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Differential Flood Stress Resistance of Two Tomato Genotypes

Steven T. McNamara[1] and Cary A. Mitchell[2]

Center for Plant Environment Stress Physiology, Department of Horticulture, Purdue University, West Lafayette, IN 47907

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Abstract. **Tomato accessions PI 128644 (*Lycopersicon peruvianum* var. dentatum Mill.) and PI 406966 (*L. esculentum* Mill.) were identified in preliminary screening trials as being relatively nonresistant and resistant to root-zone flooding, respectively. A comparative study of these accessions was undertaken to examine adaptive responses to inundation. Root and shoot growth of both accessions were inhibited by 120 hr of flooding. Aerobic respiratory capacity of secondary roots of both accessions decreased to a similar extent after 24 hr of inundation. Flooding did not significantly affect anaerobic root respiration rate of either accession. Stomatal conductance decreased after 24 hr of flooding for both accessions, with some recovery by PI 406966 after 168 hr of treatment, coinciding with development of adventitious roots on lower stems. Few adventitious roots formed on flooded PI 128644 plants. Leaf water potential of both accessions initially increased as a result of flooding, but declined to near control level by 120 hr of treatment. Total phenol content of PI 128644 roots decreased with 72 hr of flooding, while that of PI 406966 roots was not significantly affected. Factors underlying the greater resistance of PI 406966 to flooding remain unclear, but may include a lower root respiratory requirement for O_2 and greater ability to sequester or eliminate toxic substances during inundation.**

Tomato is a useful model system with which to study effects of root-zone flooding on plant growth and development (Bradford and Hsiao, 1982; Jackson et al., 1978; Jackson, 1956). Following inundation, stress symptoms typically develop in a predictable sequence: Leaf epinasty, stomatal closure, and reduced shoot growth rate all occur within 24 hr. Chlorosis and abscission of the oldest leaves are observed between 72 and 96 hr of treatment. Adventitious roots commonly develop on the lower stem by 120 hr, whereupon plants begin to recover (Jackson, 1956; Kramer, 1951).

Tomato typically is considered to be one of the most sensitive vegetable species to excessive soil moisture (Iden, 1956); however, flood-resistant genotypes have been reported (Kuo and Chen, 1980; Kuo et al., 1982; Reid et al., 1969). The physiological basis for resistance of these genotypes during initial stages of flooding remains unclear.

Screening trials conducted in our laboratory indicated that flood resistance in the genus *Lycopersicon* is relative rather than absolute. All *L. esculentum* lines examined by us were affected deleteriously by inundation, including several reported to possess some degree of flood tolerance (Kuo and Chen, 1980; Rebigan et al., 1977). We encountered difficulty similar to that reported by Poysa et al. (1987) in detecting differential sensitivity to flooding among *L. esculentum* cultivars. This difficulty may indicate that limited genetic variability exists for this trait among tomato cultivars. Therefore, comparative examination of other tomato species was used to identify differentially resistant genotypes that could be used for future gene transfer between flood-resistant and nonresistant *Lycopersicon* spp.

Plant Introduction (PI) 128644 (*L. peruvianum* var. dentatum Mill.) and PI 406966 (*L. esculentum* Mill.) were identified as being relatively nonresistant and resistant to 5 days of flooding, respectively. These observations were based on occurrence and severity of visual stress symptoms (leaf chlorosis, desiccation, and abscission, as well as vascular discoloration). The objective of this study was to characterize the relative response of these PI 128644 and PI 406966 tomato lines to flooding in terms of cumulative growth, root respiration, leaf stomatal conductance, and leaf water potential. Total phenol content of roots and leaves of both species was examined to determine whether vascular discoloration observed for flooded PI 128644 plants might be accounted for by transport of toxic phenolic compounds from root to shoot. The results of the study presented herein improve our understanding of adaptive mechanism functioning in the genus *Lycopersicon* and will enhance efforts to breed and select for improved flood resistance.

Materials and Methods

Plant culture. Seeds of *L. peruvianum* var. dentatum Mill. PI 128644 and *L. esculentum* Mill. PI 406966 were obtained from the Regional Plant Introduction Station, Ames, Iowa. For experiments involving chemical analysis of root tissue, plants were grown in 10-cm-diameter (0.5-liter) plastic pots containing coarse silica sand (Weldron) and were irrigated daily with single-strength Hoagland's No. 1 nutrient solution, pH 6.0 (Hoagland and Arnon, 1950). Plants for growth and water relations studies were grown in a medium consisting of 1 soil : 2 peat : 2 perlite (by volume), amended as follows ($g \cdot m^{-3}$): 597 KNO_3, 597 $MgSO_4$, 896 superphosphate (0N–46P–0K), and 75 trace element mix (no. 555, Peter's, Allentown, Pa.). The plants were irrigated daily with nutrient solution containing (in $mg \cdot liter^{-1}$) 517 KNO_3 and 368 NH_4NO_3, (in $\mu l \cdot liter^{-1}$) and 124 H_3PO_4 (75%), pH 6.3. Seedling culture and all experimentation were carried out in a growth chamber under the following conditions: photosynthetic photon flux of 500 $\mu mol \cdot s^{-1} \cdot m^{-2}$ (400–700 nm) from fluorescent and incandescent lamps, photoperiod 16 hr (begun at 0600 HR) on a 24-hr cycle, 68% ± 5% RH, and air temperature 26 ± 2C days/22 ± 2C nights.

Flood treatment was imposed by placing each seedling pot inside a 1.2-liter container filled with the same nutrient solution used for irrigation. Plants were immersed to 1 cm above the surface of the medium. Solutions were changed after 60 hr of

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[1]Present address: Univ. of Minnesota Landscape Arboretum, 3675 Arboretum Drive, Chanhassen, MN 55317.

[2]To whom reprint requests should be addressed.

treatment. Control plants were placed with similar containers modified with bottom drainage holes and irrigated daily. Similar-sized seedlings of PI 406966 and PI 128644 typically were 22 and 27 days old (fifth and seventh leaf stage), respectively, at the beginning of treatment.

Growth responses. Cumulative growth responses measured after 120 hr of treatment included total leaf area (LI-3000 area meter, LI-COR), stem length, and leaf, stem, and root dry weights. Tissue weight was measured after drying for 3 days at 70C in a forced-air oven.

Root respiration. Root respiration capacity was measured at 24-hr intervals over a 120-hr treatment period. Seedlings were removed from treatment and fibrous secondary roots were gently washed free of sand. Distal sections of secondary roots (3 cm long) were excised and surface-disinfested in 1% (v/v) bleach (525 µl sodium hypochlorite/liter) for 45 sec. Tissue was subsequently rinsed in running tap water for 60 sec to remove bleach. About 0.25 g of tissue was placed in a respirometer flask lined with three layers of Whatman No. 1 filter paper moistened with 1.0 ml of single-strength Hoagland's No. 1 nutrient solution, pH 6.0 (Hoagland and Arnon, 1950). The center well of each flask contained 0.5 ml of 20% (w/v) KOH to trap CO_2. Following temperature and pressure equilibration for 30 min, oxygen consumption rate was measured for 2 hr at 26C with a differential respirometer (Gilson Medical Electronics). Initial oxygen concentration in the flasks was 21%.

Immediately following measurement of aerobic respiration rate, center wells were flushed five times with distilled water to remove KOH. The gas manifold system of the respirometer was used to purge flasks with N_2 bubbled through a 45-cm-long column containing 20% (w/v) pyrogallol, pH 10, to remove contaminant O_2. Carbon dioxide production was then measured at 26C for 2 hr. Following gas-exchange measurements, roots were blotted and immediately weighed.

Water relations. Stomatal conductance rate of the youngest fully expanded leaf was measured at 24-hr intervals over a 144-hr treatment period using a steady-state porometer (LI-COR LI-1600 equipped with a model 1600-07 cylindrical chamber). Simultaneously, estimates of leaf water potential were made with a pressure chamber (PMS Instruments) on the third and fifth oldest leaves of PI 406966 and PI 128644, respectively. Control plants were irrigated to field capacity 4 hr before measurement. All measurements were made 8 to 11 hr into the photoperiod.

Root and leaf phenol content. After 72 hr of treatment, secondary roots and leaf lamina tissues were excised and quick-frozen in liquid N_2, lyophilized, and stored frozen at −10C until analyzed. Extraction and determination of total phenol content were as described by Hammerschmidt and Nicholson (1977). About 100 mg of dry tissue was placed in boiling absolute methanol (10 ml/100 mg dry weight) for 5 min. The methanol was decanted and saved. The tissue was homogenized in acidified [0.1% (v/v) HCl] 80% (v/v) methanol 10 ml/100 mg dry weight, centrifuged (5000× *g*, 5 min), and the pellet extracted twice with acidified 80% (v/v) methanol (10 ml/100 mg dry weight). The methanol extracts were combined and concentrated to near dryness at 32C by flash evaporation. The residue was suspended in 10 ml of distilled water and partitioned four times against an equal volume of hexane. Following adjustment to pH 3.5, the aqueous fraction was taken to dryness, redissolved in 2.0 ml of ethanol (95% v/v), and stored at −20C until assayed.

Total phenol content was determined with the Folin–Ciocalteau reagent. A 0.1-ml aliquot of extract was diluted 1:10 with 95% (v/v) ethanol. Two milliliters of freshly prepared 2% (w/v) sodium carbonate was added to 0.1 ml of diluted extract. The mixture was agitated in a vortex mixer and allowed to stand for 5 min. A 0.1-ml aliquot of Folin reagent diluted 1:1 (v/v) with distilled water was added to the sample mixture while being mixed. The mixture was allowed to incubate for 45 min and absorbance was measured at 750 nm in a spectrophotometer (Beckman Instruments model DU-50). Phenol content of the tissue was expressed as nanograms of chlorogenic acid equivalents per milligram of dry weight.

Experimental design and data analysis. The experimental design used for all experiments was completely randomized with a factorial arrangement of treatments. Response variables were measured for three to five replicate plants per treatment. Data were subjected to appropriate analysis of variance and nonlinear regression procedures.

Results and Discussion

Few plant species are capable of sustained growth during prolonged periods of root-zone inundation (Kramer, 1951; Valoras and Leytey, 1966; Wenkert et al., 1981). Growth inhibition occurs as a consequence of flood-induced alterations in a number of interrelated physiological and biochemical processes, including reduced water and nutrient uptake (Jackson, 1956; Kramer, 1951; Leyshon and Sheard, 1974), decreased translocation of cytokinins and gibberellins from roots (Burrows and Carr, 1969; Reid et al., 1969), stimulated ethylene production (Tang, 1982), chlorophyll degradation, leaf abscission (Kramer, 1951), stomatal closure, and reduced photosynthetic capacity (Bradford, 1983).

Overall, growth of the differentially flood-resistant tomato accessions PI 128644 and PI 406966 was inhibited to a similar extent by 120 hr of flooding (Table 1), indicating that short-term growth changes are of limited value in evaluating overall flood-stress resistance. This conclusion is supported by results of preliminary comparative examinations of 64 tomato genotypes, including several reputed to possess some degree of flood-tolerance (data not presented). Growth data failed to consistently reflect overall ability of an accession to withstand flood conditions. Flood-resistant species may adapt in ways that enhance long-term survival at the expense of dry-weight accumulation (e.g., stomatal closure) (Jackson and Drew, 1984).

Aerobic respiratory capacity has been correlated with flood resistance in various species, including tomato (Carpenter and Mitchell, 1980; Kuo and Chen, 1980). Vartapetian et al. (1978) showed that mitochondrial integrity in excised *Orysz sativa* L. and *Cucurbita pepo* L. roots was highly dependent on an available supply of oxygen. Maintenance of the aerobic respiratory apparatus in flooded roots can be supported by internal aeration from the shoot via aerenchyma (Drew et al., 1985). Root aerobic respiratory capacity of the two tomato accessions compared here, as determined by measurement of O_2 consumption rate, responded similarly to flooding treatment over time. The data, therefore, were combined over accessions (Fig. 1). The decline in aerobic respiration capacity measured for both PI 128644 and PI 406966 after 24 hr of inundation suggests that neither species was capable of transporting sufficient O_2 from the shoot to sustain the root respiratory system. The roots of PI 406966 appeared to remain viable longer during flooding than those of PI 128644. After 120 hr of flooding, PI 128644 roots developed a brown, watersoaked appearance, whereas those of PI 406966 were firmer and lighter in color. Some browning of root tips was observed for both species.

Decreased O_2 consumption by flooded roots can be caused

Table 1. Cumulative growth of flood-resistant (PI 406966) and flood-susceptible (PI 128644) tomato seedlings after 120 hr of treatment.[z]

Variable	PI 128644			PI 406966		
	Control	Flood	Change (%)	Control	Flood	Change (%)
Leaf area (cm^2)	187	58*	−69	486	220*	−55
Leaf dry wt (g)	1.11	0.51*	−55	2.93	1.37*	−53
Stem dry wt (g)	0.17	0.15	−11	0.34	0.41*	+18
Root dry wt (g)	0.14	0.02*	−86	0.37	0.11*	−72
Shoot dry wt (g)	1.28	0.65*	−49	3.27	1.77*	−46
Plant dry wt (g)	1.42	0.67*	−52	3.65	1.88*	−48
Stem length (cm)	11.47	9.11*	−20	13.97	14.43	+3

[z]Each value represents the mean of four replicate plants.
*Significant difference within rows tested by protected LSD (P = 0.05).

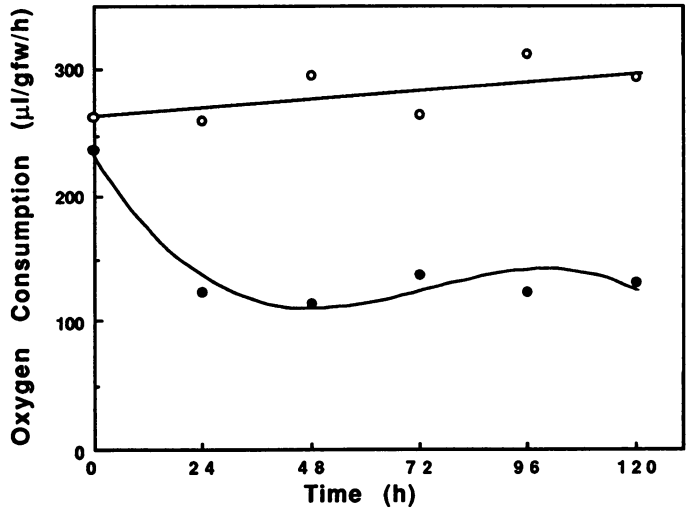

Fig. 1. Oxygen consumption by excised secondary roots from flooded or nonflooded tomato seedlings during a 120-hr treatment. Data were combined for both test species. Each data point represents the mean of measurements from roots of six plants. Open symbols represent controls and closed symbols flood treatments.
$Y_{control} = 267.10 + 0.33X \quad R^2 = 0.06$
$Y_{flood} = 234.05 - 6.11X + 0.09X^2 - 0.00042X^3 \quad R^2 = 0.46$

by factors other than deterioration of the normal cyanide-sensitive electron transport pathway. Lambers et al. (1978) reported that, although O_2 use capacity by roots of flood-tolerant *Senecio aquaticus* decreased during inundation, O_2 concentration in the roots remained high enough to maintain cytochrome *c* oxidase activity. The decreased O_2 use capacity may be attributed to inhibition of an alternative oxidase. The relative contributions of cyanide-sensitive and -insensitive respiration were not examined here. When averaged over time and treatment, the mean O_2 consumption rate for PI 128644 was significantly greater than for PI 406966, possibly indicating less-efficient use of oxygen by PI 128644 roots.

Greater viability of PI 406966 secondary roots during flooding may be reflected in their greater capacity for selective discrimination during mineral uptake. Barlett (1961) reported that species capable of rhizosphere oxidation during flooding accumulated substantially less Fe in their shoots than did other species. Jones and Etherington (1970) found that roots and shoots of highly flood-sensitive *Erica cinerea* accumulated Fe, while those of flood-resistant *E. tetralix* did not. Additionally, treatment of nonflooded *E. cinerea* cuttings with various formulations of Fe induced toxic symptoms similar to those resulting from waterlogging, including leaf desiccation. Nutrient analysis of tomato tissue revealed that leaves of flooded PI 128644 seedlings had higher concentrations of many elements, including Fe (200% of unflooded control), than did leaves of non-flooded controls (data not presented). In PI 406966, concentrations of Fe and most other nutrients were decreased by flooding. These results may indicate aerenchyma-enhanced improvement of the O_2 status of PI 406966 roots. Flooding stimulated aerenchyma development in hypocotyls of PI 406966 but not PI 128644 (unpublished observation). Secondary roots of PI 406966 were somewhat more porous than those of PI 128644, regardless of treatment. Adaptive significance in terms of facilitating internal aeration within PI 406966 is unknown.

Under anaerobic conditions, energy production by plant tissues depends on fermentation. Therefore, capacity for stimulated glycolysis during anoxia may be of significant adaptive value to flooded plants (Tripepi and Mitchell, 1984). Flood treatment did not significantly affect the anaerobic root respiration capacity of either accession. Carbon dioxide production data, therefore, were combined over treatments (Fig. 2). Accessions differed only after 120 hr of treatment, when PI 128644 had higher rates of CO_2 production. These results suggest that stimulation of anaerobic respiration probably is not a major factor contributing to the greater flood resistance of PI 406966.

Soil flooding can decrease root conductance to water (Bradford and Hsiao, 1982). In the absence of effective compensatory mechanisms, drought-like injury can occur (Kramer, 1951). Between 72 and 120 hr of flooding, the older leaves of PI 128644 plants began to show evidence of wilting and desiccation; younger leaves typically exhibited marginal necrosis. Neither wilting, desiccation, nor leaf necrosis were ever observed for PI 406966. Stomatal closure has been credited for maintaining high water potential in several species during flooding, including tomato (Bradford and Hsiao, 1982; Tang, 1982). The water-stress symptoms observed for flooded PI 128644 seedlings suggested that stomata might not close in this accession. However, stomatal conductance had decreased for both species by 24 hr of inundation (Fig. 3), suggesting they have similar adaptations for moderating transpirational water loss. Based on measurement of leaf water potential, stomatal closure appears to have had a positive impact on the water balance of both species during early stages of flooding (data combined over accessions, Fig. 4). Water potential was initially increased by inundation and then declined to near control level by 168 hr. The subsequent decline in leaf water potential of PI 406966 to nonflood values was associated with the development of numerous adventitious roots and sto-

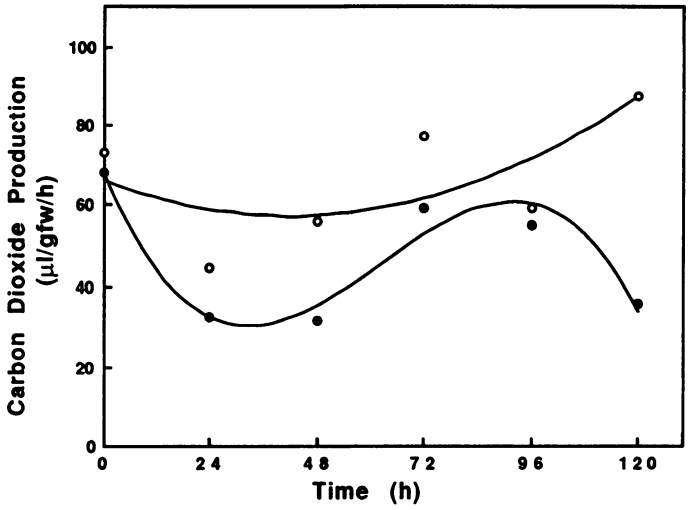

Fig. 2. Carbon dioxide production by excised secondary roots from flooded or nonflooded tomato seedlings during a 120-hr treatment. Each data point represents the mean of measurements from roots of six plants. Open symbols represent measurements from PI 128644 and close symbols measurements from PI 406966.
$Y_{control} = 65.93 - 0.42X + 0.0050X^2$ $R^2 = 0.19$
$Y_{flood} = 68.05 - 2.60X + 0.054X^2 - 0.00029X^3$ $R^2 = 0.421$

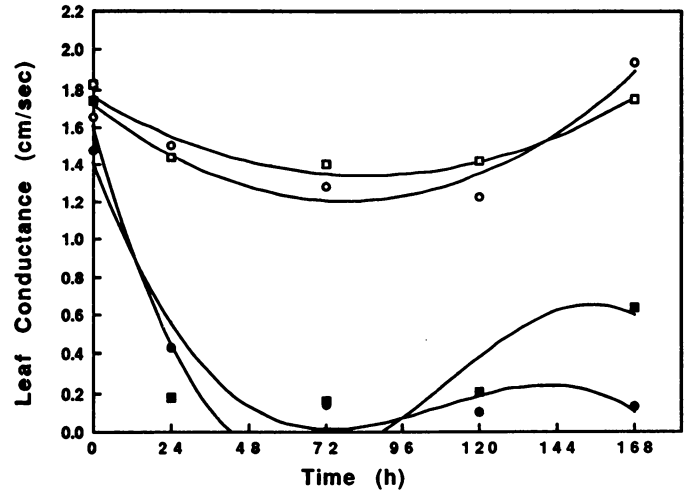

Fig. 3. Leaf conductance of flooded or nonflooded tomato seedlings PI 128644 and PI 406966 during a 168-hr treatment. Each data point represents the mean of measurement for four plants. Open symbols represent measurement of control seedlings and closed symbols measurements of flooded plants. Circles represent measurementfs for PI 128644 and squares PI 406966.
Control of PI 128644: $Y = 1.72 - 0.013X + 0.000085X^2$ $R^2 = 0.43$
Flood of PI 128644: $Y = 1.414 - 0.046X + 0.00048X^2 - 0.0000015X^3$ $R^2 = 0.95$
Control of PI 406966: $Y = 1.76 - 0.010X + 0.000060X^2$ $R^2 = 0.30$
Flood of PI 406966: $Y = 1.62 - 0.064 + 0.00070X^2 - 0.0000021X^2$ $R^2 = 0.87$

matal re-opening (Fig. 3). In PI 128644, however, water potential declined even though seedlings formed no adventitious roots and stomata remained closed, suggesting that further deterioration of the water-conducting capacity of roots occurred

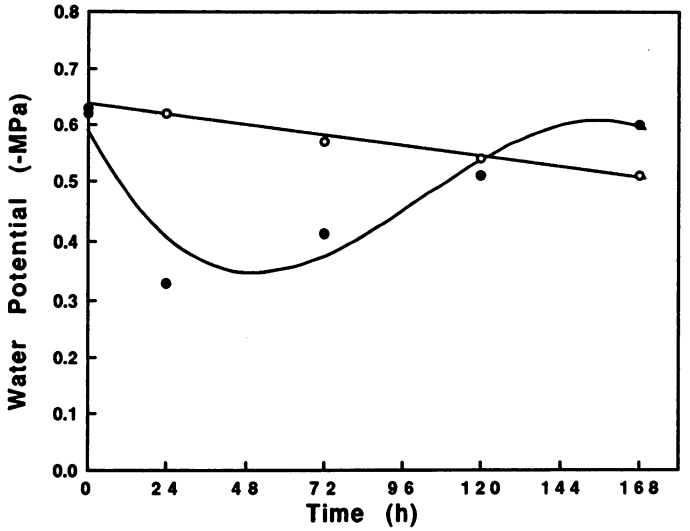

Fig. 4. Leaf water potential of flooded or nonflooded tomato seedlings during a 168-hr treatment. Data were combined for both test species. Each data point represents the mean of measurements for eight plants. Open symbols represent controls and closed symbols flood treatments.
$Y_{control} = 0.64 - 0.00076X$ $R^2 = 0.38$
$Y_{flood} = 0.59 - 0.011X + 0.00014X^2 - 0.00000046X^3 +$ $R^2 = 0.57$

Table 2. Total phenol content of root and leaf tissue after 72 hr of treatment expressed as nanograms of chlorogenic acid equivalents per milligram dry weight of tissue.

Plant part	Total phenol content[z,y]			
	PI 128644		PI 406966	
	Control	Flood	Control	Flood
Roots	90 a	29 b	58 c	49 bc
	Combined			
Leaves[x]	47 a		29 b	

[z]Each value represents the mean of five replicate plants.
[y]Mean separation within rows by protected LSD ($P = 0.05$)).
[x]Accession × treatment interaction nonsignificant. Data were combined over treatment.

during later stages of treatment. Although water stress may contribute to the death of PI 128644 plants flooded >120 hr, it does not appear to account for leaf desiccation observed during shorter periods of inundation. An alternative explanation is that phytotoxic substances accumulate in PI 128644 during flood stress. Ion imbalances already have been mentioned. Certain phenolic substances also may play a role.

Stems of flooded PI 128644 plants typically exhibited a browning of the stele not observed for control plants nor for PI 406966 plants under either treatment. This discoloration is similar to that reported for flooded *Juglans* spp. (Catlin et al., 1977). It has been suggested that, during anaerobiosis, a loss of membrane-selective permeability may release phenolic compounds from the vacuoles of root cells. These substances may inhibit cellular metabolism in the root and shoot by complexing with and denaturing protein. The content of total phenols in the roots of flooded PI 128644 seedlings was significantly lower than that of controls by 72 hr of treatment (Table 2). These

results are consistent with the hypothesis that phenolic substances are lost from root cells under low O_2 tensions. Cellular membrane integrity may be maintained to a greater extent in flooded PI 406966 roots, where total phenol concentration was similar to that of controls.

Both tomato accessions experienced increased leaf phenol content by 72 hr of inundation, despite the fact that no net loss of phenol was detected in roots of PI 406966. Change in level of phenolic compounds indigenous to leaves during flood stress (e.g., anthocyanin) complicates assessment of the impact of root-derived phenolic substances on the shoot. Ultimately, any such evaluation must consider that the relative sensitivity of a species to toxic substances may relate more directly to its ability to metabolize or compartmentalize such compounds than to totally prevent their occurrence. While the damage observed for flooded PI 128644 plants may involve metabolic poisoning of tissue, the role of phenols remains unclear.

Adventitious roots undoubtedly enhance the survival and recovery of PI 406966 seedlings during prolonged periods of inundation. However, the actual mechanism(s) supporting the greater relative resistance of PI 406966 before adventitious root development remain obscure. Internal aeration of the roots and lower root respiratory requirement for O_2 may be involved. Valuable insight into the physiological status of roots during flooding could be gained by examination of cytochrome *c* oxidase activity and levels of adenylate energy charge (Tripepi and Mitchell, 1984). The greater sensitivity of PI 128644 may result, in part, from inability to sequester or eliminate toxic substances occurring in the roots during anoxia.

Literature Cited

Bartlett, R.J., 1961. Iron oxidation proximate to plant roots. Soil Sci. 92:372–379.

Bradford, K.J. and T.C. Hsiao. 1982. Stomatal behavior and water relations of waterlogged tomato plants. Plant Physiol. 70:1508–1513.

Bradford, K.J. 1983. Effects of soil flooding on leaf gas exchange of tomato plants. Plant Physiol. 73:475–479.

Burrows, W.J. and D.J. Carr. 1969. Effects of flooding the root system of sunflower plants on the cytokinin content in the xylem sap. Physiol. Plant. 22:1105–1112.

Carpenter, J.R. and C.A. Mitchell. 1980. Root respiration characteristics of flood-tolerant tree species. J. Amer. Soc. Hort. Sci. 105(5):684–687.

Catlin, P.B., G.C. Martin, and E.A. Olsson. 1977. Differential sensitivity of *Juglans hindsii*, Paradox hybrid, and *Pterocarya stenoptera* to waterlogging. J. Amer. Soc. Hort. Sci. 102(2):101–104.

Drew, M.C., P.H. Saglio, and A. Pradet. 1985. Larger adenylate energy charge and ATP/ADP ratios in aerenchymatous roots of *Zea mays* in anaerobic media as a consequence in improved internal oxygen transport. Planta 165:51–58.

Hammerschmidt, R. and R.L. Nicholson. 1977. Resistance of maize to anthracnose: changes in host phenols and pigments. Phytopathology 67:251–258.

Hoagland, D.R. and D.I. Arnon. 1950. The water-culture method for growing plants without soil. Calif. Agr. Expt. Sta. Circ. 347.

Iden, T. 1956. Effect of oxygen concentration in the soil aeration on growth and nutrient absorption of fruit vegetables (in Japanese). J. Jpn. Soc. Hort. Sci. 25:85–93.

Jackson, M.B., K. Gales, and D.J. Campbell. 1978. Effects of waterlogged soil conditions on the production of ethylene and on water relationships in tomato plants. J. Expt. Bot. 29:183–193.

Jackson, M.B. and M.C. Drew. 1984. Effects of flooding herbaceous plants, p. 47–128. in: T.T. Kozlowski (ed.). Flooding and plant growth. Academic, London.

Jackson, W.T. 1956. The relative importance of factors causing injury to shoots of flooded tomato plants. Amer. J. Bot. 43(9):637–640.

Jones, H.E. and J.R. Etherington. 1970. Comparative studies of plant growth and distribution in relation to waterlogging: I. The survival of *Erica cinerea* L. and *E. tetralix* L. and its apparent relationship to iron and manganese uptake in waterlogged soil. J. Ecol. 58:487–496.

Kramer, P.J. 1951. Causes of injury to plants resulting from flooding of the soil. Plant Physiol. 26:722–736.

Kuo, C.G. and B.W. Chen. 1980. Physiological responses of tomato cultivars to flooding. J. Amer. Soc. Hort. Sci. 105(5):751–755.

Kuo, C.G., J.S. Tsay, B.W. Chen, and P.Y. Lin. 1982. Screening for flood tolerance in the genus *Lycopersicon*. HortScience 17(1):76–78.

Lambers, H., E. Steingrover, and G. Smakman. 1978. The significance of oxygen transport and of metabolic adaptation in flood-tolerance of *Senecio* species. Physiol. Plant. 43:277–281.

Leyshon, A.J. and R.W. Sheard. 1974. Influence of short-term flooding on the growth and plant nutrient composition of barley. Can. J. Soil Sci. 54:463–473.

Poysa, V.W., C.S. Tan, and J.A. Stone. 1987. Flooding stress and the root development of several tomato genotypes. HortScience 22(1):24–26.

Rebigan, J.B., R.L. Villareal, and Sen-Hsiung Lai. 1977. Reaction of three tomato cultivars to heavy rainfall and excessive soil moisture. Phillip. J. Crop. Sci. 2:221–226.

Reid, D.M., A. Croxier, and B.M.R. Harvey. 1969. The effects of flooding on the export of gibberellins from the roots to the shoot. Planta 89:376–379.

Tang, Z.C. 1982. Some physiological and morphological reponses of *Quercus macrocarpa* seedlings to flooding. Can. J. For. Res. 12(2):196–202.

Tripepi, R.R. and C.A. Mitchell. 1984. Metabolic response of river birch and european birch roots to hypoxia. Plant Physiol. 76:31–35.

Valoras, N. and J. Letey. 1966. Soil oxygen and water relationships to rice growth. Soil Sci. 101(3):210–215.

Vartapetian, B.B., I.N. Andreeva, and N. Nuritdinov. 1978. Plant cells under oxygen stress, p. 13–88. In: D.D. Hook and R.M.M. Crawford (eds.). Plant life in anaerobic environments. Ann Arbor Science, Ann Arbor, Mich.

Wenkert, S., N.R. Fausey, and H.D. Watters. 1981. Flooding responses in *zea mays* L.. Plant & Soil 62:351–366.