soil water. Singh and Sainju describe the influence of soil physical and morphological properties on soil temperature, water and air content, and available nutrient supply, and the resulting consequences on root growth. They also analyze the effect of soil and crop management practices that alter these properties in relation to root growth. Since optimal root growth is crucial for maximizing crop yield, we believe that papers presented at this workshop should be of benefit to a wide array of horticulturists.

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Soil Temperature and Root Growth

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Genetic diversity of root systems has been observed under optimal conditions, and may be further modified by the environment. Soil conditions, such as temperature, available water, aeration, nutrient content, and soil strength, are important factors that can impact root growth, development, and, ultimately, productivity. Temperature is the subject of this presentation. We will review pertinent information from the literature, and include some of our own observations with selected agricultural crops to highlight specific effects of temperature on root growth. Our intention is not to present in great detail all of the aspects of soil temperature/root growth interactions, but rather to provide a brief overview of the relationships to aid the reader in conducting further study.

SEASONAL CHANGES IN SOIL TEMPERATURE

Soil temperature is generally lower than that of the air, but seasonal fluctuations can occur with depth depending on soil and aboveground factors. For example, the average soil temperature taken at the 10 cm depth in Lubbock, Texas, from day of year 150 (30 May) to day of year 275 (2 Oct.), 1994, ranged from a low of 17 °C to above 30 °C (Fig. 1). The general trend is for the soil temperature to increase from early in the spring to mid-July, then decrease in the Fall. Daily fluctuations are evident, however, due to changes in evaporative demand and soil water content. Aboveground plant development, as well as changes in soil water status, can also influence seasonal changes in soil temperature at various depths (Fig. 2). As the soil dries during the

season in nonirrigated plots (Fig. 2B) the higher temperature isotherms move progressively deeper in the soil profile at a faster rate than in the irrigated plots (Fig. 2A). The soil becomes cooler as canopy closure occurs, as evidenced by the movement of the 24 °C isotherm toward the soil surface. The same isotherm also moved toward the surface in the nonirrigated plots as the canopy closed, but this occurred at a later time in the season. The dotted lines in both figures represent the predicted rooting depth as a function of changes in temperature. Note that the rate of downward root growth was faster in the nonirrigated plots.

TEMPERATURE EFFECTS ON ROOT GROWTH

Root growth is significantly impacted by changes in soil temperature (Abbas Al-Ani et

al., 1983; Bland, 1993; Cooper, 1973). Morphological changes, as well as root function and metabolism, can be influenced by such changes.

Root morphology

Changes in root morphology as a function of changes in temperature are generally characterized by differences in root length, dry mass, and branching. In general, root growth tends to increase with increasing temperature until an optimum is reached above which root growth is reduced (Brar et al., 1970; Cooper, 1973; Glinski and Lipiec, 1990; Pearson et al., 1970). McMichael and Quisenberry (1993) observed that the optimum temperature for root growth in cotton (*Gossypium hirsutum* L.) was between 28 and 35 °C vs. between 23 and 25 °C in sunflower (*Helianthus annuus*

Fig. 1. Seasonal changes in soil temperature at Lubbock, Tex., 1994 (10 cm depth) (from D.R. Upchurch and J.J. Burke, unpublished data).

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Fig. 2. Development of soil temperature isotherms (solid lines) during the growing season for Lubbock, Tex., 1992 for (A) irrigated and (B) nonirrigated plots. The solid circles represent the predicted rooting depth from soil temperature measurements (Burke and Upchurch, 1995)

Fig. 3. Development of the root systems of 10-day-old cotton and sunflower seedlings over a range of root temperatures. (McMichael and Quisenberry, 1993).

L.) (Fig. 3). The response of the primary roots of each species to changes in temperature was different from that of branch roots. Primary roots were able to grow over a much broader range of temperatures than were branch roots. In both cases no branch roots were produced during the course of the experiments at either the low (20 °C for cotton and 10 °C for sunflower) or high temperature (40 °C for both species). Cooper (1973) described the impact of changes in root temperature on root extension rates of a number of species, emphasizing the range of temperatures that were optimal for growth. Glinski and Lipiec (1990) also presented data on optimum temperatures for root development (elongation and dry mass) for a wide range of species (Table 1).

If the temperature deviates significantly from the optimum, root growth may be affected. For example, roots grown at low temperatures may be less branched (Brouwer and Hoagland, 1964). Death of the root cortex may also occur (Christiansen, 1963), followed by severe wilting of the plant. Temperatures higher than the optimum may reduce elongation rates (Arndt, 1937), or increase branching (Nielsen, 1974). Cooper and Thornly (1976) showed that as root temperature increased the fraction of the total plant dry matter accumulated in tomato (*Lycopersicon esculentum* Mill.) fruits decreased significantly.

Morphological changes in root growth can also occur as a result of the interaction of soil temperature with other soil factors, such as pathogen activity. The development of lateral roots of young cotton plants increased significantly at low temperatures (15 °C) when the plants were grown in sterile soil in the absence of pathogens (McMichael et al., unpublished data). Further research will help to determine the exact nature of this important interaction.

Root function

The impact of soil temperature on the function of the root systems has been documented in a number of species. At low temperatures water and nutrient uptake by root systems may be reduced (Nielsen, 1974; Nielsen and Humphries, 1966). Glinski and Lipiec (1990) showed that for a given level of available water, root growth rate in maize (*Zea mays* L.) decreased with root temperature. At the higher temperature (30 °C) the growth rate increased significantly as the available water increased, but such was not the case at the lower temperature (15 °C). Hydraulic conductance can decrease as root temperature decreases (Bolger et al., 1992). In the case of nutrient relationships, Cumbus and Nye (1982) showed that the concentration of nitrogen in rape (*Brassica rapus* L.) shoots was not significantly affected by root temperature, but that the highest rate of growth was associated with the highest nitrate depletion at root temperatures of 25–30 °C. Higher root temperatures can affect overall enzymatic activity of root systems (Nielsen, 1974). McMichael and Burke (1994) showed that root metabolism may become more temperature-sensitive as the mobilization of reserves in the cotyledons declines during early

Table 1. Optimum temperature for root growth of 18 species. (Modified from Glinski and Lipiec, 1990.)

Plant	Direction of change	Optimum temp (°C)	Reference
Sunflower (<i>Helianthus</i> sp.)	Root elongation rate	20	Galligar (1938)
Loblolly pine (<i>Pinus taeda</i> L.)	Root elongation rate	20	Barney (1951)
Pecan (<i>Carya illinoensis</i> L.)	Root elongation rate	30	Woodroof (1934)
Tomato (<i>Lycopersicon esculentum</i> Mill)	Root elongation rate	30	White (1937)
Maize (<i>Zea mays</i> L.)	Root elongation rate	30	Anderson and Kemper (1964); Blacklow (1972)
Cotton (<i>Gossypium hirsutum</i> L.)	Root elongation rate	33	Arndt (1945)
Soybean (<i>Glycine max</i> L.)	Taproot extension rate	25	Stone and Taylor (1983)
Oats (<i>Avena sativa</i> L.)	Root mass	5 (at maturity)	Nielsen and Humphries (1966)
Kentucky bluegrass (<i>Poa pratensis</i> L.)	Root mass	15	Brown (1939)
Strawberry (<i>Fragaria</i> spp. L.)	Root mass	10–20	Brouwer (1962)
Rape (<i>Brassica napus</i> L.)	Root extension	≈23	Moorby and Nye (1984)
Oil palms (<i>Elaeis guineensis</i> Jacq.)	Root growth	30–35	Agamuthu and Broughton (1986)
White oak (seedlings) (<i>Quercus alba</i> L.)	Root growth	24	Larson (1974)
White oak	Root elongation rate	≈17	Teskey and Hinckley (1981)
<i>Lolium perenne</i> L.	Dry mass	17	Clarkson et al. (1986)
Rice (<i>Oryza sativa</i> L.)	Root growth	25–37	Kar et al. (1976)
Maize (<i>Zea mays</i> L.)	Root mass	26	Walker (1969)
<i>Agave deserti</i> L.	Root elongation	30	Jordan and Nobel (1984)

Fig. 4. Development of the root systems of four 10-day-old exotic accessions of cotton as a function of temperature (B.L. McMichael, unpublished data).

seedling growth, indicating that temperature dependency is developmentally regulated. They showed that root growth in cotton in response to temperature is maximum within the optimal range of temperatures predicted from the Thermal Kinetic Window concept of Burke et al. (1988). The rates of reduction of 2,3,5-triphenyltetrazolium chloride (TTC) in 3- and 7-day-old cotton root systems remained high at temperatures within the defined Thermal Kinetic Window, but decreased sharply at temperatures above or below the Window. This information supports the suggestion that elevated substrate levels during periods of rapid mobilization of seed reserves favors survival of the plant, in that the temperature range for sustained metabolism is broadened.

Genetic variability

Substantial evidence suggests that genetic variability exists for root development in response to changes in temperature both between (Table 1, Fig. 3), and within species. Differences exist in temperature responses of seedlings of a number of exotic cotton accessions in both root length and branching (Fig. 4) (McMichael, unpublished data). Both the optimum temperature for root length development and the temperature response for lateral root initiation differed among genotypes. Quisenberry et al. (1981) reported similar results for older plants. Brar et al. (1970) found significant differences in the temperatures for optimum root growth (extension of main axis) in a number of forage legumes. Williams (1972) attributed part of the genotypic response to changes in root temperature in clover (*Trifolium* sp. L.) to changes in leaf area. Tachibana (1982) not only observed that figleaf gourd was more sensitive to low temperature than was cucumber (*Cucumis sativus* L.), but that cultivars of cucumber differed in sensitivity at 12 °C. McMichael and Quisenberry (1991) also observed that the genetic variability observed in root development in cotton genotypes was somewhat independent of their variability in shoot development, suggesting that breeding for more favorable root traits (i.e., deeper, more branched roots, less sensitive to low soil temperatures) might be possible. However, evidence exists for root-shoot interactions that impact the response of the whole plant to changes in soil temperature.

ROOT-SHOOT INTERACTIONS

Changes in soil temperature not only influence the growth and development of the roots, but can also impact root-shoot relationships. Gosselin and Trudel (1986) observed that increasing root zone temperatures from 12 to 36 °C tended to increase shoot dry mass as well as overall productivity of pepper (*Capsicum annuum* L.) plants. They (Gosselin and Trudel, 1985) also showed that increasing root temperature from 12 to 36 °C partly offset the negative effects of low night air temperatures (8 to 24 °C) on leaf dry mass and area of 6-week-old tomato plants. Their results demonstrated that higher root temperatures (30 °C)

are needed for maximum productivity when plants are grown at the low night air temperature (8 °C). Root development in young cotton seedlings was greater at higher root temperatures (28 °C), even when aboveground temperatures were low (20 °C) (McMichael and Burke, 1994). Lateral roots did not develop at low root temperatures regardless of the temperature of the shoots (Table 2). Total plant fresh mass was also reduced when shoots and roots were grown at the low temperatures. Based upon the number of days during the growing season when soil temperatures were favorable for root growth, and the duration of those favorable temperatures each day in 1991, Burke and Upchurch (unpublished data) also suggested that plants were probably temperature stressed for a large part of the season, leading to reduced shoot growth.

ENHANCEMENT OF ROOT GROWTH AND PLANT DEVELOPMENT IN RESPONSE TO SOIL TEMPERATURE

Enhancing root growth and plant productivity requires strategies to alter either the soil temperature or the temperature characteristics of the root systems.

Adjustment of soil temperature

The adjustment of soil temperatures is very difficult on a very large scale. This can be accomplished readily under greenhouse conditions by using a number of techniques, such as heating or cooling coils placed in the soil or temperature control of nutrient solutions used for hydroponically grown plants. In field situations, plastic mulches have been used to change the soil temperature (Ham et al., 1993; Mbagwu, 1991). Wein et al. (1993), for example, improved the yield of tomatoes with mulches. Another approach is the use of row spacing to adjust the closure of the crop canopy to effect changes in soil temperature (Upchurch and Burke, unpublished data).

Adjustment of root growth characteristics

As discussed earlier, genetic differences affect root growth characteristics over a range of temperatures. Root morphology might be altered to increase branching at adverse temperatures, thereby improving water and nutrient uptake. The function of the root system could also be changed to improve plant performance over a broad range of temperatures. For example, Oliver et al. (1995) successfully introduced a NADH-hydroxypyruvate reductase gene from cucumber into tobacco (*Nicotinia tabacum* L.) and showed that the enzyme from the transformed root had the same temperature characteristics as the cucumber roots. Further research is needed before genetic alteration can be used commercially for such purposes.

Table 2. Development of 10-day-old cotton seedlings grown at four temperature regimes (from McMichael and Burke, 1994).

Temp (°C)		Root length (cm)		Total root length	No. laterals
Shoot	Root	Tap	Lateral	(cm)	
28	20	3.08 a ^c	0.0 a	3.08 a	0.0 a
20	28	5.06 b	1.83 b	6.89 b	8.00 b
28	28	7.71 c	5.82 c	13.53 c	8.38 c
20	20	4.71 ab	0.0 a	4.71 a	0.0 a

^cMean separation within columns by Duncan's multiple range test, $P \leq 0.05$.

CONCLUSIONS

Plant roots grow and function in a diverse thermal environment. Relatively small changes in soil temperature can have significant impacts on the development of the root system, depending on the stage of growth and the durations of the changes. One aspect of the root growth/temperature relationship that is becoming increasingly important is the impact of genetic diversity on root response and the utilization of genetic potential to enhance root growth and function under a broad range of soil temperatures. Future work using genetic engineering, coupled with proper management techniques, should provide the means for increasing overall plant productivity across diverse soil environments.

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Soil Water and Root Growth

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Healthy, functioning root systems are critical to survival and productivity of land plants. Roots serve the combined functions of anchorage, support, and water and mineral nutrient uptake. Root growth, development, and function are largely determined by genetic information, but respond, often substantially, to available carbohydrate supply and local environmental conditions encountered during growth. Soil attributes that affect the extent and morphology of growing root systems include water content, strength or mechanical impedance, thermal regime, and structural development. The extent and function of plant root systems, in turn, directly or indirectly modify these soil conditions.

Weaver (1919, 1920) performed intensive characterizations of plant root systems in the field that, in many respects, remain unequalled to the present day. That roots exhibit sometimes profound morphological responses to environmental factors (Weaver, 1919, 1920; Weaver and Clements, 1929), and that "...the ideal root system is...one that fully occupies the soil to an adequate depth and throughout a radius sufficient to secure at all times enough water and nutrients" (Weaver and Clements, 1929), were clearly recognized by these and other early workers.

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Despite early and continued efforts, there is growing need for better knowledge and understanding of root growth and root function as related to soil water status. Intensive management of soil-plant systems is required in many cases to enhance resource use efficiency and to minimize potentially harmful effects of inappropriate water or chemical inputs. Despite considerable progress in some areas, however, knowledge of root growth and function is seldom applied directly to management of farms, nurseries, and other plant production enterprises (van Noordwijk and van de Geijn, 1996). Increasingly stringent statutory policies in some European countries may well portend stricter controls on agricultural inputs in the United States, as public concern for environmental quality continues to grow. Intensive water and fertilizer nutrient management, and improved predictions of the fate and transport of soil-applied chemicals, emphasize a need for more detailed information concerning root system responses to soil water status. Increasingly sophisticated computer simulation models, including the ability to provide 2- or 3-dimensional characterization of transient soil water and chemical distributions, require accurate knowledge of how growing root systems react with the soil environment if they are to be truly useful management tools.

We will not attempt to reiterate the accumulated knowledge concerning soil water effects on plant root growth in this paper. Our emphasis will be on how spatial and temporal characteristics of soil water may impact root growth and hence root function, and the importance of knowledge concerning the local

root growth and root function responses to soil water in enhancing our ability to effectively manage plant, soil and water resources.

THE SOIL ENVIRONMENT FOR ROOT GROWTH

Soils are complex amalgamations of physical and biological components, properties and processes, many of which are highly variable in space and time. Although the distributions of many soil physical properties and/or processes are seemingly random, they often have identifiable spatial and temporal structures at some scales of observation. Substantial variation in soil water and other attributes is also a direct result of plant activities (Hook et al., 1991; Jackson and Caldwell, 1993). Considerable progress has been made in characterizing and accommodating soil environmental heterogeneity during the past decade, particularly with respect to stochastic (rather than deterministic) representations. Some of this information is finding its way into computer models that simulate the space and time distributions of water and chemicals in the soil-plant-atmosphere continuum (e.g., Ma and Selim, 1997). A substantial limitation of these models at present is the relative lack of comparable information concerning root system growth and behavior in response to variable and transient conditions in the soil environment (Klepper and Rickman, 1990).

The increased tendency toward reduction of cultural practices, such as tillage, favors development and persistence of aggregates, and of structural voids and biopores in the zone of highest root activity. Water and dis-