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SCREENING FOR DROUGHT RESISTANCE IN CEREALS : A SOIL SCIENCE PERSPECTIVE

R. E. SOJKA AND A. BAUER[1]

USDA-Agricultural Research Service
Soil and Water Management Research Unit
Route 1, Box 186
Kimberly, Idaho 83341, U.S.A.

Man's appreciation for the relationship between water and crop production predates recorded history, and has been linked to the rise of most of the world's ancient civilizations. In the early 18th century A.D. the English clergyman Stephen Hale attempted to quantify effects of environmental variation on plant water use and growth[1]. The formulation of Mendel's laws of heredity, and Wollny's establishment of the first modern principles of soil physics, both late in 19th century, set the stage for the 20th century's assault on drought susceptibility of crops.

Unlike breeding for such relatively simple traits as color, size, morphology, or even pest resistance, breeding for drought resistance has proven substantially more elusive. This results principally from the dynamic interaction of many hereditary and environmental factors which together bring about the plant processes and conditions that result in quantity and quality of growth and yield[2]. Furthermore, the breeding effort may be hampered by a continuing failure to distinguish between drought resistance *per se* and the collection of traits that can be associated with drought resistance[3]. This difficulty reflects what is perhaps a more fundamental dilemma, namely the lack of a universally accepted definition of drought resistance. The authors would also point out the need to assess soil-derived sources of variability in field evaluation of cereal responses to drought.

Understanding Drought Resistance

Darwin's insight that success and proliferation of a species is related to survival of its genetic makeup in a harsh and competitive environment is a guide to understanding the screening for drought resistance. Regardless of what approach a breeder takes in assembling the genes that constitute an individual cereal plant, the test of its drought resistance lies in the survival and proliferation of those genes. Fortuitously, in cereals gene survival and proliferation are synonymous with grain yield. Cereals are not generally grown for vegetative biomass, and, being annuals, multiyear survival and production need not complicate the assessment of its drought resistance. Also, fortunately, each cereal plant under optimal conditions produces an abundance of seed (not simply one vs none under stress); whereas under stress, cereals compensatorily reduce the number and size of viable seed gradually and systematically, allowing a relative assessment of stress severity among genetic individuals or cultivars.

In addition to surviving drought, each cultivar must respond well to such local factors as temperature, light, fertility, insects, diseses, and cultural practices. For this reason, Sojka[3] suggested that the most effective means of assessing relative drought resistance is

1. *USDA-Agricultural Research Service, Northern Great Plains Research Laboratory P.O. Box 459. Mandan, North Dakota 58554, U.S.A.*

to index yield to a quantifiable measure of stress severity in a large germplasm collection. Furthermore, comparisons of rate of change of yield over the range of drought severity may be the most appropriate way to evaluate relative drought resistance. These rates can be expressed as the slope of an individual variety's yield plotted against the mean performance of all varieties for a series of quantifiable drought levels[4,5]. Alternatively, they can be expressed as the slope of an individual varietal yield plotted against an absolute index of environmental stress severity such as water potential[6]

These yield vs. stress relationships may not always be linear. In fact, it may be unreasonable to expect linearity across the full range of stress severity. Yields will likely diminish at different rates, depending on stress severity, as various physiological functions are affected in a stepwise mannner. The instantaneous slope of a curvilinear yield response at a specific level of stress severity can be interpreted as the sensitivity to that degree of stress severity. Examples of some physiological thresholds capable of producing non-linearity might be critical water potentials for stomatal closure[7,8] or the critical crop water stress index for enzyme dysfunction[9]. Where non-linearity is found, the shape of the function will also influence the evaluation of drought resistance in accordance with specific knowledge of the stress environment.

Drought resistance may need to be related specifically to drought types. Begg and Turner[10] pointed out that the type of drought will be influenced by the timing and duration of the stress. In addition, the severity of the stress, and the point within the soil plant atmosphere continuum which is the stress origin should be considered[11]. Various workers have suggested that if drought occurs before anthesis, at midseason, or if it is intermittent, then stress recovery must be considered in evaluating drought resistance[12,13,14]. This growth stage dependency is intensified in determinate plants[15]. The specific plant traits which favor production under uninterrupted drought may be less beneficial or prove negative in intermittent or early drought. Similarly, in comparing cultivars, care must be exercised to avoid comparing results from divergent maturity classes. While earliness is a viable drought avoidance strategy, it does not influence a genotype's ability to withstand drought when encountered within its life cycle. If an early cultivar is susceptible to stress in its life cycle, then the traits causing susceptibility could be transferable in a cross.

Strategies and Traits of Drought Resistance

An effort must be made to distinguish between the reality of drought resistance *per se*, and strategies or traits associated with drought resistance. An analogy might prove useful. There is a difference between actual flight, and the traits of an airplane or a helicopter. Each of the latter represent a strategy for achieving flight, dependent upon successful combinations of traits. An airplane has wings and flaps, a helicopter has a rotor and tail rotor. Each strategy for flight is different. Each has unique traits. The traits alone, however, do not constitute flight. Either vehicle may fail to fly for a host of reasons even though they appear to have good strategies and the traits associated with them.

Drought resistance is the ability to minimize yield loss under stress. An ideotype or strategy for drought resistance may involve a large collection of drought resistance traits, but the resulting plant must be field tested in a drought environment to prove it can indeed "fly". As Schmidt[14] stated in his review, few preconceived "can't miss" crosses (based on parental traits alone) turn out productive lines. Well planned yield tests under stress are a must.

Some of the strategies and traits seen to contribute to drought resistance seem contradictory. Passioura[16] described two such contradictory strategies, 'conservative' and 'prodigal'. Conservative plants are sensitive to small increments of environmental stress and react to it by immediately reducing water loss through various mechanisms such as partial stomatal closure. Prodigal plants remain unaffected by the early stages of drought, with all physiological systems functioning at maximum levels until a stress threshold is crossed, resulting in total plant shutdown. Conservative traits are beneficial in prolonged or unbroken terminal droughts. Prodigal traits are usually beneficial for short intermittent droughts, provided there is no danger of extending into metabolic shutdown, particularly at some especially sensitive growth stage, such as flowering in a determinate plant.

Another general approach to achieving drought resistance has been to seek improved water use efficiency (WUE). This can be a less than satisfactory approach if WUE is not properly defined[17,18]. Fischer and Turner[19] stated that increased WUE must be defined as increased dry matter yield per unit water transpired and they recognized that the ratio of grain yield to total dry matter can change. This suggests a strategy of increasing the grain yield fraction of dry matter produced while also increasing the transpirational fraction of water evapotranspired. Either of these approaches runs the risk of confusing improved yield potential or improved yield due to better water use related cultural practices as improved drought resistance, particularly if WUE's are not compared over a quantified range of water shortage[20,21,22]. Furthermore, the timing of drought within the life cycle will have a significant impact on whether yield or vegetative matter is more severely reduced, thus influencing a yield based WUE.

Because plant desiccation can involve soil related drought (low soil water potentials and/or low unsaturated soil hydraulic conductivity), or desiccating atmospheric conditions (low vapor pressure deficits), or both, plant drought resistance breeding strategies are sometimes aimed separately at the desiccation sources. Aerial architecture (leaf structure, etc.), stomatal performance, and cuticular resistances are frequently the focus of efforts to reduce atmospheric desiccation. Rooting is the major focus of soil related drought. A recent review by Schulze[11] suggests that indeed stomata are regulated bimodally in response to stress. A feedback response via leaf water status brings about stomatal closure when zero leaf turgor is reached (presumably due to failure of the root system to adequately provide transpirational needs). A so-called feed forward response regulates stomata in accordance with the difference in mole fraction of water vapor between the leaf and air. This leads to a complicated and confusing situation for use of stomatal response as a trait associated with drought resistance. In a large sense this may explain the poor potential seen for increasing drought resistance in cereals through manipulation of stomatal anatomy and physiology[23]. Quizenberry[24] noted that xeromorphic traits should be hereditarily based, but that this expression should vary in intensity as the environmental stress level varies. He pointed out that epicuticular wax deposition is one of the best examples of such a trait. Furthermore, he notes that in the absence of adequate cuticular resistance, well adapted stomatal traits cannot be effective.

Leaf rolling under stress, leaf erectness, and leaf pubescence have also been the focus of some interest. O'Toole and Cruz[25,26] and O' Toole and Chang[27] found that relative transpiration of rice *(Oryza sativa L.)* was greatly reduced with leaf rolling, especially at higher wind velocities. Similar relationships were noted for a number of species by Begg[28].

He also noted that leaf erectness minimizes exposure of upper canopy leaves to radiation during diurnal peak stress periods[29]. It is not entirely clear, however, whether a mere redistribution of radiation within the canopy can produce a net conservative effect? Leaf pubescence has been shown to impede water vapor diffusion across the leaf air interface and to reduce radiation absorption at the leaf thereby lowering peak leaf temperatures, favoring photosynthesis[30].

The trait probably best associated with resistance to soil derived drought is production of a deep and prolific root system. Unfortunately root characteristics are very difficult to observe let alone quantify, and when quantified they produce very high variances. In the field, roots are subjected to nearly all the climatically induced sources of variation common to shoots, but in addition are subjected to discontinuities in time and space of fertility, soil moisture characteristics, soil strength, pH, salinity, temperature, and oxygen regime. Nonetheless, it is believed that a variety of root characteristics are heritable traits[31]. Taylor[32] proposed that four of the most important root characteristics influencing plant access to water are : rooting depth, root length density, root axial resistance to water flow and root radial resistance to water flow. Conceptually, imposing a velocity (l/t) consideration to the first two of these would also be desirable, since the vigor or speed with which they are expressed can significantly affect their drought combatting effectiveness, which (in all but the most optimal soils) can advance to serious proportions within a matter of days.

A new technology which may significantly enhance the breeder's ability to routinely consider rooting characteristics (at least depth and root length density) is the use of the mini-rhizotron[33,34,35]. The coupling of automated image analysis and compact video technology now make it feasible to observe large numbers of breeding lines in the field (*in vivo* and *in situ*). This has not previously been possible. Perhaps the greatest potential exists for implementation in third world breeding centers. There the major cost of manual observation tube insertion could be minimized. The mini rhizotron technique can allow a true field assessment of rooting depth and root length density. Furthermore, time series observations can allow comparisons of relative vigor, or rapidity of root extension. The singular success of the Swift Current, Saskatchewan drought resistance breeding effort through concentration on rooting characteristics[36] behooves a greater interest in this approach.

Passioura noted that despite being severly water stressed, many crops leave substantial amounts of apparent available (1.5 MPa) water unused in the soil[37]. This would imply that there are genotype-related differences limiting potential extractable soil water as defined by Ritchie and co workers[38,39,40]. The latter concept would be highly beneficial for discriminating among genotypes, provided methodology could be developed allowing sufficiently extensive and rapid determinations. Sojka[41] used thermocouple psychrometers to follow water extraction in his terminally stressed wheat comparisons. These instruments are costly for extensive field use, and all but the shallowest placed instruments must be regarded as expendable at the season's end. In soils prone to cracking, some thermocouples will eventually lose contact with the soil and provide spurious data;nonetheless the approach is at least feasible. New soil water monitoring technology including time domain reflectometry (TDR) or use of fiber optics may eventually make the concept of intensive soil water monitoring in drought breeding programs more attractive for wide scale field use[42,43,44].

Plant water status has been viewed as a good indicator of stress resistance, particularly if linked to yield. However, it is severely limited in breeding trials by the excessive time required for these kinds of measurements. Sojka[3] reported on various approaches using water status to determine drought resistance. Blum et al[46] and others have suggested using infrared derived plant characterization to speed up the process and possibly allow large numbers of daily evaluations. Development of the crop water stress index (a relative index of plant stress based on canopy temperature) has provided a conceptual basis for interpreting such data at least from cloud free arid climates[46]. In the most recent application of this kind of technology to cereals[47] the results suggest, unlike Hurd's[36], that a conservative drought resistance strategy resulted in the greatest maintenance of yield under stress. However, it should be recognized that Zipoli *et al's* stress was unbroken terminal stress, whereas some stress relief from rain can be expected in most years in Saskatchewan where Hurd's work was done.

Technical Considerations for Conducting Field Experiments

For any field experiment, a carefully developed statistical plan is a requisite to selection of the appropriate experimental design as well as the appropriate analysis of variance. Proper experimental techniques are required to prevent mistaking unrelated affects for genotypic drought differences, assuring correct data interpretation. Standard designs generally assume field site uniformity. Lack of uniformity as identified by variations in soil series, texture, profile depth, fertility, etc., should be isolated as much as possible in identifiable sub-units (such as within a replication).

Quantifying soil water status at frequent intervals throughout the growing season is desirable for interpreting experimental results from any field experiment. A capacity to frequently assess the soil water status within the plant rooting zone with precision is essential in drought studies. Characterizing water status should include the soil water supply, its distribution within the soil profile, and the proportion available at given matric potentials. Medium and moderately fine textured soils have a higher available water capacity than fine, moderately coarse, or coarse textured soils. But coarse textured soils hold the largest proportion of their available water capacity (up to 90%) at tensions ≤ 0.1 MPa. Proportions held at this tension decrease with finer soil texture[48]. Hence not all so called available soil water is equally available between field capacity and the 1.5 MPa permanent wilting point. The ease of water up take by plant roots diminishes as the soil water potential decreases i.e., becomes more negative[49]. This was subsequently quantified by Brun et *al*[50] with respect to both evaporative demand and soil water content. In drought studies, especially comparisons between or among sites of different soil textures, maintaining between-site similarity of soil water potential regimes is necessary if a direct comparison of the results is to be made.

The consequence of a plant stress is a decrease in yield potential. Vegetative plant portions usually decrease linearly with water supply, but reduction in grain yield potential is related to the stage of plant development when the stress occurs. The most cri[illegible] developmental stage for cereal crop grain yield appears to be at anthesis, because [illegible] number per ear is being determined at that stage. Although reduced grain [illegible] result in heavier kernels, the added weight per kernel does not generally pro[illegible] yield compensation for the reduction in kernel number. Plant develop[illegible] therefore, heading and anthesis, can differ among cultivars[51]. Impositio[illegible] conditions based on other than plant development stage may not have the same impact on yield of different cultivars being compared in the same field under identical cultural practices.

Capability to irrigate (or supply supplemental water to) a single plot or single treatment independently of the plots or treatments is essential in evaluating drought related studies. As indicated above, plant development rate can vary with cultivars, hence separate water supplementation may be required to assure stress imposition or relief at the desired development stage. Crop water use rate is, in part, a function of leaf area. Leaf area differences can be affected by soil variation and cultural practices such as fertilizer application rate. Basing the addition or the withholding of water on a soil water content measurement in a single treatment can result in either applying insufficient or excess water quantities on others. Care must also be exercised when applying and metering irrigation water to assure that the soil infiltration rate is not exceeded, resulting in runoff of the excess water.

Quantifying developmental growth stage is facilitated by the use of scales which assign a numeric or alphabetic designation to morphological features recognized visually or by feel. Scales to designate plant development stage are available for many crops[52,53], and for small grain cereals there are several[54]. Scales to describe small grain cereal development stage, however, are not equally sensitive to recognizable changes of morphological features. This should be a consideration affecting the selection of a particular descriptive scale.

Establishing uniformity in seedling populations among cultivars is significant to field-conducted drought studies, especially those focussed on cultivar comparisons. Numerous yield studies with corn show the relation of grain yield to plant population[55,56]. Less information on seeding population effects on grain yield is available for other cereals, but studies such as conducted by Black and Bauer[57] illustrate the same type of relation. Kernels (seeds) of cultivars often differ in size and weight. This affects both the unit area delivery rate of seed and individual seeding vigor. Hence, seed size and weight must be considered when determining planting rate based on total seed mass. Whenever possible, seeds should be selected from identical seed lots or of known non-stressed production conditions, since antecedent conditions can affect seedling vigor. Planting rate must also include adjustments for percentage germination and kernel water concentration[51].

Soil variability in field studies is largely unavoidable since homogeneity even in easily recognized soil properties generally is limited spatially within a soil type[58]. The degree of variablity and its impact can be reduced by adjusting plot size and placement to improve the probability of greater site homogeneity of soil properties having a bearing on the experiment's outcome. This is important if plant responses are not to be mistakenly attributed to genetic variation among genotypes when, in fact, the source of variation is environmental and may even mimic a drought response.

SUMMARY

Although a cultivar may exhibit the traits of a given drought resistance strategy, their presence does not guarantee drought resistance *per se*. Drought resistance is best defined as the ability to minimize yield loss in the absence of optimal soil water availability. A high yield baseline which allows a cultivar to do well over a range of environments does not of itself imply drought resistance. Drought resistance is best determined through yield testing in the field over a quantified range of stress. Such testing can provide the unique relationship between an individual cultivar's seasonal water status and its yield. The challenge to those seeking to breed for drought resistance has remained unchanged: to combine minimal yield loss due to drought with a high yield baseline. Progress in recent years has occurred in understanding the role and extent of field variability and developing stress quantifying instrumentation to better determine quantified stress/yield relationships. The complexity of the challenge to produce drought resistant cereals demands a close and harmonic cooperation between breeders, soil/environmental scientists, and plant physiologists if the goal is to be realized.

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