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Understanding Root Systems to Improve, Seedling Quality

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SUMMARY. Root architecture can be very important in plant productivity. The importance of studies on root morphology and development is discussed to improve seedling growth. Root systems of dicotyledonous species are reviewed, with emphasis on differences between growth of basal and lateral roots. The presence of different types of roots in plant species suggests possible differences in function as well. The architecture of a root system related to its functions is considered. Classical methods for studying root systems comprise excavation of root system, direct observation, and indirect analyses. While the first method is destructive and the third is effective in understanding root architecture only on a relatively gross scale, observation methods allow the scientist a complete a nondestructive architectural study of a root system. The three groups are reviewed related to their potential to give valuable information related to the root architecture and development of the seedling, with emphasis on the availability of a medium-transparent plant-growing system, enabling nondestructive daily observations and plant measurements under controlled environmental conditions. Effects of CO_2 enrichment on seedling growth is reviewed, emphasizing the effects of CO_2 on root growth.

Vigorous root systems are as essential as vigorous shoots for growth and development of healthy plants. Early seedling root growth and development determine the optimum root system throughout the entire life of a plant, consequently affecting growth during this period and potentially leading to optimization of yields (Leskovar and Stoffella, 1995; Lynch, 1995). The spatial distribution in the soil of the root system can determine the potential of a plant to exploit the soil's resources, which are unevenly distributed on Earth's surface or subjected to localized depletion by the roots (Lynch, 1995). The production of a primary root system, i.e., the primary branching from the radicle, may have a major impact on growth and survival of a plant (MacIsaac et al., 1989). A primary root system increases the surface area available for the uptake of water and mineral elements. In addition, with its architecture, a primary root system provides physical support to the developing shoot.

Morphology and development of young roots in dicotyledonous species

Seedling root morphology differs between monocotyledonous and dicotyledonous species (Fahn, 1982; Leskovar and Stoffella, 1995; Sutton and Tinus, 1983; Zobel, 1975, 1986, 1995, 1996). Dicotyledonous species were described as presenting three types of roots: radicle, adventitious, and lateral (Esau, 1965, 1977).

The radicle forms the taproot (primary root), adventitious roots are initiated from the hypocotyl, and lateral roots are from the taproot. Beginning with Zobel (1975), several researchers have identified a fourth type of roots-basal roots. Zobel (1986) indicated that initiation of basal roots is under different genetic control than initiation of lateral and adventitious roots. In fact, a double homozygote from a lateralless tomato mutant (recessive mutant called diageotropica, *dgt*) and an adventitiousless tomato mutant (recessive mutant called rosette, *ro*) originated roots in the hypocotyl and upper portion of the taproot. Assuming only three types of root, the double homozygote should have had only a taproot. Because these roots were genetically not lateral, nor were they adventitious, Zobel (1975) classified these roots as basal roots. Basal roots have been reported to be produced by mungbean (*Vigna radiata* L.) (Leskovar and Stoffella, 1995), bell pepper (*Capsicum annuum* L.) (Leskovar et al., 1989; Stoffella et al., 1988), tomato *(Lycopersicon esculentum* Mill.) (Zobel, 1975), beans (*Phaseolus vulgaris* L.) (Stoffella et al., 1979), and lettuce (*Lactuca sativa* L.) (Nicola, 1997).

Evidence that basal and lateral roots differ in terms of morphology, point of origin from the taproot and development was reported by Nicola (1997) in lettuce seedlings grown in transparent medium (Fig. 1). Basal and lateral roots in lettuce seedlings originated from two distinct regions of the taproot and developed differently. A thicker, short upper radicle was visibly distinguished from a smaller, long, lower radicle 2 d after seeding (DAS). This distinction was even more evident 3 and 4 DAS. A restriction area

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separated the two portions of the taproot. Basal roots originated at two opposite sides of the short upper portion of the taproot and located close to the hypocotyl, and did not produce secondary branches during the first 18 DAS. Lateral roots originated at ~120° apart along the longer portion of the taproot and produced secondary branches. Basal roots presented a horizontal extension in the medium, while lateral roots presented a growth extension downward into the medium. The number of lateral roots 18 DAS was 2- to 3-fold the number of basal roots.

Adventitious roots cannot be confounded with lateral roots for two main reasons. First, adventitious roots originate from the stem, while lateral roots originate from the taproot. Second, the former type originates from tissues other than the pericycle, while the latter type originates from the pericycle. Conversely, basal roots are not clearly classified with respect to their point of initiation. Zobel (1986) demonstrated that basal roots initiate from the pericycle of the lower hypocotyl and upper taproot. Consequently, basal roots were not adventitious in anatomical origin, nor lateral or adventitious in genetic control of their initiation (see above).

Detailed information of the sequence of events occurring in root branch formation of young seedlings could be valuable to further determine the root development of field-grown plants. In bell pepper seedlings, basal roots emerged prior to lateral roots (Stoffella et al., 1988) and only after full cotyledon expansion. A similar development was found in lettuce seedlings (Nicola, 1997). In tomato seedlings, lateral roots emerged before basal roots (Aung, 1982). Weinhold (1967) described basal roots as arising acropetally (toward the shoot apex) from the germinating seedling, while lateral roots arose basipetally (toward the radicle apex). Nicola (1997) reported in lettuce a similar development only for the first 8 to 10 DAS, thereafter basal and lateral roots emerged also between older primary branches, contemporary to emergence of basal and lateral roots that followed the respectively original acropetal and basipetal patterns. Charlton (1996) defined lateral roots as "roots derived from lateral endogenous primordia formed in preexisting roots" (p. 149). The author said that lateral roots appeared at a relatively constant distance behind the tip of a growing root, that lateral roots initiated in rows or ranks, and that within each rank they appeared to initiate and emerge in acropetal sequence under normal conditions. Charlton (1996) reported that between the basipetally emerged lateral roots, particularly in dicots, additional laterals may arise for a long period in roots with secondary growth. Esau (1965) referred to these additional lateral roots as adventitious.

The architecture of a root system related to its function

Fitter and Stickland (1991) and Lynch and van Beem (1993) suggested that the architecture of a root system may have ecological implications for uptake of water and nutrients from soil. Fitter (1986, 1987, 1996) suggested that, in general, plants with a more herringbone-like distribution of roots, that is, with branches mainly along the central root axis, may occur under low soil resource availability, whereas in plants with a dichotomous-like distribution, secondary branches increase when resources are present in abundant supply, thereby increasing acquisition of water and nutrients. Variation in root architecture among species was indicated by Seiler (1994) to be an important factor determining differences in drought tolerance among species. Early, rapid root growth and branching were suggested to confer an adaptive advantage in more efficient use of soil water. Root elongation can be advantageous to plants in drying soil, and may be particularly important for seedling establishment. Growth of new plants is restricted largely to surface soil layers that are vulnerable to drying (Sharp et al., 1988).

Basal roots differ from the three more classic types in terms of morphology, gene expression, and development (Nicola, 1997; Zobel, 1996). This suggests possible differences in function as well. The differentiated functions of basal and lateral roots have not yet been fully understood, but several authors have hypothesized that basal roots would provide a means for plants to uptake surface-applied nutrients and water during crop production, and they may also play a role in supporting the plant (Bole, 1977; Eshel and Waisel, 1996; Jackson, 1995). Findings in lettuce that lateral roots originated in three directions with respect to the taproot, at 120° apart and extending deep in the soil, is an indication that lateral roots can explore more soil volume for resources than basal roots, thus lateral roots may be able to reach and exploit localized patches of nutrients in the soil (Lynch, 1995). Conversely, basal root bidirectional and superficial formation gives the root system a horizontal extension in the soil surface, assuring the basal roots the capacity to exploit the most fertile portions of agricultural soils (Bole, 1977; Eshel and Waisel, 1996).

Zobel (1996) reported that species that demonstrated the most drought tolerance had the most deeply penetrating root system, implying that plants with an extensive lateral root system would be favored in these instances. Eshel and Waisel (1996) suggested that the major function of basal roots was to exploit the most fertile portions of agricultural soils more efficiently than lateral roots. In addition, Bole (1977) found that basal roots of rape (*Brassica campestris* L.) were capable of absorbing phosphorus more efficiently

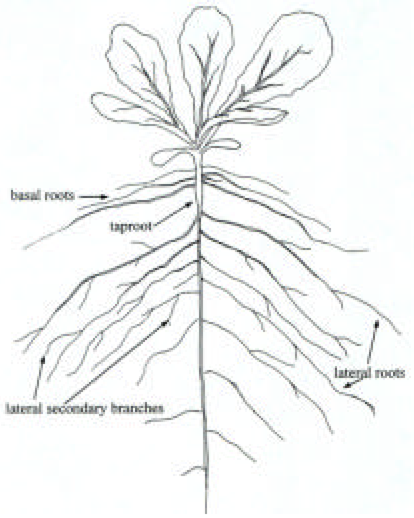

Fig. 1. Diagram of lettuce seedlings 18 d after seeding. The different types of roots present in lettuce seedlings are shown: taproot, basal and lateral roots, and lateral secondary branches

than lateral roots. Eshel and Waisel (1996) reported that basal roots were less sensitive to gravity than lateral roots, and therefore could extend the root system horizontally.

Studying seedling root systems

Studies on root morphology and architecture have attracted much research in the field of forestry and fruit crops, since these species have a long life span and have a high dependence on water supply, fertility, soil physical property, and aeration. As early as 1927, Weaver and Bruner (1927) lamented the lack of studies on how a root system functions. During the 1980s interest in studying roots increased, particularly related to the regulation of root growth and development (Feldman, 1984).

Measurements of root biomass and root length are typically used to describe root distribution in the soil profile, but analysis of root morphology and architecture can improve the understanding of water and nutrient extraction from soil (Fitter, 1985). However, field methods to study root development with repeated direct observations of undisrupted root growth have been extremely limited (Mackie-Dawson and Atkinson, 1991).

CLASSICAL METHODS. Methods to study the root system and reviewed by Mackie-Dawson and Atkinson (1991) include 1) excavation of the root system, 2) direct observation, and 3) indirect analyses. Methods from the first group require the removal of the root system from the soil, usually by washing, and can cause a major loss of root material when dealing with young seedlings. Early in development, much of the root system is very fragile, making full excavation and architectural analysis extremely difficult (Jackson, 1995). In studying root systems actively growing in soil, Jackson (1995) felt that a major difficulty was the extraction of fine roots and the measurement of root architectural variables.

Observation methods require a viewing surface that is inserted into the soil (Mackie-Dawson and Atkinson, 1991). The development of the root system in situ can then be seen through a window into the soil, allowing the same volume of soil and root system to be observed continuously. The major constraint in using these methods is that only a portion of the root can be observed, and extrapolation of the root measurements to the entire root system may be not representative. If a whole root viewing surface could be developed, observation methods could represent a major advance for study of the root system. Although hydroponic liquid culture allows direct observation of the entire root system, present growing conditions prevent normal root hair development.

The extent and activity of the root system have been indirectly measured by relating the root function to supply of water and mineral nutrients to the plant (Mackie-Dawson and Atkinson, 1991), For example, a relationship between root length and maximum soil moisture depletion was observed in pasture species by Evans (1978). Consequently, variation in soil moisture with depth as determined by measurement of soil water potential has been used for estimating root activity through mathematical models. Similarly, the absorption of ^{32}P was found to be correlated with root length by Atkinson (1989). This relationship was studied using a combination of an observation window in a laboratory study and the injection of the radioisotope in the soil. These indirect methods can be effective in understanding root architecture, however, only on a relatively gross scale (Mackie-Dawson and Atkinson, 1991).

MICROPROPAGATION METHOD. Another approach to the study of early seedling root growth is that of micropropagation in tissue culture, particularly where all external carbon is derived from CO_2 (Kozai, 1991). In this type of autotrophic culture, growth and development are largely influenced by physical environmental factors which include light, CO_2, humidity, air flow speed, temperature, and O_2. However, use of photoautotrophic micropropagation of whole seedlings is fairly new, and considerations should be taken as, e.g., how the physical environment affects photoautotrophic growth and development of whole seedlings.

Seedlings originated from seeds and grown in vitro do not require a supply of growth substances as does an explant or a cutting and they can grow autotrophically if provided sufficient CO_2. When using airtight vessels for growing photoautotrophic seedlings, the CO_2 concentration was often measured to be as low as the CO_2 compensation point (less than 100 µmol?mol^{-1}) during most of the photoperiod (Fujiwara et al., 1987; Kozai et al., 1992). Using loose caps or gas permeable film for capping the growth vessels resulted in CO_2 concentrations often <200 µmol?mol^{-1} (Kozai, 1991) (which is lower than the atmospheric concentration of 350 µmol?mol^{-1}). During the dark period, CO_2 concentration rose to 3000 to 9000 µmol?mol^{-1}, but remained low (100 to 200 µmol?mol^{-1}) for the entire light period.

IN VITRO METHOD. Little research has been conducted in vitro using seeds and even fewer studies have been done using in vitro culture to study root architecture and morphology. Stoffella et al. (1988) used test tubes filled with gelled medium (gelrite) supplemented with mineral nutrients and sucrose as a carbon source (photomixotrophic growth), to characterize the early root morphology of bell pepper seedlings. A whole-plant observation method was implemented to study the early root growth and development of lettuce seedlings (Nicola, 1997; Nicola et al., 1996). Nicola et al. (1996) and Nicola (1997) used test tubes filled with Phytagel gelled medium supplied with mineral nutrients and sucrose to grow lettuce seedlings and study root morphology and architecture [photomixotrophic whole plant culture (PMWPC)]. Plants were grown 9 d in the tubes and then removed. The lack of recyclable air and depth for root extension did not permit further growth. Consequently, a photosynthetic whole-plant culture (PWPC) system was designed and built by Nicola (1997) to study seedling root growth, which attempted to remove the exogenous sucrose supply as a carbon source and introduce circulating fresh air into the plant container to avoid the lowering of CO_2 concentrations during the light period. Glass 1-L bottles were used to accommodate a large quantity of transparent nutrient medium, thus permitting the growth of seedlings for up to 18 DAS without supplying sucrose as a carbon source. Filtered and calibrated air was allowed to flow in and out the bottles, thus permitting the seedlings to use their photosynthetic capacity. Environmental conditions of the growth room such as temperature, relative humidity and light were preconditioned and controlled throughout the duration of the experiments. The growing system developed was easily constructed, calibrated and monitored during lettuce seedling root growth studies, and enabled direct nondestructive plant observations and measurements, under controlled environmental conditions. During the studies a pregerminated seed was transferred one into each bottle and grown until plant harvest. Number of lateral and basal roots, number of secondary root branches and of leaves could be counted daily by visual observation through the bottle. The root growth observation method developed could represent a valuable tool to investigate root morphology and development in different species, to improve selection and breed new varieties based on root architectural characteristics.

Increasing root growth with CO_2

Increased concentration of CO_2 in the atmosphere has received more interest in recent years (Eshel and Waisel, 1996). Plant adaptation to rising CO_2 concentrations in the atmosphere is a paramount priority presently, because it is estimated that CO_2 in the atmosphere will double from the 1978 average concentration of 338 µmol?mol^{-1} by the middle or later part of the 21st century (Murray, 1995).

Enrichment of atmospheric CO_2 has been reported to increase growth rate and yield of a wide variety of plant species, and it is used in greenhouse crop production in northern latitudes for cucumber (*Cucumis sativus* L.), tomato, celery (*Apium gravoeolens* L.), and lettuce (Calvert, 1972; Calvert and Slack, 1975; Challa, 1976; Gent, 1984; Knight and Mitchell, 1988; Tremblay et al., 1987; Wittwer and Robb, 1964). Sonnewald et al. (1996) reported that the initial response to elevated CO_2 in the atmosphere could lead to about a 50% increase in leaf photosynthesis. The increase in atmospheric CO_2 increases photosynthetic efficiency in terrestrial C_3 plants because the present CO_2 concentration is insufficient to saturate the ribulose-1,5-bisphosphate carboxylase/oxygenase enzyme system (Rubisco) and the increased CO_2 competitively inhibits ribulose-1,5-bisphosphatc oxygenation and photorespiration (Long et al., 1996). However, an acclimation effect occurs, and the rate of photosynthesis again declines in many species, mainly due to a decline of rubisco activity (Evans, 1983,1987; Geiger and Servaites, 1991; Kramer, 1981; Sage et al., 1989; Sonnewald et al., 1996; Torisky and Servaites, 1984).

Tremblay et al. (1987) increased growth rates of shoot and roots of celery transplants raised in greenhouses with 1000 µmol?mol^{-1} CO_2, compared to ambient CO_2 concentration. Lettuce yield in a tunnel was enhanced by enrichment of CO_2 in the air (Enoch et al., 1970; Wittwer and Robb, 1964). Del Castillo et al. (1989) found that soybean (*Glycine max* [L.] Merril) plants grown in growth chambers under elevated CO_2 concentration had greater root mass than those grown under normal atmospheric CO_2 concentration. However, CO_2 concentration did not affect the rate of elongation of individual roots. The number of branches increased because of CO_2 enrichment, resulting in an increased total root length, without an increase of the volume of soil explored by the roots. Aguirrezabal et al. (1993) studied root systems in hydroponically grown sunflowers (*Helianthus annuus* L.) as affected by carbon nutrition. The results they obtained indicated that the control of carbon partitioning among various components of a single root svstem was determined by a combination of the distance of each sink from the source and its level of branching. Studies of Nicola (1997) on lettuce seedlings grown in a controlled environment have indicated that enriching the atmosphere up to 2000 µmol?mol^{-1} CO_2 enhanced root branch formation in the seedlings, particularly basal roots, compared to the control of 350 µmol?mol^{-1} $C0_2$, without affecting plant biomass 18 DAS. The ecological and physiological implications of such altered root morphology and architecture are also related to water and nutrient acquisition capacity from soil of the root system (Fitter, 1985; Fitter and Stickland, 1991; Lynch and van Beem, 1993). Using CO_2 enrichment in a controlled environment would be a valuable approach to increase early root branching in seedlings during greenhouse transplant production.

Conclusions

Root growth, development and architecture are important aspects of seedling growth. Stresses reduce root growth, root volume and extent of root soil exploration. If root growth declines due to stress, the supply of water and nutrients to the shoot may be reduced, with a subsequent reduction in shoot growth. However, conditions that limit photosynthesis can reduce shoot growth, limit assimilate translocation to the roots, and in turn, can limit root growth. Therefore, stress originating in either the root or shoot affects whole plant growth (Brown and Scott, 1984; Miller, 1986).

Studies relating the effects of the environment immediately after radicle protrusion can provide valuable insights into implications of root perturbation on early seedling growth and subsequent plant development. Understanding root architecture is important to improve transplant quality and production. Lack of methods to study root growth, which enable direct observation of the roots without their disruption, generally limits the study of root architecture. A medium-transparent whole-plant method for studying early root growth is available and might be used for precise and accurate nondestructive plant measurements under controlled environmental conditions. It could be a valuable tool to investigate root morphology and development in different species, to better study, select and breed new varieties based on root architectural potential. Although architectural changes of root systems caused by environmental conditions may occur without noticeable biomass changes in the whole seedling, they might affect the transplant stand establishment and subsequent yield of vegetable crops.

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