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BREEDING STRATEGIES FOR STRESS AND DISEASE RESISTANCE IN DEVELOPING COUNTRIES[1]

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Introduction

Adaptation of plants to the local environment with all its physical and biological stresses is the substance of evolution. Plants in general have done very well and can inhabit remarkably hostile environments. We need only look in the ocean, on salt flats, on mine dumps, in mangrove swamps, in the tundra, in deserts, and in degraded tropical forest soils to realize that plants in the broad sense have remarkable adaptations—genes—that have evolved and been selected in combinations enabling them to survive and perpetuate under what would normally be considered severe adversity.

But how well have our major crop plants been able to adapt through breeding efforts, to less than ideal physical and biological environmental conditions? Specifically, in the third world where food/population ratios are precarious and food crop yields are quite low, the amount of productivity lost because of unnecessarily high susceptibility to diseases, insects, and an adverse physical environment is probably very large, although the situation is poorly documented. Even in the USA, losses for major crops due to physical environmental factors were calculated as 66.5% (compared to 9.3% for losses to all biological factors of diseases, insects, and weeds) (7). One may question the assumptions underlying these figures as they were based on differences between average yields and record high yields, but the impact of negative physical effects of the environment on productivity is undoubtedly very high.

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Historical Perspective

In the tropics and subtropics, attempts to improve food crops were minor prior to the second world war. With a few isolated exceptions it was only with the Rockefeller Foundation-based efforts in the 1940s on wheat and potatoes in Mexico and then on rice and maize in Latin America that a strong beginning was made to improve the adaptation, quality, and yield developed locally by farmer selection. Out of these efforts grew the International Institute System (CGIAR) (9, 62), which has dominated crop improvement in the third world ever since. Before judging this tardiness as myopia one should realize that scientific crop improvement actually resulting in large-scale replacement of farmer-varieties anywhere is quite recent. It began out of necessity and with little science in the 1850s following the catastophic new encounter of *Phytophthora* with potatoes (72). It was undertaken again with wheat and some horticultural crops from 1900 onward (84), often in response to new-encounter imbalances generated at first by crop or pathogen movements but later by genetic isolation created by former resistance breeding efforts (11).

One may generalize that crop improvement efforts in modern times have had the following course:

1. Overcome disease susceptibility.
2. Utilize heterosis—first with maize.
3. Overcome nitrogen and density limitations to yield.
4. Overcome insect susceptibility.
5. Overcome physical environmental limitation to yield.

A concern for unique quality features has long underlain these five points, especially with industry breeders for horticultural and specialty crops.

Four of the five major goals involve overcoming an adverse factor inhibiting potential yield. Current breeding programs generally have a major component involving two or three of these objectives—overcoming disease susceptibility, insect susceptibility, and physical factor limitation to yield.

Success in overcoming nitrogen limitation to yield (a unique physical factor) has been so great for smaller cereals due to use of dwarfing genes that this target has been considered attained. Even with cereals, though, where nitrogen is relatively cheap, farmers have utilized nitrogen to the point of requiring further lodging resistance, especially in rice in high technology regions. The original effort was to ensure nitrogen responsiveness, but changes in plant height and architecture have caused a positive change in harvest index (ratio of grain yield to that of grain plus straw) regardless of nitrogen level (1). In fact, the major achievement in plant breeding has been this increase in harvest index and standability in cereals, a trend that has largely run its course (3). Even in maize where dwarfing was not utilized, the increase in yield (38–57%) of

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hybrids developed in the 1970s over those from the 1930s was due to a reduction in barrenness at higher and at optimum densities, and this change increased the harvest index (73).

Very little if any increase in total biomass has been achieved in any food crop. Thus, in crops such as potatoes and root crops where harvest index and biomass production were both already high, little change in yield potential has been achieved by breeding. This is especially true for forages, where the harvest is most of the biomass. The remaining area for progress, other than possibly increasing biomass and, more remotely, increasing photosynthetic efficiency, is largely one of overcoming some adversity inherent in the environment. Thus disease, insect, and physical factor limitations to yield remain major components of food crop breeding programs and they are especially important in the third world. Success in these areas is not yet general. What are the reasons for this continued need, and can they be addressed to advantage?

TEMPERATE COUNTRIES Major food crops were domesticated locally from wild plants in the tropics and subtropics. They were selected for thousands of years from naturally breeding populations for maximum local adaptability. Numerous landraces were developed in each locality, and as man moved to new environments away from the crop homeland in either distance, latitude, or altitude, adaptations to new ecosystems and pathosystems evolved, and unnecessary genes for former adaptation needs were lost. Only small parts of the early landrace genetic base were moved intercontinentally into Europe and North America from the Middle East, Africa, Asia, and tropical America in the early years of migration and conquest—hence the emphasis in modern breeding courses in temperate countries on returning to centers of origin and obtaining new material for disease resistance genes, drought resistance genes, and so forth. The genetic base was often limited for the diverse environments of the new homelands. To deal with intractable diseases, pests, and other adversities, chemicals or other capital-dependent high-technology techniques were developed and substituted for inadequate levels of genetic resistance.

With the growth of state university breeding programs in the USA, and country programs in Europe, varieties of most crops have been developed with high local adaptability for the state or country or a part of the state or country. This high local adaptability has been developed with local (or ecosystem banded) on-site selection from segregating populations, rather than from varietal trials of a few presumptive high yielding lines originating elsewhere. More recently, "broad adaptation" and coordinated multilocation trials have come into vogue even in these temperate locations.

TROPICAL AND SUBTROPICAL COUNTRIES In the third world homelands of major food crop species the history has been quite different. Maximum local

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adaptability has evolved for thousands of years. As a result, landraces have "local ecosystem adaptation" in the peasant agriculture in which they have evolved. They are adapted to the diverse physical stresses and biological problems of local areas where they are grown under low inputs and low densities, sometimes in mixed cropping systems.

With the invention of the dwarf gene high N responsiveness package and its extension into the third world since 1960, spectacular changes in yield potential have occurred in small cereals. However, this has led to the displacement of locally adapted landraces due to deployment of "international" varieties on a grand scale. This has also led to the rise of one disease or insect problem after another. It was only after new "miracle" rice varieties, developed in one or a few locations, were deployed widely in tropical Asia that the major diseases of tungro virus and bacterial blight were discovered in that region (13). Likewise, green leaf hoppers and brown planthoppers became major pests only after deployment of the new varieties. The new "high yielding varieties" (HYV's) performed poorly in some soils where local landraces had evolved in situ and performed well. Later, such soils were found to present problems of zinc deficiency, iron and manganese toxicity, salinity, acid sulfate toxicity, aluminum toxicity (for upland rice and wheat), iron deficiency, and nutrient imbalances in general (80, 87), and breeding for resistance to these physical factors began, especially for rice (51, 63). It is emphasized that adaptability had already evolved to local adversities in the regions of crop domestication and this local adaptability and local adversities, including local pathosystems, were largely ignored at first as international varieties swept vast regions.

For each "new" disease or insect pest that developed into prominence the incorporation of resistance then became the breeding target. Thus, relatively few pure varieties, often carrying vertical resistance (VR) to major pathogens, were spread over large areas previously covered by a mosaic of many local varieties, presumably carrying both VR and horizontal resistance (HR). This development has increased risk of serious epidemics and these are particularly damaging to poor farmers and poor societies. Simmonds discussed these issues in a recent book on crop improvement, stating, "the risk having been recognized, the correct response is clearly to promote diversity among varieties and to favor HR over VR" (76). He adds, "this is now, of course, no more than conventional wisdom." Unfortunately, this view is much too optimistic, as little support exists or effort is expended today on HR research or breeding, and much effort is expended to saturate large areas with a few varieties, often introduced with little analysis of the local ecosystem or pathosystem.

Broad adaptability A recent publication (36) states that the rice variety IR 36 is now on 11 million hectares—an area greater than for any variety of any crop in history. A program able to develop such a variety and promote it over such a

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large area can be admired; but one may question the wisdom of having 60–90% of a country's staple food crop in one single variety, as is (or was) the case for the Philippines, South Vietnam, and Indonesia (36).

This publication on IR 36 emphasizes the need to reduce farmers' and societies' risk. However, this emphasis is followed with: (this) "world's most popular rice . . . has eliminated some of the risks." In discussing the parentage of this variety, it becomes evident that newly perceived or newly evolved problems developed earlier on the HYVs parental to IR 36. No insurance exists against the rise of new major problems on IR 36 due to new races or biotypes, effective against the vertical genes it carries.

The relationship between international and national programs and the effectiveness of local country breeding programs may be questioned when varieties from distant sources outcompete all of those from the local breeding efforts. Alternatively, the dogma of genetic vulnerability and the dangers of genetic uniformity and vast monoculture (21, 52, 56) may be questioned and reexamined. But, once begun, the strategy to develop international varieties that carry VR becomes self-perpetuating and involuted, as the particular gene combinations giving maximum yield potential to the high yielding varieties are conserved as one resistance after another becomes perceived as important and is incorporated into the old HYV, often by a backcrossing procedure. The HYVs in rice are closely related (17) and new resistances are added, usually as single vertical genes (35). The variety becomes resistant but also vulnerable, to the extent of potential variability of the particular pathogen for which a vertical gene was used and fitness of new pathogen genotypes that will be selected.

Local adaptation The strategy involving use of high N-responsive dwarf genotypes in small cereals has resulted in vast new tonnages of yield in both developed and underdeveloped regions. The basic concept has been questioned on sociological/economic grounds (19, 43) but it is unlikely to be overthrown. The real question should be somewhat different: in breeding and selection methodology accompanying the incorporation of this character, how much thought and effort went into (and should now go into) a concern for maximum adaptation to adversities of the local ecosystem and to a consideration of the differences between the local eco- and pathosystems and the center for breeding?

Because the N-responsive dwarf-gene package was so powerful, and because local diseases take time to become epidemic on new genotypes from a low-level base on old varieties under low inputs, it was possible to neglect fundamental biological principles. Moreover, the "miracle variety" mentality for small cereals dominated development of new institutes and new breeding programs for other crops in which a simple plant-type change was not the solution to low yield, and should not have been expected to be the major

solution. Thus, for crops such as potatoes, sweet potatoes, cassava, yams, taro, maize, sorghum, millet, beans, cowpeas, chickpeas, groundnuts, and many vegetables, tropical and subtropical production remains low for many biological, physical, social, and economic reasons. Improving such crops—and further useful improvement in small cereals—will require much greater insight and study of the constraints of local eco- and pathosystems, in which human culture and economics are also considered major components (14).

Environmental Adversity and Stress

Environmental adversity in relation to plant or crop productivity can be viewed as the cause of stress on a particular genotype, and it will vary with the genotype. Adversity can be grouped under six broad headings: (*a*) water, (*b*) mineral, (*c*) air, (*d*) temperature, (*e*) light, and (*f*) biological. Levitt (46, 47) makes a strong case for common terminology "applicable to all environmental stresses, even those induced by the organismal environment" (48).

"Stress" is considered an external factor acting on an organism and "strain" is the resulting response. Stress resistance can be divided into "avoidance" and "tolerance." In stress tolerance, stress reaches the tissue and causes strain; the strain, however, is either avoided or tolerated (48). It is much easier for physiologists to view drought or salinity stress in terms of principles of mechanics of stress and strain than for pathologists to so consider diseases. However, pathologists have developed a large number of definitions and qualifications for resistance, tolerance, and susceptibility that do not fit a neat logical conceptual framework. Pathologists could well examine Levitt's proposals in detail and attempt to restructure their terms within a holistic logical frame. It is a useful exercise to attempt to relate pathologists' terms to this conceptual system. I have attempted to do so for two types of pathogen classes (Table 1). The difficulty seems to involve the systems level (68) at which one attempts integration, i.e. cellular, tissue, whole plant, or population. A further difficulty is the dynamic nature of the host-pathogen encounter and subsequent feedback influencing the interaction over time. An initial challenge by a pathogen may be avoided at the whole plant level by either cellular immunity or cellular high-susceptibility, which results in hypersensitivity and exclusion of the systemic pathogen or nondevelopment of the localized pathogen. But how do we view resistance mechanisms that reduce (rather than prevent) rapid growth and multiplication or systemic spread of the pathogen? These mechanisms result in less injury to the plant and thus the plant *avoids* some (but not all) of the potential stress of its more susceptible relatives. The extent to which disease develops then has to be examined in terms of stress tolerance. Stress tolerance involves the effect of strain on the plant. Strain is either avoided or tolerated. If tolerated, it is through reversing or repairing the strain during development (47).

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Table 1 Nature of stress resistance[a]

Potential stress	Condition of resistant plant cells exposed to the stress and surviving due to: Avoidance	Tolerance
Low temperatures	Warm	Cold
High temperatures	Cool	Hot
Drought	High water potential	Low water potential
High radiation	Low absorption	High absorption
High salt	Low salt	High salt
Flooding	High O_2	Low O_2
	Condition of whole-plant/pathogen interaction due to: Avoidance	Tolerance
Virus challenge (systemic pathogen)	Immunity or hypersensitivity	Low virus reproduction or low virus systemicity
Leaf spot (localized pathogen)	Immunity or hypersensitivity or lower pathogen growth and reproduction	Reduced response to injury or compensation for injury or high source/sink ratio

[a]Upper half of table is from Levitt (46).

Adversities In Developing Countries

Most developing countries are in the tropics and subtropics. Environments range from arid to very wet, and from warm or hot lowlands to cool uplands. Soils are often depleted or even unbalanced, with salinity in arid regions, ranging to very acid, low cation exchange capacity (CEC) and aluminum-toxic conditions in the old rainforest soils. The leached acid soils (Oxisols, Ultisols and Inseptisols) of the tropics occupy about one billion hectares (16).

The most general departures from optimum conditions in farmers' fields in the tropics are low nitrogen, low phosphorus, and periodic water deficits. Cultivars that can ameliorate or overcome these effects are desirable. Also, often important but more localized are conditions of low K, low Zn, Fe, and other micronutrients, and toxicities of Al, Mn, and other elements. Locally, and less general, excessive cold and heat are important, and light may be low in the monsoon tropics.

The literature is voluminous on drought and drought resistance (4, 15, 27, 38, 41, 42, 44, 47, 49, 55, 59, 64, 67, 77, 80, 82); considerable on mineral stresses (10, 15, 16, 22, 28, 37, 49, 63, 81, 86, 87); less extensive on salinity (23, 47, 61, 75) and cold and heat stress (34, 43, 46, 50, 53, 55, 57, 82). Air pollution stress (49) is hardly mentioned from the tropics. Space limits an extensive general review and the more interested reader may refer to cited references, especially to review papers and to recent symposia volumes. I wish

only to highlight some general concepts and viewpoints that could influence the development of new cultivars in relation to adversities in the tropics.

To a person long involved with the complexities of disease resistance breeding, wherein a variable pathogen population and its flexibility is a major and elusive enemy, breeding for abiotic environmental stress appears simple. But progress has been small or sporadic and a voluminous literature has grown, mostly on the complexity at the physiological, biochemical, and molecular level, of various types of physical stress.

It is utopian, however, to expect high plant productivity without adequate water, nitrogen, phosphorus, and potassium, as well as the required minor elements. Moreover, cultivar superiority in extraction of any limited resource has only a temporary advantage. Breeders cannot expect to abrogate the fundamentals of plant physiology. With this caveat, which are the adversities most worth pursuing? Probably of first importance are the mineral toxicities, such as Al, Mn, Fe; for certain crops and situations, salinity and alkalinity; the minor element deficiencies with a large soil reserve (Fe) or those induced (Zn) by complexing with added macronutrients; and possibly P efficiency, where roots can locally reduce P fixation (58).

What about drought? Plant soil/water relations reducing potential productivity are probably the most complex area for adversity breeding. Potential progress in drought resistance may range from zero to moderate, depending on the pattern and type of drought as well as on the crop, methods, and effort. A holistic overview and analysis (27, 41) is needed, but in general I believe progress in this area will be less than many expect, except for modification of cultivars to provide drought avoidance.

One wonders, however, if the biochemical and physiological complexities of stress resistance may not have somewhat overwhelmed the efforts and approaches in breeding to include stress resistance as a component of overall breeding objectives. Possibly the breeder can make more progress than he thinks, using innovative approaches.

ECOSYSTEM FOCUS If an old local variety seems unaffected by an environmental stress but is plant-type yield-limited, and introduced high-yield-potential varieties are affected and yield relatively poorly, the solution should be readily apparent: (*a*) utilize a backcrossing approach to introduce only the plant-type character (a single gene) into the locally adapted type, or (*b*), mutate the adapted variety to dwarf plant type. With the first approach one is confronted with the complexities of establishing a uniform stress environment in which selection in segregating and backcross generations will recover the full adaptation of the local parent. Many slips are possible here and the literature is replete with the difficulties (4, 15, 25, 39, 49, 53, 57, 64). But the second approach avoids this problem, since selection need be only for plant type. For

rice in California, where cold was the problem, with all its physiological/phenological complexities and yearly variations, the second approach (mutation to dwarfness of locally adapted types) led to quick success and major yield increases (74). Once the major advance is achieved in this way, the improved plant type of a locally adapted variety can be crossed with other locally adapted varieties to recombine other needed traits for optimum disease and insect resistance, quality, and yield. At this stage, refining of uniformity of stress challenge is needed. This approach of relying on already evolved local adaptability (or adaptability to a similar environment elsewhere) should be especially useful for mineral stresses of problem soils (22, 86).

It is emphasized again that western plant breeding is dominated by its development in areas distant from centers of origin and with a limited germplasm. The genes we wish to incorporate for some purpose in our "almost perfect" variety have already evolved and exist out there somewhere and we get material from a germplasm collection and screen for them. Rarely does one go to a matching ecosystem in the crop homeland to collect material, and a collector rarely has pathosystem and ecosystem focus. The germplasm collection system so far provides little, if any, useful ecosystem data.

In developing countries, where our crops evolved, or for which, if they did not, matching ecosystems can be found where they did, crop improvement could have a different approach and goal: *balanced ecosystem adaptation*. Such a focus permits the exploitation of past evolutionary selection for an environment. Upland rice varieties that evolved in highly acid leached Oxisols have resistance not just to aluminum but to the whole complex of factors (largely not understood) accompanying such an acid-soil environment.

There are old rice varieties that do well in a swamp ecosystem in which a high level of soluble iron influences uptake and utilization of many ions, which results in an unbalanced nutrition in nonadapted varieties. Does one screen in isolation for resistance to high soluble iron, or does one screen in the ecosystem and soil system in which high iron occurs? The difference in approach may seem subtle but it is, I think, fundamental. If the target is to increase yields in high-iron swamps one must screen maximum germplasm and segregants in such swamps. If the target is to obtain resistance to iron toxicity per se, then one refines a technique for that—but may end up with a variety that does poorly in the whole iron-toxic-influenced environment. This point is highlighted in an article on screening rice for tolerance to mineral stresses (63): "Developing techniques for screening of rices for tolerance to mineral stresses is beset with difficulties. First, a mineral stress in rice soils rarely occurs in isolation; it is usually compounded by the presence of other mineral stresses and by environmental problems. Second, the magnitude of the stress varies spatially and with time . . ." Although these statements are true, they reflect a desire to isolate specific toxicity from general physiological and environmental complexities

occurring in the toxic environment. Such isolation makes for cleaner research and more acceptable scientific papers. But it may inhibit progress in breeding toward obtaining what is really needed—yield increases under the existing adversity *complex*. Where there is an interaction between the primary adverse factor and other physical factors, screening for the complex can be straightforward, with later analysis of the mechanisms, genetics, and so on—while the farmer already benefits from increased production. Where there is an interaction also with pathogens and disease development it becomes even more important not to separate selection for an adverse physical factor from interacting disease effects. By combining selection for increased resistance to both blast and drought in rice it has been possible to raise blast resistance levels far above what was obtained by selecting for blast resistance alone under non-adverse environmental conditions (12, 13).

NATURAL AND INDIRECT SELECTION FOR STRESS ENVIRONMENTS Our concept of "optimum environment" influences our view of non-optimum or stress conditions. Sufficient water to kill wheat is optimum for rice and moisture optimal for maize is excessive for safflower. Thus, "optimum" is crop-specific and based on past natural and primitive man's selection of the crop and its progenitors, and generalizations are difficult.

In modern breeding programs also, there is much indirect selection for conditions less than optimum (49). Selection for good performance and yield in the target area for the new variety will automatically select for tolerance to the stress of that environment. Much of this process does not reach the literature, unless a new variety developed elsewhere is moved into the area and shown to be less tolerant to some factor of the new environment. Thus, sugarbeets and cotton developed in California were more resistant to oxidant air pollutants than varieties developed in less air polluted environments (49). This was an indirect location effect on selection, realized only after the fact. Similarly, wheat and barley varieties developed in the acid soils of eastern USA were more tolerant of aluminum toxicity than those from Indiana, where high available soil aluminum does not occur (29). Breeding soybeans for high yield under normal field conditions in Illinois apparently selected for superior midday water status in the new varieties (8).

There are many such examples that are seldom highlighted in discussions of breeding strategies and methods. All the intangibles and unknowns of an environment are represented in the selection process, be they soil chemical imbalances or toxicities, drought periods, low light levels, temperature extremes, air pollutants, or endemic diseases and pests. The degree of inadvertent tolerance or resistance obtained reflects the constancy and degree of stress, the diversity and size of the genetic base material, plus recombinational ease and extent.

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Two examples of indirect selection where unknown adverse but supposed "soil factors" were involved are especially interesting (13, 20). In southern Brazil wheat breeding started in 1919. When foreign introductions died before flowering it became evident that local cultivars had tolerance to some unknown condition. Farmers used no lime or fertilizers, and selection for lines yielding 1000 kg/ha was considered satisfactory. Later it was realized that this condition, termed "crestamento," was due to aluminum toxicity which inhibited root growth and thus phosphorus and water uptake. The same region was appropriate for soybeans, and as the limited soybean introductions had no aluminum tolerance, liming was started, which increased take-all disease of wheat in the rotation. Later, introduction of high-yielding Mexican wheats proved a failure (due to high susceptibility to aluminum) but even so, the importance of breeding for tolerance to aluminum was contested because of the supposed resolution by liming and the belief that tolerance factors meant low yielding ability. These mistaken ideas were not accepted by Brazilian wheat breeders, but they influenced Brazilian breeders of soybeans and maize, who ignored, until recently, breeding for such tolerance (20). Only later was it realized that Al-tolerant wheats were low-yielding because of various diseases, especially favored both by the climate that generated the high-Al soils and by interaction with soil factors in general. Recently, southern Brazil was chosen as one location for the FAO program on horizontal resistance breeding, and considerable success has been obtained in a very few years with massive recombination and holistic recurrent selection against all negative environmental factors (2). Even earlier however, the determination by Brazilian wheat breeders to select for yield under realistic farm conditions despite whatever stress the environment offered, even without understanding that stress, resulted in considerable progress. But because the soybean breeders did not do so and liming became necessary, a new set of conditions developed in the wheat-soybean rotations, and now even wheat varietal tests are performed on limed soils on experiment stations (20).

The other illuminating example of selection against an adverse condition was in Indonesia on rice (13). Dutch researchers thought an area in Java had a soil problem, called "mentek," seen through stunting and oranging of rice. Tolerance was found in a Bengal variety, and by using a four-location field screen of segregating populations from a cross made in 1934 the tolerant variety "Peta" was developed. This variety later became the mother of IR8 and thus it helped initiate the green revolution in tropical rice. In this case, however, tolerance to "soil sickness" turned out to be resistance to rice tungro virus and its vector. This was realized only many years later. These examples illustrate that if the environment provides a relatively consistent stress, of whatever nature, and if much germplasm is available and used wisely, resistance or tolerance will become an automatic component of selection for performance and yield for that environment.

DIRECT SELECTION UNDER ADVERSITY There are several areas of controversy in crop improvement relative to stress. One argument centers around whether genetic advance can be attained more readily by selection under stress or under optimum conditions (31, 32, 71). Good mathematics and abstract theory support the contention that selection for stress tolerance will result in reduced yield in nonstress environments, and in slower advance even for stress environments because of low expression of genetic variance and heritability (39, 71). However, the validity of the assumptions underlying the rationale is open to question. The diversity of biological phenomena implied by the words "stress" and "stress resistance," and the complexity of "adaptability" and "stability," make simple generalized conclusions suspect. In fact, the definitions of "adaptability" and "stability" are at the root of this basic controversy as the question in most papers is the relationship (among cultivars) in relative performance across a range of environments (in time or space) which vary in degree of stress from a theoretical optimum of zero. The more "stable" cultivars automatically respond less well to optimum conditions by this "relative performance" criterion of stability. For already-developed cultivars, regression of cultivar mean yields onto overall environmental mean yields has been used successfully to judge adaptation to different environments (26, 83). An additional approach would be to focus on an ecosystem as a breeding target, learn the range and proportion of various levels of stress in the ecosystem, and weigh selection in early generations (14) by this knowledge.

Certainly a plant pathologist would not agree that disease resistance (often considered by breeders as a type of stress) could be attained by selection in a nonstress (nondisease) environment. The belief that greater progress for high mean yields across a set of environments can be attained by selection under optimum conditions is based on both valid and invalid assumptions. High yield responsiveness (largely to N) is best expressed in ideal environments with high N. Such selections will usually do relatively better also as environments become less ideal, due to their high harvest index, and thus they support the belief. But they no longer support it when moved to a location where drought is severe, or where a new pathogen, aluminum toxicity, or air pollution are present. Little breeding effort (as compared with cultivar testing) has been expended specifically for stress environments, and thus comparing normal cultivars with the few cultivars actually developed for stress conditions is like comparing a model-T Ford with a current model. They are invalid comparisons.

The reluctance to breed for stress conditions maintains the status quo of superiority of materials bred in "optimum" conditions. Moreover, this situation supports the bias that materials bred for stress *must* be (70) less good in optimum conditions than those bred for optimum conditions. This idea cannot be a universal truth biologically or genetically. A few genes for stress resistance

(to nutrient toxicities, deficiencies, disease, drought) need not mean lower productivity in nonstress conditions—they may not even be switched on in nonstress environments. The goal is to combine stress resistance genes with high yield potential under good conditions. Seen thus, the problem becomes how to challenge in *early segregating generations* to detect both stress and nonstress productivity. We need to improve methods with a strategy based on sound biological and physiological principles. However, an interesting and logical concept was advanced earlier (60) that should be followed up: that species and populations evolved on infertile or droughty sites have slower growth rates, this characteristic giving evolutionary selective advantage for adaptation to limiting levels of environmental factors in general.

Calculations of low heritability and observations of low expression of genetic variance under stress are rooted partly in the methods used and the conditions of the experimental environment. With absolute uniformity and quantification of stress challenge I see no inherent reason for low heritability or poor repeatability of results. The variable microenvironments where assessment is made and the differing levels of stress in a repeat trial make for the low values of heritabilities and genetic variances. Methods need to be improved to reduce this internal variability and to quantify the range of stress so that segregating materials can be evaluated across this range, with subsequent recombination from the extremes.

There will be types of stress and stress resistance that preclude high relative yield in both environments, but these will be special cases, understandable on the basis of sound crop physiological principles. Short determinate soybeans ideal for optimum conditions are less able to compensate for early season drought than standard height cultivars (18). Drought resistance mechanisms exist that preclude high productivity in high moisture conditions, such as for CAM pathway plants. Sufficient height in cereals under severe drought conditions may result in excessive tallness under full moisture and hence in low potential yields in normal areas.

Few reports have appeared of selection from the same cross being done under different levels of deviation from optimum conditions with later comparison across the range of selection environments. An exception was selection from a winter wheat cross in Japan at three fertility levels; more lines superior for adaptability at all three levels and with higher heritability of yield advance were obtained at the lowest fertility level (32). For rapeseed, advance in yield in a droughted environment was greater if selection for yield was practiced in a droughted environment and weighed with an appropriate selection index involving harvest index (65, 67).

In contrast, in studies with oats (31) a droughty, low fertility location gave less discrimination and lower heritability. A perusal of such papers and my own unpublished experiments with rice and maize lead me to believe that the

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problem with selection under stress environments is mainly one of nonuniformity of the stress in the experimental field. Innovative approaches to reduce this variability are needed. Additionally, improvement should follow recurrent reciprocal selection among progenies derived from crosses made from the best selections from representative farm acreage extremes of environments occurring in the target area for a new variety. This approach means that the target will be defined within more narrow limits than the theoretical maximum stress and theoretical optimum growing conditions. There are two basic sources of error: (*a*) internal plot variability that reduces discrimination and heritability of selected phenotypes, and (*b*) movement of selected genotypes into environments too different from that where selection was made.

A second area of debate in stress research concerns the extent to which one must understand the physiological or biochemical mechanisms controlling resistance responses in order to make progress in breeding (7, 64). The same debate also applies to disease resistance (79) and extends to the genetics of disease resistance (54) in relation to obtaining greater disease resistance.

A wish to understand plant biochemistry, physiological control of resistance mechanisms and the underlying genetics is laudable. To believe, however, that this understanding is essential before substantial breeding progress can be made is not true, and it may engender a self-defeatist attitude that will inhibit progress. It then becomes easy to say we don't know enough, and to expect others in more basic research to supply us with selection criteria. We thus avoid doing innovative research that would enable us to select for high stress and disease resistance and to combine these with high yielding ability.

For outbreeding crops (or inbreeders that can be made to perform as outbreeders) the potential of gene recombination is so great that there is little possibility that reductionist techniques based on specific mechanisms can ever outperform holistic selection to the whole environmental complex. The main needs are to improve uniformity of the selection environment and to reduce the error between selection environments and farmers' fields. Farmers' fields will have some range of variability, which should be studied for incorporation into the selection (and recombination) procedures and environments (14, 38).

The more internally uniform a selection environment can be made, and the more an experimental design can reduce internal variability, the less need there is for reductionist techniques to divide a gross stress into different mechanisms of resistance and to select for each mechanism separately in isolation. Small additive variances visible phenotypically will be genetic and heritable. This makes breeding in developing countries easier, as expensive equipment and analytical methods, often applicable only to very small numbers of plants, are not needed for refinements of field uniformity, improvement of plot designs, and recombination enhancement which will improve genetic advance.

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Mineral stress The mineral excesses and deficiencies are probably the easiest of the stresses to breed for in terms of few mechanisms of resistance and ease of creating internal plot uniformity for stress. Where reductionist techniques should be easiest, such as seedling tests for tolerance or resistance to a pathogen challenge, they have resulted in major errors of nonrepresentation of the complexity of disease epidemic development and of pathogen evolution (14). These biological discrepancies seem to be absent when measuring tolerance to physical factors such as toxicities of aluminum or other minerals, and thus here they should be more potentially useful. But even here the interaction with other elements makes questionable such isolation of specific tolerance from related effects in an uncertain environment. Clark (16) lists the patterns of change of different elements in sorghum tissues that occur with an excess of a single element. The frequency of change (either higher or lower) with 21 different element excesses ranged from 5 for K to 11 for P in leaves and from 9 for Zn to 17 for Mn in roots. Indeed, the complexities of interaction are great and will provide physiologists with decades of research ammunition. But these complexities need not inhibit breeding for ecosystem adaptation and high productivity in an ecosystem. Rather than breeding for resistance to Al in isolation one needs to breed for performance on ancient acidic soils where, although Al toxicity occurs, many imbalances are generated, including low calcium and an aerial environment conducive to many pathogens. Farmers will require productivity in the face of all the interrelated negative factors.

How is it possible that one may see yellow iron-deficient oat (16) and soybean varieties alongside dark green varieties, both developed recently in good breeding programs? The answer is simple: the green varieties were selected in soils with a high pH, the yellow varieties were selected (and were green) in a soil of low pH. The Fe-inefficient cultivars became recognized—and were a problem—only as they were moved elsewhere onto soils where differing pH radically alters microelement availability. So, in the tropics and subtropics, areas of similar soil pH and geomorphology can be grouped as an ecosystem breeding target and also searched as a source of similarly adapted germplasm. Within this soil group other subdivisions can be made when their characteristics are accurately measured, such as Ca and P level, Al level saturation, and CEC. But in general, a breeder would be interested in materials from the main group (low pH) first and should let local details be sorted out initially by the germplasm. Moreover, as low soil pH results from high rainfall levels over time, one can expect correlative disease resistances to have evolved (say to fungal leaf pathogens) at least so far as nonspecific resistance is involved.

Drought stress Research on drought has been the most extensive in looking for reductionist factors that might be used in selection (4, 27, 40, 64, 66). There

are so many different physiological processes and morphological and phenological characters affecting plant water status and stress under reduced water availability that breeders find it difficult (probably rightly) to rely on a simple reductionist selection factor to detect "drought resistance." Quisenberry (64) deplores the failure of breeders to utilize the many mechanisms identified by crop physiologists and attributes this to "(*a*) difficulty in measuring the mechanism, (*b*) lack of convincing evidence to support a relationship with increased productivity, (*c*) insufficient knowledge about inheritance, (*d*) poor communications with crop physiologists, and (*e*) a sense of helplessness associated with the phenomenon of drought."

It may well be that reductionist approaches can improve what is now done in selection for drought resistance. To be most useful, however, specific drought resistance traits will have to be detectable for individual plants *within large populations of plants in breeders' plots*. Different drought resistance mechanisms may work against each other and some less-than-maximum expression may be the ideal in an overall whole-plant integration of productivity in the face of a variable stress. Thus the breeder may rightly prefer to rely on yield or yield plus harvest index under some degree of drought stress rather than relying on leaf water potential or xylem vessel diameter or another specific criterion of a subsystem for selection.

Several breeders have advocated the use of leaf temperature (low) under a drought challenge as a selection criterion, and this has been refined for large scale use (5). Although this is a specific criterion superficially appearing to be reductionist, it is really an integrator of many subsystems affecting plant water status. An even more innovative technique has been developed to select for tolerance to drought stress (6) and to *Septoria* leaf blotch (88) that seems to satisfy a logical definition of tolerance and the need to have a uniform challenge applied at a specific phenological stage. Wheat is defoliated with magnesium chlorate on a specific day after flowering. Subsequently, lines that more effectively fill the grain are identifiable and are highly correlated with lines found resistant to drought by more cumbersome methods.

But for developing countries in general, it seems to me that greater effort to do the following would yield results most quickly: (*a*) accurately assess the degree and pattern of drought and its variations in the target growing area; (*b*) develop a very uniform soil environment for field plots which expresses soil/water relationships uniformly as water is extracted; (*c*) during periods or in areas where rainfall absence allows drought to occur, utilize a line source sprinkler system (33, 41) such that germplasm lines can be assessed across a gradient of stress; (*d*) assess maximum germplasm across the gradient, picking the section of the gradient representing the range of the drought target and selecting lines performing maximally within that part of the gradient; (*e*) make maximum recombination among selected lines, assessing F_2's and F_3's in

two uniform environments representing the least amount and largest amount of drought stress of the target environment; *(f)* assess F_4's to fixed lines across the gradient and repeat the recombination, thus following a recurrent selection breeding system.

Breeders in much of the tropics are in the most favorable position to make progress as two selections (and up to three generations of most food grain crops) can be grown per year, with one selection generation completely controllable for drought stress (with the proper irrigation system) in the dry season. This generation is immediately followed by a rainy season with its unpredictable drought but with its close approximation to farmers' conditions with realistic levels of diseases, insects, and other adversities that interact with the major stress.

Resistance to Diseases and Pests

This topic is complex and full of conflicting views (14). Much of the problem concerns dissatisfaction with durability of resistance, when previously bred resistant cultivars become susceptible.

In a practical breeding program two aspects should be considered and separated clearly: 1. How much resistance is really needed for the potential ecological (farm) target? 2. How much durability is needed for the level of resistance that is otherwise satisfactory? If one addresses these two questions directly with good logic, knowledge, and intuition, this aspect of a breeding program should become straightforward. However, the continued preeminence of disease (and insect) resistance in breeding programs generally is a signal that this issue has not been satisfactorily resolved in spite of all the efforts and all the papers on disease and insect resistance. Thus we must acknowledge openly the inadequacy of past approaches and ask what can be changed to advantage.

Two points are considered fundamental and they relate to the two points above: 1. The concept of resistance/susceptibility should be considered as only one aspect of the ecological relationships that occur within a crop ecosystem, in which man's activities are a major part. 2. Any existing complex of relationships in host-pathogen population interaction has evolutionary roots and an evolutionary future. Breeding is a manipulation of the evolution not just of the crop, but of many other organisms as well.

The first need is to establish a target location where a new potential variety would be grown. Eight steps have been proposed for practical breeding programs in the tropics (14). These steps are:

1. Ecosystem and farming system analysis.
2. Pathosystem analysis.
3. Choice of selection sites.
4. Analysis of the germplasm base.

5. Selection of parents.
6. Recombination (crossing).
7. Pest/pathogen challenge, breeding plot designs, and selection.
8. Getting new varieties used.

Each of the eight deserves examination in detail, but this is impossible here. However, the types of error and their diversity in relation to pest/pathogen challenge and selection are emphasized. One should be able to see how individual plants in segregating populations suppress population growth of pest or pathogen, and how they suppress the development of symptoms. As these relationships also reflect environmental conditions and the initial challenging dose, one must know the pathosystem well enough to make these factors both realistic and successful for normal disease development. One must obtain disease, but not favor disease unrealistically and obscure minor genetic differences in plant response. The longer-range target is to estimate how effective selected single plant performance will become when present as a homogeneous population of similar plants. Suppression of population growth of pest or parasite or of the development of symptoms or damage during ontogeny is a dynamic process over time. Therefore, a static single instance of observation for "resistance" is a poor reflection of the developmental process.

Even with repeated observations, however, there are three major sources of error: (*a*) the heterozygous nature of the plant on which judgment is made (for nonclonal crops); (*b*) the difference between single plant performance in an unusual setting (the heterogeneous populations in breeders' plots) and performance of a homogeneous population in relation to "r" in the future farmers' fields; and (*c*) the genetic structure and variability of the challenging pathogen population in relation both to host plant resistance genes and to the pathogens' potential variability.

The problem is to recognize clearly the possibility of errors of three distinct types and to try to reduce each of them in the field. Environmental variance is a component of each of these errors, and many statistical studies of genetic-environment interaction (30) and heritability (h^2) have determined that heritability of complex characters is often quite low. However, statistical treatments of heritability usually do not unravel specific sources of error resulting from different biological phenomena in the field. Since yield and disease resistance are interrelated yet dependent on different biological phenomena, it is useful to affect field manipulations to minimize major sources of error in situ.

HETEROZYGOSITY ERROR This error is not a problem for clonal crops as the heterozygous response is maintained intact by cloning. For seeded outbreeders the error can be minimized by selfing and progeny testing for a generation or

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two, to expose hidden susceptibility. The problem is greatest for seeded inbreeders in which unfixable heterozygosity is involved in judging vigor, yield, and disease response of F_2 (or F_1 of top crossed) plants. Several studies in wheat have indicated that selection within F_2 is no better than random; the solution is to select only among F_2 populations, bulking the best and selecting plants only in F_3 or F_4. This forces great seed carryover into F_3 or F_4, making these generations very large. It is not clear, however, how consistent across species is the inability to select positively in the F_2, nor how much this inability might be rectified by different field designs. Research on both points is needed for tropical crops. In fact, it is not known how much of the inability to select positively in the F_2 is due to heterozygosity per se, or to interplant interference among heterogeneous phenotypes, or to alloinoculum bias in interpreting disease response. These latter problems can be reduced by wide spacing, which, however, introduces a new problem—that of relating wide spacing performance to normal close spacing in farmers' fields. Again, research is needed on this question. Wide spacing can be combined with reduction of environmental variance by gridding the field or by the ultimate grid of a hexagonal design with an internal check in each hexagon (24, 25). This hexagonal design provides each plant with equal space and identical relationship with all neighbors, one of which is always a standard check, against which performance can be compared.

HETEROGENEOUS ERROR IN RELATION TO PEST/PATHOGEN BUILDUP Disease will not develop at the same rate on a plant surrounded by neighbors genetically different in resistance as on one surrounded by genetically similar plants. This point is the basis of recent work with mixtures to reduce disease (85). In breeders' plots in segregating generations individual plant performance will not be the same as later in solid stands, even excluding the heterozygosity inherent in an F_2 or F_3 generation. This difference is due purely to epidemiological factors of inoculum buildup and dilution. To minimize the alloinfection component of this error, widespacing was suggested for F_2. This can be repeated with hexagonal planting in F_3 but it becomes very cumbersome if one desires family selection. A different design has been used successfully for rice blast (12). A challenge of inoculum is presented at one end of long plots, perpendicular to them so that a gradient effect is obtained in time and space. The challenge is a spreader band of seedlings of diverse susceptible genotypes. This spreader can be infected either naturally or artificially from different diseased varieties in the area. Inoculum impinges on nearby plants and begins to develop as autoinoculum, family by family, spreading down the plot. Depending on the environment/family-genotype/pathogen interaction, selection may take place at any distance from the spreader at which optimal differences are visible.

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Alternatively, inoculation of *all plants* is carried out, but at low doses, so that polycyclic autoinfection and inoculum production over time become major factors in judging resistance. This approach may be especially useful where disease/pest buildup is spotty with gradient challenge, and is especially useful for vectored systemic pathogens, such as viruses. However, for polycyclic fungal diseases, several advantages accrue with the gradient method for families. To make the low-dose challenge work well, some background research is required to determine dosages that best reveal genetic differences in resistance, yet still prevent escapes. An inherent problem is that as resistance increases a given dose will result in fewer diseased plants (more escapes). This still permits selection among families on the basis of frequency of diseased plants, but there is a fine line between too low a frequency and too many escapes. It is not easy to know whether one is dealing with an accidental escape or an escape due to higher resistance acting on ease of infection.

Careful study is required for each case to make selection accurately reflect resistance. If disease development during full ontogeny is to be revealed, dependent on autoinoculum generation and release, the artificial challenge should be designed not to obscure these aspects.

In both gradient and low-dose challenge methods, interplot interference among families can be reduced by interplanting a neutral crop and/or increasing spacing. Interplant interference within families can be reduced by increasing spacing.

ERROR DUE TO PATHOGEN POPULATION STRUCTURE AND POTENTIAL VARIABILITY This cryptic error has two components, both essentially contributed by VR and by pathogen genes overcoming VR host genes. The first component of this error can be illustrated by an F_3 family in which different plants have different numbers of VR genes and the challenging fungal population (say blast on rice) present on a mixed spreader band has individuals with different numbers of vertical genes for pathogenicity. Spores with four vertical genes are present and they infect plants with four matching VR genes but do so late and provide only a few lesions. These plants develop only two cycles of infection before the epidemic stops and, as they appear only slightly diseased at heading, are selected over their neighbors because they are less diseased. Although highly susceptible, they produce apparently resistant progeny due to a repeat of the same phenomenon since major local inoculum sources are not from four-VR gene hosts. Such lines may be brought out as a new variety only to collapse in a few years.

The second component of this error is less subtle, where no matching spores are available in breeders' plots or nearby areas, and a line has no lesions and is promoted as resistant. After several years of large acreages, disease appears

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and the following year a major epidemic ensues. A very rare fungal mutant or recombinant was selected that was not present or detectable earlier.

This problem has been most intractable for the inbreeding small cereals with their polycyclic coevolved pathogens. Robinson (69) has suggested a solution of mass polycrossing with all parents being VR-susceptible to a single race composing the major challenging inoculum. Selection is then only for plants with some symptoms, presumably due to HR. This problem is at the heart of debate over VR and HR. It is, in essence, a question of how to breed crops so as to slow pathogen evolution (45). It will take new research and many years to resolve the issue. Meanwhile, are there any practical approaches?

For rice and blast two approaches have been taken (13) and are suggested for other intractable "breakdown" type diseases. The first component can be attacked by observing less-diseased plants often and carefully during an epidemic. If disease builds up rapidly from only a few initial lesions (but still remains relatively low) they can be considered too susceptible. If one is uncertain to what extent a low disease level is due to a low initial compatible inoculum dose, the question may be resolved for the few lines being promoted by isolating the fungus (or lesions) and challenging the next generation with this possibly specialized inoculum. If the specialized inoculum can cause only slight disease, one assumes that there is high HR. The second component of this cryptic error can be eliminated by avoiding all plants that show no disease whatsoever.

A quite different approach is to carry out a specialized breeding program with much pathologist involvement in which different VR genes from different source parents are identified, and pyramided or rotated (35). This procedure might seem simple but it is difficult to carry it out accurately and difficult to stay ahead in yield competition.

The above three types of cryptic error are influenced by the overall environmental conditions. Often the environment does not favor disease in breeders' plots, so the magnitude of any one of the three errors cannot be estimated. Selection is done blindly (on plant type and yield potential), which is more often the case than one usually thinks.

Success of any selection involving resistance depends upon environmental conditions over time which allow normal (but slightly over-favorable) disease or pest buildup. It also depends upon high heritability of selected traits, which in turn is dependent on uniform (constant or gradient) challenge with a "realistic" dose and absence of escapes. In general for the tropics, I recommend letting nature do the job, but being innovative in manipulating nature to advantage. Areas can usually be found where a major pest or pathogen develops consistently annually, and screening can be carried out in such areas at least once a year. Alternatively, biological/ecological studies may indicate simple beneficial

manipulations of the environment, including extra nitrogen and irrigation, or growing susceptible host plants adjacent to screening plots and in the off-season. For pathogens that can be grown in the laboratory there is a long history of successful artificial inoculation. For viruses and MLO's, accurate identification and maintenance in stocks is often difficult in the tropics. This problem has recently been reduced by development of a low-cost, insect-proof screenhouse for raising plants at ambient temperature (71). Costly greenhouses and costly cooling equipment are not required.

For insect pests (including virus vectors) in the tropics, successful rearing is still in its infancy. In temperate zone programs it is still uncommon, although for corn borer resistance work, millions of egg masses are raised each season by the USDA in Iowa and distributed to corn breeders throughout the country in a well-organized scheme.

Simpler schemes can be developed in the tropics and used on a smaller scale for careful checking of field results or for off-season generation-advance and screening. Large low-cost screenhouses that are not insect proof but do conserve insect populations have been successfully used for maize and rice stem borers and for developing virus resistant maize (78).

Conclusion

Developing countries contain both the centers of origin of our major crops and great genetic diversity useful for local ecosystems and adversities. Great improvement has been made in plant type in the small cereals generally, giving nitrogen responsiveness and higher harvest index. These advances were accompanied by an objective of broad adaptation and a few cultivars have been extended to vast acreages in the tropics and subtropics. Now there is a new opportunity, for the small cereals and many other crops, to concentrate on maximum adaptation to local adversities, of which there are many. Breeders and their colleagues in developing countries are in the best position to make this advance because of the diversity of local landraces evolved for local conditions, and/or the possibility of matching a local ecosystem and its adversities with a similar one where the crop genetic diversity evolved. Moreover, the possibility of two to four generations per year, with manipulative control of drought stress in the off-season, should enable the tropical breeder to make rapid progress. There is a need to recognize the local opportunities, increase local agroecosystem and pathosystem analysis, improve strategies and improve methods to increase uniformity of stress in breeders plots where plants are selected. There is also a great opportunity to apply hybrid breeding approaches to several tropical crops to increase not only yield potential but stress and disease resistance. Greater effort is needed on horizontal resistance, to reduce the risk of collapse of new varieties, which poor farmers and poor societies cannot afford.

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