

Transplant Growth Control through Water Deficit Stress—A Review

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SUMMARY. The theme of this review is modulation of extension growth in transplant production through restraint of watering of the seedlings. The purpose of the modulation is to produce transplants of 1) appropriate height for ease of field setting and 2) adequate stress tolerance to withstand outdoor environmental conditions. Physiological responses of the plant are discussed in relation to the degree of water deficit stress and are related to the degree of hardening or stress tolerance development in the transplants. Optimal stress tolerance or techniques for measuring same have not been fully defined in the literature. However, stress tolerance in seedlings is necessary to withstand environmental forces such as wind and sand-blasting after the seedlings are transplanted in the field. It is also imperative that the seedlings undertake a rapid and sustained rate of growth after outdoor transplanting. Water deficit stress applied to plants elicits many different physiological responses. For example, as leaf water potential begins to decrease, leaf enlargement is inhibited before photosynthesis or respiration is affected, with the result of a higher rate of dry matter accumulation per unit leaf area. The cause of the reduced leaf area may be a result of reduced K uptake by the roots with a concomitant reduction in cell expansion. Severe water deficits however, result in overstressed seedlings with stunted growth and poor establishment when transplanted into the field. In transplant production systems, appropriate levels of water deficit stress can be used as a management tool to produce seedlings conducive to the transplanting process.

The scope of this review encompasses seedling water management practices and the effects of varying degrees of water deficit stress on the physical, physiological and mechanical stem strength attributes of transplants. It also details the implications of slight or severe water deficit stress on hardening or stress tolerance development in transplants. The overall objective of water management in transplant production is to modulate growth in order that the seedlings withstand the temporal physical conditions in which they are transplanted and after establishment undertake a rapid and sustained rate of new root and shoot growth.

Stress-tolerant transplants

Transplant producers growing seedlings in the greenhouse intuitively regulate watering level to restrain excessive growth. The restraint is necessary for survival of the seedlings in the field after outdoor transplanting (Latimer, 1990; Riviere et al., 1990) and for easy and proper seedling placement during the transplanting procedure.

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Water restraint can result in hardened or stress-tolerant seedlings. This stress tolerance is important for holding transplants when field establishment cannot be done immediately (Marr and Jirak, 1990), for a high percentage survival in the field (Liptay, 1987), and a more rapid rate of establishment (Liptay and Nicholls, 1993). The goal in transplant production is to achieve an optimal seedling size with the appropriate level of stress tolerance to withstand environmental or other stresses when the plugs are transplanted into the field.

Varying water deficit stress

Water deficit stress can be applied in varying degrees to seedlings or plants. One effect of water deficit stress at moderate levels is a reduction in plant leaf area. Frensch and Hsiao (1994) reported that the rate of solute flow into maize (*Zea mays*) plants can become rate limiting for cell expansion under conditions of mild water deficit stress. This also was shown to occur in soybeans (*Glycine max* L. Mer.) and sunflower (*Helianthus annuus* L.) at about -400 KPa (Boyer, 1970). However, when plants were rewatered following drought stress the leaf growth rate did not recover to the original rate of enlargement. Photosynthesis and respiration were not inhibited until more severe water deficit stress was imposed.

Muchow et al. (1986) also reported similar results for soybean. In addition, at very low water potential, where biomass production was reduced, the decrease was associated with lower stomatal conductance but was not associated with specific leaf N content. Schulze and Bloom (1984) reported similar results for *Raphanus raphanistrum* L., a wild type of radish and tomato (*Lycopersicon esculentum* Mill.). In white clover (*Trifolium repens* L.), short drought periods reduced leaf area and the number of stolons but had no effect on leaf number. With longer drought periods the number of leaves was also decreased (Belaygue et al., 1996). The decrease in shoot growth (Kuchenbuch et al., 1986b), was linear with decreasing water content of soils for onions (*Allium sativum* L.).

Sharkey and Seemann (1989) reported that reductions in whole leaf photosynthesis was primarily the result of stomatal closure rather than damage to chloroplasts. Ben et al. (1987) reporting on varying levels of water deficit

stress, indicated that the CO₂ saturation rate of photosynthesis under high light conditions was the most sensitive stress parameter. Furthermore, mild water deficit stress did not affect quantum yield of photosynthesis but, acute water deficit stress damaged chloroplasts. Thus there appear to be several degrees of water deficit stress; the less severe being desirable for transplant production while the more severe are too restrictive on growth.

Water stress and morphology

The primary root of maize continued slow growth at low water potentials which completely inhibited shoot growth (Sharp et al., 1988; Saab et al., 1990). Root growth in tomato seedlings behaved in a similar manner (Liptay and Tan, 1985). However, in all cases the roots had lower rates of volume expansion and were very thin. Wu et al. (1994) reported that an increase in cell wall loosening contributed to the maintenance of primary root elongation at these low water potentials. Moreover, low water potentials had no effect on osmoticum deposition close to the apex but did decrease deposition in the more mature tissues (Sharp et al., 1990). Wu et al. (1996) reported that growth in the root apical region at low water potentials involved an increase in cell wall extension properties such as an accumulation of expansin. Sharp (1996) indicated that abscisic acid accumulation may help maintain primary root growth and inhibit shoot growth under low water potentials. Mulholland et al. (1996) demonstrated that leaf expansion can be enhanced by exogenous application of synthetic abscisic acid either to the rooting environment or directly to the xylem sap. Moreover, Sharp (1996) recommended caution when interpreting the effects of hormones applied to well-watered plants because hormonal sensitivity or response of tissues varies with water status.

Plasma membranes of living cells have been shown to be freely permeable to water while creating a barrier to other molecules (Chrispeels and Maurel, 1994). The water channels were proteins called aquaporins which allowed water to pass freely while excluding ions and metabolites. In plants, aquaporins are in the vacuolar membranes (tonoplast) and may be present in the plasma membrane. The driving forces of water, which cause irreversible expansion of

cells, are hydraulic and osmotic. Maize plants have been shown to respond to water deficits by hydraulic signals from the roots and by hardening of the cell walls (Chazen and Neumann, 1994). There is a different response between the differentiating tissue and the more mature tissue and also among organs (e.g., the root vs the shoot).

Mechanical properties

Water deficit stress has an effect on the mechanical strength of a seedling or plant stem and this response varies with plant species (Niklas, 1991). Niklas and Moon (1988) used elastic modulus as a measure of the bending strength of a stem that can support a weight on the stem tip or continue to grow vertically. The elastic modulus of a stem depended on stem water content (Niklas, 1989b) and also on the ratio of cell wall to protoplasm (Niklas, 1989a). Buckling of the stem in chives (*Allium schoenoprasum* var. *schoenoprasum* L.) occurred at -1300 KPa (Niklas and O'Rourke, 1987). Nonami and Boyer (1990) discussed elastic and plastic properties of cell walls. They found elastic deformation was instantaneous, reversible, independent of time, and was present only when the force applied to the plant tissue changed and followed Hooke's law. Plastic deformation was not instantaneous, not reversible, occurred continuously at a rate proportional to the force applied and was Newtonian in nature. At low water potentials the plastic properties and conductance of water of the cell walls decreased, but, there was little effect on the elastic properties. From a practical point of view, the reversibility of deformation, part of the elastic properties discussed above, is a desirable and necessary feature of stress tolerance. The property allows the plant to return to and retain its basic shape even after severe bending caused by wind or other forces. Thus specific water deficit stress could result in desirable improvements to the strength of the transplant and the seedlings' stress tolerance.

Growing medium and water deficit stress

Decreasing the water content in a soil decreased K uptake by onion roots; the drought resulted in an increasingly steep K gradient around the root (Kuchenbuch et al., 1986b). In soybean, the K content of the xylem sap decreased with decreasing water po-

tential (McQuate et al., 1986). This osmotic adjustment was different in different plants. Kuchenbuch et al. (1986a) also found similar results for onion plants. Less K uptake under lower water potentials may explain reduced leaf area (Boyer, 1970), as a result of reduced cell expansion at reduced K levels in the cells (Marchner, 1986).

Transpiration

Increased field survival in hardened or stress-tolerant transplants may result from their altered stomatal regulation. For example, Spence et al. (1986) reported that plant stomata, adapted to drought stress, maintain stomatal opening at lower plant water potentials than nonadapted plants. Stomata from drought-stressed plants were smaller, had a different shape and had a mechanical advantage over nonstressed plants in opening. The pores of stomata of drought-stressed plants required only 1.9 times the turgor pressure of the surrounding epidermis to initiate opening vs. 2.4 times for pores of the guard cells from well-watered plants.

Plants may use several mechanisms in response to drought stress. Sorghum (*Sorghum bicolor* L.) plants delayed the onset of plant water deficit by producing more xylem vessels (Fernandez and McCree, 1991). Tomato plants have more and larger stomata than black locust (*Robinia pseudoacacia* L.) and are more prone to drought stress (Hinckley, 1973). Gu et al. (1996) reported that upon rewatering, after a drought stress event, tomato plant transpiration returned to normal but growth rate did not.

Physiology

Water deficit did not appear to promote ethylene synthesis in cotton (*Gossypium hirsutum* L.), bean (*Phaseolus vulgaris* L.), or rose (*Rosa hybrida* L., 'Bluesette') (Morgan et al., 1990). Though leaf area was smaller in plants experiencing drought stress, the biomass of the seedlings was greater per unit area than for nondrought-stressed plants (Latimer, 1990). The larger biomass may be part of the development of stress tolerance in plants. Solute concentration in tissue increased after growth rate had fallen. Glutathione reductase, an indicator enzyme of drought stress, increased under stress conditions (Burke and Hatfield, 1987).

Guralnick and Ting (1987) reported the time required to restore various physiological processes after a prolonged drought for portulaca as follows: water potential and CO₂ uptake were normal after 24 h; ribulose diphosphate carboxylase was normal after 3 d; the crassulacean acid metabolism pathway was normal after 5 d; chlorophyll levels were higher than normal after 5 d; phosphoenol pyruvate carboxylase and phosphoenol pyruvate carboxykinase activity were normal after 6 d; the chlorophyll a/b ratios returned to normal levels only after 27 d. Sells and Koepe (1981) reported that proline oxidase activity decreased in mitochondria after only a slight water deficit stress while proline increased in drought-stressed plants (Stewart et al., 1977). Another factor associated with water deficit stress may be antioxidant concentrations. Gogorcena et al. (1995) reported a decline in antioxidant levels associated with drought stress in peas. However, Castillo and Layzell (1995) reported that oxygen limitation plays only a minor role during drought stress. There are a number of scientists experimenting with the role of antioxidants in relation to development of stress tolerance in plants.

Incident radiation and water deficit stress

The volume of water used by plants in the greenhouse is generally related to incoming radiation and air movement (Hesse, 1985; Musard and Dupuy, 1972; Stanhill and Albers, 1974). There appears to be a linear relationship between the amount of water consumed by the plants and the amount of incoming solar radiation plants received. Wiertz and Richter (1987) have developed an irrigation model which includes this relationship.

Conclusions

Seedling growth control for transplant production in greenhouses can be achieved by regulating the amount of water available to the plants. The severity of water restriction is critical. A desirable level of water restriction results in stocky, stress resistant seedlings able to withstand environmental stresses after transplanting outdoors. If water restriction is too severe, seedlings die or are overhardened, slowing new shoot and root growth. The dif-

ference in the severity of stress tolerance is related to various levels of physiological restraint on growth, the more severe being detrimental to plant development. In conclusion, more studies are needed to quantify and understand the physiological responses of the plants related to water deficit stress.

For commercial practices, though, the physiological studies, support the concept of limited water application to achieve an acceptable restrained shoot growth and also a level of stress tolerance. This level of stress tolerance does not appear to limit rapid new root and shoot growth once the seedling is transplanted outdoors into the field.

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