Kim, 1993b).

General misunderstanding of tolerance and horizontal resistance

There is a general misunderstanding of horizontal resistance. We expect the uniform expression of resistance of a host crop against all races of a pathogen. However, levels of the horizontal resistance varies depending on the environment, location, inoculum pressure, temperature, and soil fertility and the response trend is more or less horizontal.

Another example of the misunderstanding of tolerance (horizontal resistance) is with the parasitic plants, *Striga* and *Orobanche*. Expression of the polygenically controlled *Striga* resistance (tolerance) depends on inoculum dose, nitrogen level (soil fertility), and soil moisture (Kim, 1991; Kim and Adetimirin, 1997a). Selection based only on *Striga* attachment and/or emergence may result in single-gene controlled, hypersensitive type of vertical resistance. So far we have not found the vertical resistance gene to *Striga* species in maize. Use of vertical resistance gene shall end up the break-down of the resistance. Knowledge of quantitative and population genetics, epidemiology and host-pathogen homeostasis in co-evolution of a parasite and an host are important aspects to understand the concept of tolerance (horizontal resistance) with crop germplasm.

Tolerance is a type of horizontal resistance

Tolerance has been variously defined, but it is generally accepted as “less yield loss or less quality loss with similar level of pathogen, insect and parasite infestation” (Buddenhagen and de Ponti, 1983). It has an inherent or acquired capacity to endure a pathogen or a parasite and contributes for more production of grain yield and/or stover dry matter. From the standpoint of relative sensitivity, tolerance and hypersensitivity appear to represent the two extremes in host plant resistance to infection (Nelson, 1973). The tolerant plants withstand the impact of pathogen and parasite. Thus, tolerance accomplishes the same net result as active resistance mechanisms. Tolerance negates infection by a desensitization of the plant, whereas hypersensitivity negates infection by localizing infection sites. Plants with tolerance can ‘live with’ a certain amount of a pathogen's or a parasite's infection without having appreciable ill-effects. Most of high tolerance is based on oligogene controlled horizontal resistance. Ontogenetic changes in tolerance are exhibited towards the late growing stage of the crop, therefore the yield and its components of tolerant plants are less affected than the susceptible plants. The chance of new races that overcome tolerance arising is low as it does not exert high directional selection pressure against the pathogen. For a practical breeder, whether a variety yields well in the presence of disease or parasite pressure as a result of its tolerance or its resistance makes little difference (Buddenhagen and de Ponti, 1983). Plants showing least effects of the disease and good yield at maturity will have the highest tolerance. Therefore, breeding for tolerance to systemic pathogens such as viruses, soil borne wilt fungi and bacteria was recommended highly (Buddenhagen, 1981). The behavior of *Striga* is similar to the soil borne wilt fungi and a great portion of the wilted *Striga* plants have been seen at all maize testing sites (e.g. Abuja, Mokwa and Ferkessedougou) in West Africa. In conclusion, the author believes that tolerance is a type of horizontal resistance.

How to identify sources of tolerance

Under severe MSV infection, maize plants with tolerance genes such as inbreds of IB32 and TZi 3 seemed to be susceptible at the seedling stage (leaves below the ear), but streak symptoms often ameliorated ontogenetically (leaves above the ear). At flowering and two weeks after flowering only a few streaks were visible on the top leaves, while susceptible plants showed streak symptoms continuously. Ontogenetic changes for tolerance are more clearly seen in foliar diseases such as *Puccinia sorghi* rust (Kim *et al.*, 1980). Plants of a crop with partial infection would be regarded as a signal of

tolerance or horizontal resistance. Genotypes with the reported tolerance or horizontal resistance are durable and they showed moderate susceptibility at high inoculum dosage. Low temperature and high elevation also increased streak symptoms of the resistant lines in maize. Tolerance can be selected simultaneously with high grain yield; both of these characteristics are controlled by polygenes and quantitatively inherited. Multilocational testing would be a good approach to select for tolerance across wide environmental conditions. For example, over 100 open-pedigree maize lines were tested internationally against seven virus and virus-like diseases. A relatively high proportion of the inbreds showed high or moderate resistance to maize dwarf mosaic virus strain a (MDMV-A) (49%), maize mosaic virus (MMV) (42%), and sugarcane mosaic virus-MB (SCMV-MB) (33%), while fewer were resistant to corn stunt (CS) (23%) and maize mosaic virus (MSV) (17%) (Brewbaker *et al.*, 1991). Genes for tolerance cannot be effectively selected under a mild infection of the pathogen or an erratic natural epibiotic conditions (Kim, 1991; 1993a). The slow progress in breeding of corn stunt spiroplasma, transmitted by *Dalbulus maidis* leafhoppers, in Mexico, Central and South America might be caused by the lack of uniform artificial infestation (Brewbaker *et al.*, 1991). This was true in parasitic weed, *Striga* and *Orobanche* research worldwide (Kim, 1996a).

Time to observe tolerance

The most appropriate time for taking evaluation on tolerance (horizontal resistance) is around two weeks after flowering. Selections for tolerance at seedling stage in both laboratory and field conditions are not reliable. Plants with tolerance show continuous variation in symptoms under different environmental conditions. Application of genetic engineering and biotechnology to breeding for tolerance and horizontal resistance is difficult because most of the resistance is controlled by more than one gene with quantitative inheritance.

Breeding methods for tolerance

Breeding for tolerance (horizontal resistance) differs somewhat from breeding for vertical resistance. Selection can be achieved only under high and uniform infection of the pest (Kim, 1993a; 1993b; 1994b). Because of variation in levels of natural infection, artificial infestation with a uniform challenge provides a better opportunity to select lines for tolerance. Mild or nonuniform infection often dilutes the progress made in the previous selection cycle. Vertical resistance genes are easily transferred into a susceptible line or

cultivar through a conventional backcross method. In contrast, conversion or accumulation of horizontal genes and tolerance depends on the number of genes and the gene action involved. If resistance is controlled by a few major genes (oligogenic resistance), a modified backcross method (e.g. selfing-backcross-selfing-backcross - -) may work. If several minor genes with additive gene action are involved, the recurrent selection method can be effective. Inbreeding and hybridization would be more effective if the resistance is governed by nonadditive or dominant gene action.

To maximize the potential use of resistance sources in crosses, conversion and incorporation of exotic genes of resistance would be better from sources in the same heterotic group. Approximately 25% of exotic genes from temperate germplasm for the tropics and from the tropical germplasm for the temperate regions would be appropriate (Goodman, 1992; Kim, 1990b; Kim *et al.*, 1988a). Genetically-fixed homozygous inbred lines offer the highest chance minimizing negative effects of deleterious genes in crosses. Experimental data showed that host plant resistance plays a major role in genotype x environment (G×E) interaction for maize germplasm tested in West Africa (Kim, 1990a). Only approximately 15% of variance belonged to G×E, which was much smaller than expected. Horizontal resistance of maize germplasm to biotic stresses across environments could contribute to the low interaction of sums of squares. Conversion of temperate germplasm in West Africa and Hawaii proved that a few major genes for resistance to important diseases can change the adaptation of temperate germplasm to the lowland tropics (Brewbaker, 1983; Kim, 1990b; Kim *et al.*, 1988a).

CONCLUSION

A crop cultivar with a good level of tolerance is different from a cultivar developed by vertical resistance or genetically modified organism. Significant variation is present among crop germplasm in the level of tolerance. A plant with tolerance can be selected for only under high and uniform infection of a biotype. Genetically homozygous inbred lines of a crop can be used as sources of tolerance. Environmentally safe, economically feasible and sustainable control of pests in a crop can be achieved by combining different tolerance genes into a cultivar against major biotic stresses.

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