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FITTING CROP GENOTYPES TO ABIOTIC STRESS ENVIRONMENTS: PROBLEMS AND PROSPECTS

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Plant breeding efforts have substantially increased yields mainly of crops grown under (near) optimum conditions, especially during the last half century. This, with or without deliberate efforts, has resulted in an increase in adaptability of cultivars and stability of grain yields, even in abiotic stress environments. In order to ensure nutritional security for the growing population, especially in the tropics with its dwindling and degraded land resources, we constantly need newer crop production technologies. Even in highly developed temperate agricultural systems, 60 to 80% of the seasonal variation in crop productivity is attributed to weather fluctuations (Thompson 1975; Boye 1982). In the tropics where the intensification of crop production and extension of crops to more marginal areas are the order of the day, increased research on crop productivity, especially in stress environments is called for.

In the short run, crop management may be as efficient in achieving stress amelioration as is genetic improvement. Because certain plant traits or characteristics are now recognised as important for abiotic stress resistance of crops genetic improvement as a means of stress amelioration is becoming more feasible. In the long run farmers must be given options combining both genetic and management components of crop production in dry areas. These options are briefly discussed here.

The extent of adaptation, is limited to the ranges of environmental factors (e.g., minerals or water availability) in which plants have evolved during their existence. When subjected to excess (e.g., water logging) or deficiency of these factors (e.g., nitrogen deficiency), the plant is regarded to be under stress. For example, use of high population densities and nitrogenous fertilizer will result in higher demand for water and other nutrients, as well as on radiation to sustain maximum growth rates. Hence definition of 'stress' in agricultural context, is any environmental condition that results in limiting a crop (and plant) for realizing its potential for growth, development, and reproduction. Optimum conditions for field crops can not be fully extrapolated from results obtained with the single plants in controlled environments, and vary significantly with developmental stages, and the changes in other significant elements of the environment.

Stress physiologists generally choose the most limiting factor for their study, but application of such studies may not have sufficient relevance to practical crop production unless the nature and quantum of interaction with other factors is also elucidated. Most physiologists study the individual processes in isolation, and poorly quantify the relative significance of each process in stress tolerance. Processes such
as cell enlargement and cambial activity respond rapidly to water stress than metabolic processes or photosynthesis. For example, in sorghum, brief stress periods during differentiation of pistil and stamen primordia can irreversibly reduce seed number and yield, but photosynthesis may return to normal following relief from stress (Eastin et al. 1983). Although cost-benefit-ratios of adaptations to stress by specific processes have been investigated by several (Gutschick 1987) there are only a few instances where they have been applied in a practical crop improvement program. Relative merits of adaptations also change with age; for example, increased root-shoot ratios as a means of drought avoidance are agronomically more sound at seedling stage than that at panicle development or grain filling stages.

CROP IMPROVEMENT FOR STRESS RESISTANCE

Admittedly our knowledge of both physiology and molecular biology of stress resistance is too meagre to be readily applied in crop breeding, and hence need continued search for new knowledge, and refinement of existing knowledge and techniques. The genetic diversity in a major food crop, like sorghum, & the environmental conditions under which it is grown are wide enough to give hope to make significant headway even with the conventional approaches, and working at plant and crop levels. Hence efforts to integrate the stress physiology research into the ongoing breeding programs is taking precedence over the long range objective of understanding the basic mechanisms involved in stress resistance.

The genes for yield, adaptability, and resistance to stress are separate, at least at some of the loci, and hence stress resistance can be reasonably combined with yield and adaptation without unduly sacrificing yield potential or quality (Seetharama et al. 1982). The methodology for adaptation to environmental stresses is same as that for adaptation to biotic stresses. However, the former is more complicated as resistance to biotic factors generally have no or less yield penalty than the same in case of resistance to physical stress factors. The approach to solve the problems related to yield limitations imposed by physical stresses include (i) understanding the specific problems, (ii) establishing methods to screen sources of resistance, (iii) determining whether useful genetic variability for adaptation exists or not, (iv) attempts to select for improved adaptation, and finally (v) field evaluation in the target region on an operational scale.

The above stepwise approach is illustrated and discussed in the following sections using the problem of crop establishment.

IMPROVEMENT FOR CROP ESTABLISHMENT

Many factors—edaphic, atmospheric, and biological—exert their influence at different times from sowing to harvest of crop. Seed germination and seedling
emergence are two important stages susceptible to these factors and may limit crop production. This phase of crop establishment has to be examined as a good seedling stand forms the first step towards the realisation of a good crop and high yield under local conditions. We provide few examples of such a treatment of the problem, below.

**Soil crusting**

Soil crusting could limit seedling emergence and establishment. A technique was developed in an Alfisol (with 54% coarse sand in the upper 3.1 m) at ICRISAT Center which crusts naturally when rainfall is followed by bright sunshine (Soman et al., 1984).

The soil is disced and rotovered. Ten 1.5 m wide broad bed are prepared between the sprinkler lines and smoothed with a bedshaper. Seeds are sown at a specific depth (50 mm) with four-cone commercial planter in 2 m long plots. After sowing, the beds are again smoothed to make the soil surface even. Thirty five mm of water is then applied using two parallel lines of the sprinklers. The plots are left to dry for three days, after which the surface becomes firm. The crust in the control treatment is broken without damaging the plumules of germinating seeds using a roller with nails mounted on it.

We measure crust strength, bulk density, moisture, and temperature of the soil and record the number of seedlings emerged in both the crust and control treatments. The genotypic variation is assessed on the ability to emerge through crust over different years.

**Soil temperature**

Soil surface temperature similarly inhibits seedling emergence. This problem may occur more widely than soil crusting in the tropics. In India, and West Africa soil surface temperatures commonly exceed 45°C which inhibit the emergence of seedlings resulting in poor stand.

Measurements of germination in constant temperature incubators are not necessarily relevant in the field where soil temperatures vary diurnally. Therefore development of a technique was necessary to study response to soil temperature at seedling emergence where soil water was not limiting and surface crust absent.

The technique for above study is described in detail by Soman and Peacock (1985). Briefly, porous clay pots, 0.3 m in length and 0.1 m in diameter, are filled with sieved top soil (10-20 cm depth) from an Alfisol field. The pots are placed in a tall water tank such that only the top 0.07 m of the pot is above the water level, The
soil surface is 20 mm below the top of the pot. The soil in the pots were heated by lamps fitted to a frame above the tank. The temperature of the soil surface can be altered by varying the height of the frame above the soil surface, to obtain temperatures of 35, 40, 45 and 50°C measured at 20 mm depth below the soil surface. The wet soil column in the pots provided a steady water supply for the seedlings while allowing them to be affected by the temperature of the soil. The design is simple, and the total cost of the unit is approximately one tenth of a commercial growth chamber.

Seeds are sown at 50 mm depth in the soil in the pots. Soil temperature is measured every two hours in each pot using copper-constantan thermocouples. Water is added to the tank daily to maintain a constant level. Emerging seedlings are counted 5 and 6 days after sowing (DAS), and the percentage of emergence calculated based on the number of seeds sown. This figure is used to differentiate (or group) genotypes.

Soil moisture

Lack of sufficient moisture in the soil and inhibits both germination and emergence thus affecting crop establishment. A technique was developed in the field where a line-source gradient irrigation (~30 mm, maximum near the sprinkler line; 0.0 mm at 12 m away from it on either side) was applied to seeds sown in dry soil (ICRISAT 1987). This set up, under a high evaporative demand condition in the field simulates a series of (2 to 4) combinations of soil moisture levels and soil temperatures. This technique provides an example of an interactive environment where more than one factor is involved; the level of interaction can be controlled by the experimenter by choosing the appropriate level of irrigation, type of soil, and other factors.

The problem solving approach elucidated above in three case studies have several distinct features. Not only the identification of desired traits that are present in widely varying genetic background, but also the availability of a particular trait in combination with others are emphasized. This latter information could be very useful in fitting genotypes for problematic environments.

CROP IMPROVEMENT FOR DROUGHT RESISTANCE

It is now appreciated that timing, intensity and probability of drought and its effect on crops - both in quantitative and quantitative terms - can vary widely depending upon locations and cultural conditions. Hence crop genotypes and cropping systems suited to the local conditions have been duly emphasized. Better analysis of climatic and edaphic data, and synthesis of knowledge of various crop production aspects through crop simulation modeling (Huda et al. 1986) have been increasingly put to practical use.
Progress in breeding for drought resistance in crop plants is still not satisfactory, especially if we exclude drought escape by early maturity in many recently released cultivars. While some may still consider that breeding for drought resistance is a waste of resources (Arnon 1980), a more realistic approach is possible if one is willing to accept the reasons for slow progress in this field. A more pragmatic approach of combining the traditional fragmented approaches of empirical screening (numbers game of breeders), and isolated studies on a few selected components of drought resistance believed to contribute to growth under stress (mechanistic approach of of physiologists) is called for (Seetharama et al. 1982). Multilocation and multiple testing of a large number of selections is the backbone of most breeding programmes; however, timing and severity of stress over years are seldom sufficiently uniform to provide reliable, and repeatable test environments with respect to moisture, as well as other principal factors essential for determining the degree of success. Use of rainout shelters and dry locations where one can manipulate stress profiles are helpful in simulating most probable conditions of target environment. Drought intensity for selection should be decided based on expression of critical response studied, and the probability of that response being useful across different growing seasons.

In young crop improvement programmes empirical screening seems to work but soon one would find out it is difficult to make further progress without better techniques. In spite of the limitations in the mechanistic approach, there are some definite advantages in using physiological selection criteria as outlined in Table 1. Knowledge of breeding for specific physiological or morphological traits is still fragmentary, and much of the available information has been inferred from experiments or breeding programs designed to answer more general questions. Though it is possible to identify useful traits with respect to physiological approach for breeding for drought resistance, the elucidation of complex interactions among the traits, and the environment is quite difficult and expensive. This explains why physiological approach is not adequately practiced.

The trade-off between yield potential and drought resistance is well discussed (Seetharama et al. 1983). As no immunity to physical stresses is possible, the question one would ask is how much less susceptible chosen genotype can be. Only a few characters, that too to a specified degree, can be selectively ‘switched on’ (induced) under stress, thus avoiding drainage of plant’s energy for this adaptation, or opportunity to increase productivity under good condition of growth. Leaf rolling serves as an example of such a trait, but one should note that its significance is only within certain ranges of stress, and useful only if conditions are expected to improve later.
Table 1. Advantages of physiological selection criteria

1. Yield is generally affected by many factors of the environment exercising their influence on crops throughout the growing season, but individual traits are affected mostly by the events occurring during the (shorter) time periods during which such traits are expressed.

2. Relationships between component traits and yield may not be always be linear, or even absent; such traits as those enabling plant survival or establishment are still valid as selection criteria.

3. Compensation between some component traits are always possible; hence their real role can only be known when studied independently; this should be done before attempting to assign a definite role for the component traits in yield formation.

4. Yield per se is not heritable, but component traits or processes are. Yield measurements, especially in poor environments, are highly variable, and hence unreliable and may not be cost-effective.

5. Yield assessments under severe or long-duration stress situations is unreliable for comparison of genotypes or agronomic treatments. Same magnitude of yield reductions can result because of entirely different reasons or mechanisms.

Table 2. Considerations in selecting physiological traits for crop improvement for drought resistance.

1. The range or set of conditions under which the character is useful (or counter-productive) should be known.

2. The character must have a demonstrated role in drought resistance.

3. Measurement of character must be simple, rapid, cost-effective, and preferably capable of being used during early growth stages.

4. There must be sufficient genotype variation for the character.

5. Assessment of character should preferably involve single (set of) measurements rather than multiple measurements.

6. Reasonable/sufficient knowledge about the inheritance of the character and its interaction with other characters, and adverse side-effects (or pleiotropic effects) must exist.

7. The inclusion of the character should fit into the over-all plant improvement strategy for the target environment.
As the number of traits contributing to yield stability under drought are numerous (e.g. of more than 20 in sorghum, (Seetharama et al. 1982) environment following the criteria listed in Table 2. The desirable type/level of it is essential to carefully select them to suit the needs of each target drought resistance (or its component traits) for one production area may be different from another depending upon the average level of drought (and temperature, nutrients, etc.) prevalent in the area and crop husbandry practices. The usual method of establishing usefulness of a physiological trait is to incorporate it into an adapted material and compare its impact on agronomic performance of lines in which the trait is expressed or not expressed (near-isolines). Physiological process/adaptation considered individually are not necessarily correlated with yield. Broader perspective of crop production in the target area should be developed simultaneously to detail interacting factors limiting yield (Sojka 1985).

Equal yields could be achieved by different mechanisms, and hence the need for physiological analysis of yield under stress continues to exist. With a highly selected battery of tests uniquely suited to the needs of a target environment, the researcher can ensure that the parents chosen for crossing have several desired characteristics. Care must be taken to ensure that the progenies retain useful combinations of traits in them by manipulating reasonable repeatability of stress pattern and severity of the target location, each year during varietal development.

Three major research areas relevant to productivity under stress environments are recognized: (1) manipulation of crops and their environments in ways which avoid or reduce stress injury, and increase productivity, (2) exploitation of genetic potential by developing new cultivars of crops adapted to environmental stress, and (3) elucidation of the basic principles of stress injury and resistance in plants, and evaluation of the scope and nature of stress damage to the crops, in order to refine our ability to deal with crop production problem in the future.

Though breeding for stress tolerant genotypes with agronomic elitesness is the ideal solution, most researchers would attempt the crop management approach in the short run, especially under highly variable and harsh environments. The biggest challenge is to bring together diverse adaptive features showing complex interactions with an array of crop growth environments faced with stresses of different kinds varying in space (plant organs) and time (growth stages). Physiologists must also note the differences between tests for presence of a trait or response associated with drought, and field tests that finally prove the stress resistance of a cultivar. Attempts to integrate many facets of plant activity under stress should be actively considered while working on plant parts or processes under stress.
REFERENCES


