Genetic and Environmental Aspects of Roots and Seedling Stress

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Soil is a complex agglomeration of soil particles, micro- and macro-organisms, organic matter, chemicals, roots, water, and gases. The exact mix of these is unique to specific soils and environmental situations, and no two pots or plots can be identical. Despite this diversity, many generalizations are possible, and specific approaches to stress tolerance or avoidance in seedlings can be identified.

Stress symptoms are the phenotypic and physiological result of a negative interaction between a plant and its environment. The majority of plant stresses occur because of environmental or biological factors impinging on the plant through the root system. Four general aspects of the rhizosphere can be involved in the induction of these stresses: soil chemistry, soil environment, soil physical structure, and soil biology (Zobel, 1992a, 1993). As will become apparent, no one aspect affects the plant in isolation from the other three. Before we can discuss the specific stresses these rhizosphere aspects can induce, the nature of seedling roots, and their interaction with their environment, must be considered.

BACKGROUND

Within the published literature, there has been a remarkable lack of consistency in root terminology (Zobel, 1991a). When two types of roots with distinctly different physiological and/or morphological responses to the same environment are considered to be a single type of root or are simply not differentiated, no valid conclusions are possible. When a study of a specific type of root is reported, but in actuality involves research on an entirely different type of root, confusion is the least of the problems. Because all roots have similar anatomy and external morphology, it is often difficult to distinguish different root types in the field. For consistency, I use here the root nomenclatorial standards described by Zobel (1991a).

Klepper (1991) provides a description of the developmental pattern of wheat (*Triticum aestivum* L.) roots and, by extension, corn (*Zea mays* L.), barley (*Hordeum vulgare* L.), and other grass root systems. The first root to emerge from the seed is the taproot or radicle, followed by basal roots (often called seminal roots; see Zobel, 1991a), and then lateral roots. These then are followed by adventitious (nodal) roots. Nodal adventitious root development normally takes place beyond the seedling stage; therefore, there are only three types of roots present in monocotyledonous plants during the seedling stage. Dicotyledonous plants, such as soybean (*Glycine max* Merr.), tomato (*Lycopersicon esculentum* Mill.), and brussels sprouts (*Brassica oleracea* L. Gemmifera Group), also have the radicle, basal roots, and lateral roots as component parts of their seedling root systems, and their seedling root system developmental sequence is essentially identical to that of the monocotyledonous species (Zobel, 1991a).

Most studies of stress tolerance have focused on seedling root systems and, therefore, these three types of root. Different types of root are genetically, developmentally, and functionally distinct (Waisel and Eschel, 1991; Zobel, 1991a; Zobel et al., 1992). Because there are at least five or six types of roots in mature plants (Zobel, 1986), generalizations from seedling responses to mature plant stress responses may not be valid. However, greenhouse and growth chamber growth conditions are not representative of field conditions during seedling development, and, therefore, results developed under these

conditions should be used with caution when applied to hypotheses about seedling growth under field conditions.

Functional differences between root types, and even temporal changes in the function of different types of roots, can be critical to any assessment of stress response and possible alleviation of that stress. Waisel and Eschel (1992) demonstrated that mineral uptake differs between root types, and Brekle (1991) demonstrated that the growth of lateral roots is stimulated by excess heavy metals, while growth of the radicle and basal roots are suppressed by the same concentrations. Zobel et al. (1992), using ion-specific microelectrodes, have demonstrated that, in tomato, K and NO₃ uptake rates differ along the length of the root. When basal roots begin to elongate, uptake of these two ions by the radicle diminishes. The pattern of uptake along the basal root is similar to that of a radicle of similar developmental age, though quantitatively different. When lateral roots begin to elongate, NO₃ uptake by basal roots reaches to the same low level as that of the radicle. Again, the pattern of uptake along the lateral root is similar to that of the other two types at similar developmental ages, though quantitatively greater. Spatially and temporally, therefore, the three types of seedling roots behave differently (see also Waisel and Eschel, 1991). These results emphasize that the type of root demonstrating stress tolerance or sensitivity must be taken into consideration when assessing overall seedling responses. Zobel (1991b) has demonstrated that genetic variability in various root types can be manipulated. Thus, conceivably, the types of roots tolerant to a stress can be increased while the number of the sensitive type(s) can be decreased.

O'Toole and Bland (1987) have summarized the literature on genotypic variation in crop root systems, and Clarke and McCaig (1993) have taken a further look at possible breeding protocols. Both groups concluded that a primary constraint to root system improvement is its extensive morphological plasticity. Morpho-plasticity and its counterpart, physio-plasticity, are the direct result of genotype $\times$ environment interaction ($G \times E$)-based changes in plant root systems (O'Toole and Bland, 1987; Smith and Zobel, 1991; Zobel, 1975, 1992b). This plasticity can result in a drastic change in the root system morphology (or physiology) of a homozygous genotype across even small experimental plots within a single soil class. Unless the pattern of interaction can be identified, it is difficult, if not impossible, to identify the genetic component of this $G \times E$. However, plants need this plasticity if they are to survive in diverse soil environments. There is extensive $G \times E$ in field-grown root characteristics (Smith and Zobel, 1991; Zobel, 1990, 1992a), suggesting a potentially broad genetic base for providing stress tolerance. However, a large $G \times E$ also can cause difficulty in identifying the genetic pattern of response to stress situations. When the inherent temporal and spatial variability of various rhizosphere factors is included, genetic studies can be difficult.

The opacity of the soil and lack of suitable experimental systems to analyze root system responses to perturbations in their environment nondestructively are constraints to studying morphological aspects of stress responses. However, a statistical procedure (additive main effects and multiplicative interaction—AMMI) capable of dissecting the $G \times E$ responses of root systems now is used by many geneticists and breeders to analyze the plasticity and to characterize it morphologically, physiologically, and genetically (Royo et al., 1993; van Eeuwijk, 1992; Zobel, 1990, 1992a, 1992b; Zobel et al., 1988).

Now that some of the limits and constraints to studying rhizosphere stress have been identified, and a common nomenclature and understanding of roots stated, we can review the research on stress and discuss its implications for developing tolerance or avoidance. Many types of stresses produce very similar response patterns. As a result,

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the solution to stress is frequently the alleviation of the response rather than removal or avoidance of the stress. Both duration of the stress situation and the severity of the stress are significant attributes that must be taken into account when considering "solutions." This need holds equally for all factors. Most stress situations are unique to the specific site where the stress problem is found.

SOIL STRESSES

Moisture stress

Drought stress. Moisture stress, in the form of drought stress, is one of the most pervasive forms of stress. The simplest drought stress is the presence of moisture deeper in the soil profile than the plant root system penetrates. Eghball and Maranville (1993), Elizondo (1991), Hamblin and Tennant (1987), Hays et al. (1991), Lorens et al. (1987), and Mishio (1992) have demonstrated genetic variability for depth of rooting in a wide variety of crops. Another, straightforward drought situation is one where the total water reserves in the profile are inadequate for production of the crop (Passioura, 1972). A reduction in root growth or in xylem vessel size have been reported to be effective responses to this difficulty (Passioura, 1985). Numerous reports document the existence of sufficient genetic variation (Baker et al. 1992; Klepper, 1991) to implement these approaches through effective breeding pressure. These two forms of drought stress appear to be fairly straightforward. However, when acid subhorizons or plough pans that restrict rooting depth are combined with inadequate rainfall for even short periods during seedling development, the situation becomes much more complex.

Oxygen deprivation. The inverse of drought stress is flooding stress. Plant response to the resultant reduction in O_2 is normally characterized by a dramatic increase in ethylene in the stem or roots at the air–water interface. Ethylene is a powerful plant growth regulator and may be responsible for modifying auxin relationships and stimulating the induction of adventitious roots. Ethylene also is known for disrupting microfibril orientation and causing cell leakage and eventual cell wall degradation. Root growth under O_2 deprivation has been reviewed recently by Drew and Stolzy (1991). In rice (*Oryza sativa* L.) and other aquatic species, the roots normally develop extensive aerenchyma, their suberization retards O_2 efflux, and lenticels that develop above the water–air interface bring in additional O_2 . Justin and Armstrong (1987) described 91 species based on their level of response to excess water.

Temperature stress

Temperature stress in some forms, e.g., heat stress inhibition of fruit set, freezing of nonhardy species, is extremely well known. In other forms, it has been generally ignored; soil temperature stress via the root system is a major under-recognized form of stress. Bowen (1991), in a review article, suggests that most temperature stress takes place in that part of the shoot that is below the surface of the soil for a large part of the growing cycle. This is certainly true of seedlings of many monocotyledonous crop species, but it discounts the effects of soil temperature during the portion of the season when the shoot apex is aboveground. Cooper's (1973) very thorough review of the effects of root temperature documents effects on all plant growth aspects.

Root-zone temperature data presented by Cooper (1973), Klepper (1987), and Bowen (1991) suggest that species have characteristic temperature minima and maxima with a broad optimum. For example, based on an assessment of 50% reduction in root elongation, Bowen (1991) and Klepper (1987) suggest species/cultivar-specific lower threshold temperatures for maize (17°C), kidney bean (*Phaseolus vulgaris* L.) (12°C), and strawberry (*Fragaria* spp. L.) (5°C). The maize threshold temperature appears rather high, but Cooper's (1973) review suggests that many crop plant species have a similar threshold. These thresholds question the validity of routinely using a 10°C threshold for calculating growing degree days.

Most research on rhizosphere temperature stress has dealt with seedling emergence and growth. Some efforts to deal with excessively high or low soil temperatures have involved using mulches to cover the

soil and reduce solar heating, or building up ridges to increase solar heating in the root zone (Allmaras et al. 1973). The soil temperature below the plough layer is one aspect that deserves more thorough consideration. Zobel (1992a), in a brief review of the effects of root-zone temperatures, cited work by Rykbost et al. (1975), Kaspar et al. (1984), and others to suggest that temperature stress in mature plants takes place at soil depths well below the plough layer and is most important at anthesis and during seed and fruit development.

Temperature stress is not limited to restricting root growth into deeper layers of the soil profile. The literature reviewed by Cooper (1973) suggests that marginal root-zone temperatures in seedling and mature plants limit or even strongly modify normal shoot growth and development. However, very little is known about the interaction between soil temperatures and marginal stresses from other causes. Where temperature and other stresses have been studied, lower (at or below threshold) root temperatures appear to ameliorate some of the stress symptoms (Bowen, 1991), while higher temperatures appear to stimulate stress symptoms.

Mineral stress

Many locations around the world have been identified as mineral deficient. Many other locations are transient mineral deficient—when soil temperatures are low, the plants express mineral deficiency symptoms that dissipate as soil temperature increases. The opposite problem is associated with sites that contain an excess of minerals. An increasing number of locations in the world suffer from excess salts or are irrigated with saline water. These are frequently thought of as mineral-excess sites. Heavy metals increasingly are becoming a problem in industrial countries as well as in many developing countries with mines and mine spoils.

Deficiencies. Plant (root) response to nutrient deficiencies is diverse; the potential for improvement is equally diverse. Recent reviews by Krikun (1991) and Wilcox (1991) describe some of the interactions of roots with mycorrhizae and the benefits of this symbiotic relationship under nutrient-limiting conditions. This association is best known for the improved uptake of P in infected vs. noninfected plants. Gabelman and Loughman (1987) edited a collection of reports on genetic aspects of plant mineral nutrition, and Gabelman et al. (1986) reviewed the genetic variability for nutrient uptake. Much of the work cited by these authors is the result of studies with seedlings and/or single types of root. Zobel et al. (1992) and Waisel and Eschel (1991) demonstrated that mineral uptake differs between root types. These findings suggest the possibility of designing root systems to present an appropriate balance between root types for each specific soil.

Marschner (1991) and Bar-Yosef (1991) have reviewed the effect of root exudates, including H ions, on the availability of nutrients to the root. These compounds sometimes have direct effects, such as chelating relatively insoluble ions; on other occasions, they modify the soil environment. A modified soil environment will change the activity of soil microorganisms, which can produce siderophores and other chelating compounds to make minerals more available.

Excess. Root responses to soil chemical factors, excess salt, and excess heavy metals have been reviewed by Foy (1992), Kafkafi (1991), and Breckle (1991), respectively. Plant roots respond to mineral excess and deficiencies morphologically and physiologically. The primary focus of research on adjustment to mineral excess has been involving physiological adjustment. However, roots generally respond to mineral excess by becoming thicker and growing more slowly (Kafkafi, 1991). In addition, Breckle (1991) notes that growth and initiation of second- and third-order lateral roots are stimulated by heavy metals, while the taproot and first-order laterals (seminal/basal roots) are suppressed. Snapp and Shennan (1992) reported that tomato plants subjected to excess salinity have reduced root growth in sensitive and insensitive lines. They also demonstrated that the sensitive line had excessive lateral root dieback, while the insensitive line did not. Apparently, as with mineral uptake, different types of roots have different levels of tolerance.

Mozafar and Oertli (1992) found that salt stress in at least some cultivars of barley is sensitive to root-zone temperature. If the root

zone is kept at 15 to 20C, rather than 10 or 25C, the effects of NaCl concentrations of up to 60 mmol-liter⁻¹ were significantly reduced. This result has implications in testing for salinity tolerance. Screening should be performed under several temperatures because a significant number of low-tolerance escapes may be selected inadvertently due to interactions of temperature with the salinity, or genotypes with temperature-insensitive salt tolerance might be missed. In this situation, lines with shifts in temperature optima, lines with changes in salinity tolerance, or both types might provide a solution.

The interaction of high Al and drought sensitivity (Goldman et al., 1989) also is of interest. They found that Al and drought acted synergistically in soybean; i.e., when both stresses were applied simultaneously, leaf water potential, relative water content, and transpiration were significantly lower than was predicted by simple additive action between the two stress factors. This result suggests that the two stresses are acting on the same or complementary biological pathways. If this is the case, germplasm tolerant to one stress factor will have a high likelihood of tolerance to the other stress. Identification of the biological pathway involved is of greatest importance for future screening programs.

Physical stress

Mechanical impedance causes shortening and thickening of roots, with irregularly shaped roots being a hallmark of root systems growing in physically constraining soils (Bennie, 1991). Roots will grow down cracks (either artificial or natural) and then explore lower, less-compact layers of the soil profile. When roots are unable to penetrate soil aggregates that contain moisture and minerals, they may change morphology or, alternatively, initiate a new type of root to allow more efficient removal of moisture (De Freitas, 1988). Numerous reports suggest that, for intermediate compaction levels, larger (thicker) roots can penetrate where normal roots cannot (Materechera et al., 1992). This finding has been the basis for several selection programs. Voorhees (1992) has reviewed implement-induced compaction stresses.

Carbon dioxide

In a review paper, Zobel (1992a) criticized some of the soil environment generalizations made by soil scientists in the mid-1960s. Zobel (1992a) stated that, contrary to their (Grable, 1966) and, incidentally, his own (Ycas and Zobel, 1983) published theories, soil CO₂ levels in excess of 1% are the rule rather than the exception under field conditions (Buyanovsky and Wagner, 1983; Evans, 1962). Pot cultures, hydroponics, and other greenhouse and growth chamber plant culture techniques have minimal soil mass and, therefore, would be expected to have CO₂ levels more similar to atmospheric conditions than bulk field soil. Theoretical research suggests that optimum root growth and function occurs at 0.5% to 1% CO₂ in the root environment (Geisler, 1969; Yurgalevitch and Janes, 1988; Zobel, 1992a). Based on these conclusions, results determined under controlled greenhouse or growth chamber conditions need to be confirmed under field conditions before they are accepted as typical.

ADDITIONAL CONSIDERATIONS

Zobel (1993), in a brief review of root systems and soil stresses, suggests that stress symptoms frequently develop when two or more marginally stressful conditions act synergistically. For example, soil temperature significantly ameliorates (15–20C) or enhances (10 or 25C) barley sensitivity to root-zone salt (Mozafar and Oertli, 1992). Breeding for tolerance to a stressful environment, or the development of modified cultural practices to avoid stress, requires that *all* environmental conditions be documented and assessed for stress potential.

As mentioned in the section on drought stress, stress avoidance can be achieved by faster growth rates, resulting in deeper roots or modified uptake rates. An experiment to document the effect of temperature on the gravitropic response of maize taproots (Matthews and Zobel, 1995) demonstrated that Cargill, Hytest, DeKalb, Eastland, and Pioneer genotypes changed gravitropic response with increasing temperature (Table 1). Three different patterns of response were

Table 1. Final radicle angles (up = 0°) of five hybrid corn seedlings germinated for 5 days at four temperatures (recalculated from Matthews and Zobel, 1995).

Hybrid	Radicle angle(°)			
	Germination temp (°C)			
	17.5	20.0	25	30
Cargill 4327	145	142	154	145
DeKalb 524	136	133	144	135
Eastland 541	115	129	148	142
Hytest	113	125	142	136
Pioneer 3751	141	146	160	152
Grand mean	139			
LSD _{0.05}	9.4			

observed, with Pioneer demonstrating the most vertical growth under all temperatures. In a soil with an acid subsoil, Eastland/Hytest seedlings might demonstrate significant acid subsoil tolerance through avoidance at germination temperatures of 17 to 20C, but would be less tolerant at 25C. However, Pioneer seedlings presumably would be much less tolerant of the acid subsoil, but, perhaps, better able to penetrate a pan layer at 25C because of the steeper angles. These temperatures are well within the normal growing temperatures of corn seedlings and probably on the high side for northern New York, where they are commonly grown. Many agricultural areas in northern New York also have acid subsoils. With a difference in angle of taproot growth of 47° (Hytest at 17.5C = 113°; while Pioneer at 25C = 160°), there appears to be more than adequate genetic and temperature variability in gravitropic response to postulate breeding for specific stress avoidance conditions for maize seedlings.

CONCLUSIONS

From the data and review, I conclude that before generalizations about seedling stress tolerance are made, 1) diverse cultivars must be checked for differential responses, 2) morphological responses of the root system to stress conditions should be checked, 3) environmental variables in the field soil in question should be documented and mimicked in any greenhouse or growth chamber research, and 4) differential responses of diverse root types need to be checked.

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