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Root Systems of Vegetable Crops: A Brief Introduction

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Roots have several vital functions in crop plants, including providing anchorage, absorbing and conducting water and nutrients, providing a "sink" (and sometimes a storage location) for assimilates, and synthesizing certain phytohormones. Yet, the statement made by Weaver and Bruner in 1927 (5) remains true today: "The roots of plants are the least known, least understood, and least appreciated parts of the plant". This lack of understanding can be attributed to the fact that roots are usually out of sight, and to the tedious and difficult nature of root studies in situ.

The aerial environment indirectly influences the root system through the shoot. The soil environment similarly affects the shoot through its influences on the root system. Growers generally can exert more control over the soil environment than over the aerial environment (5). Indeed, most cultural practices directly or indirectly affect the root-soil environment (3). Several possible benefits of improved knowledge of vegetable crop root systems may accrue to growers. Answers to cultural questions such as the best time or method for applying fertilizer or irrigation water would be based on more direct evidence. Cultivars may be selected not only for climatic adaptability but also for adaptability to specific soil conditions. Efficiency of plant arrangements in the field can be improved. Intensive cultivation by intercropping or succession cropping will be favored by knowledge that roots are well-distributed throughout the soil volume (5). Crops may be selected for tolerance to high or low levels of plant nutrients or other dissolved elements in the soil solution (1). Losses from lodging may be reduced or eliminated (4). Ultimately, root-centered mathematical models will be developed for computers that can be used to help farmers make cost-effective management decisions (2, 3). The overall result will be increased yields.

Considerable progress has been made in root-system research during the past 2 decades. However, much remains to be done. The following list of research needs was compiled by Klepper et al. in 1983 (3): "More specific information is needed on: phenology of root system development relative to shoot development under field conditions; above- and below-ground environmental effects on root growth and death; functional relationships among roots, between roots and soil, and between roots and shoots under field conditions; genetic variation in root anatomy and rooting patterns; [and] effect of variability in the landscape, soil profile, and plant populations on operation of models of the soil-root system." This list was compiled for field crops. If anything, it is even more applicable to vegetable crops, for which even "baseline" root data are minimal.

Papers in this symposium provide current information on methods of studying root systems in the field, rhizogenetics of vegetable crops, root system effects on lodging of vegetable crops, root systems in relation to stress tolerance, root-related differences in nutrient acquisition efficiency, and mycorrhizae in vegetable crops. Needs for additional research will be discussed. It is hoped this symposium will stimulate an increase in the small number of research scientists studying root systems of vegetable crops.

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Methods of Studying Root Systems in the Field

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Growing plants require photosynthetically active radiation (PAR), water, 15 to 20 elements (37), and the absence of lethal factors. Although most of the water and mineral elements used by plants is absorbed by roots, root systems have been studied in much less detail than plant tops. Part of this deficiency may be due to the "out of sight, out of mind" syndrome, but most of the deficiency occurs because root studies usually are much more time-consuming, more labor-intensive, and more costly than shoot studies. As one example, several related experiments were conducted during the 1979 growing season to obtain insight into the reason(s) why narrow-row soybeans (*Glycine max* L. Merr. 'Wayne') outyield soybeans grown in conventional meter-wide rows (2, 13, 16, 17, 21, 22, 25, 34). Much more data were collected above-ground than below the soil surface, but the above-ground measurements required only about one-half as much labor as the below-ground measurements.

Root studies are often so tedious and time-consuming that one should use the simplest possible procedure that will furnish the desired information. A simple spade slice through the plow layer into the subsoil may be sufficient to detect a pressure pan (plow sole) (Fig. 1) or nematodes. Several spade slices can be observed in a few minutes at very little cost. Often, however, a more quantitative answer is required than is possible with a spade. This paper describes techniques requiring greater intensity of effort than use of a spade. Boehm (5) and Schuurman and Goedewaagen (29) provide greater details on root study methods than is possible in this short article.

Fig. 1. A title spade is used to determine effects of soil cracking on cowpea (*Vigna unguiculata* L.) root development.

DESTRUCTIVE METHODS

Excavations

General architecture of the root system and extent of rooted volume of soil can be determined by excavating the entire root system or a segment of it. A trench is first dug around the plant. A support is provided for the plant top. Soil is removed from around the roots by using needles, air, or water pressure. The location and extent of the root system can be drawn on a plastic sheet, photographed, or mounted (Fig. 2). This technique may be the only feasible one in a rocky or gravelly soil or if the rooted volume of soil is not symmetrical. Many small roots are lost during excavation, and the technique is time-consuming. Preston (20) estimated that one person needs 5 weeks to excavate, measure, and record the root system of a 15-year-old pine tree. Rogers and Booth (24) calculated that about 60 tons of soil was removed in excavating the root system of a mature fruit tree. Weaver (41) and Weaver and Bruner (42) used this technique in many of their investigations.

Monoliths

The monolith method requires removal of a soil block and separation of roots contained in that block. Sometimes a trench is dug for access to the profile. Blocks of soil are removed from successively deeper layers until the bottom of the root zone is reached. Each block is soaked in water and soil is washed through a mesh grid leaving the roots. Alternatively, some type of container is forced into the soil deep enough to enclose the deepest roots. The container is pulled from the soil and either the monolith is cut into depth increments or small rods are forced horizontally through the soil. Soil is then washed from the roots.

Nelson and Allmaras (18) mechanized the monolith method. Trenches are dug around a soil block, leaving it free-standing in place. A steel and plywood frame, containing predrilled holes in the plywood, is lowered around the free-standing block. The frame is constructed to tighten against the block as it is lifted from the hole (Fig. 3). Small rods are driven horizontally through the soil, using the predrilled pattern of holes. The soil block is submerged in water, usually overnight. Soil is then washed away, leaving the root system held in place by the network of rods. The root system is cut into segments, each representing the roots found in a specific volume of soil. Roots are weighed or their length is measured using techniques discussed later.

Sivakumar et al. (30) collected soybean roots that floated free during washing. Some of these roots belonged to plants with tops outside the space enclosed by the frame. These roots were cut by the trencher. Other roots were cut by the small rods during insertion and others were broken during the washing process. Lengths of these loose roots were from 5% to 12% of the total length in the soil block. In addition, short segments of dead roots (last year's or this year's roots?) usually float away during washing; this removal reduces sample cleanup time. Boehm et al. (6) estimated labor requirements for one framed monolith to a 1.8-m depth at 1560 min (Table 1).

Cores

Core methods involve removing cylindrical core samples from the soil profile and washing the soil from the roots. Cores are

Fig. 2. Parts of the intertwined root systems of 2 soybean [*Glycine max* (L.) Merr.] plants are exposed by washing away the upper layers of Ida silt loam soil.

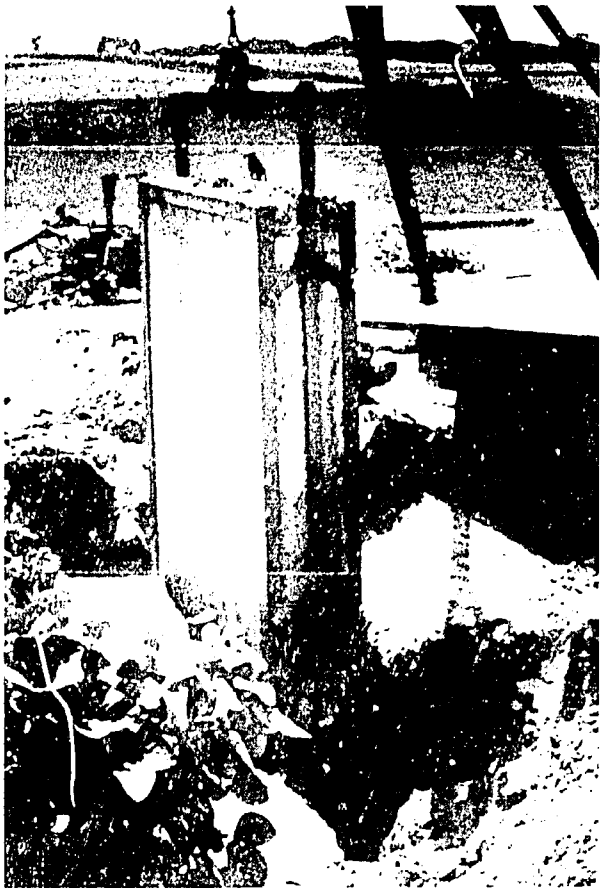

Fig. 3. The framed monolith method of Nelson and Allmaras (15) is used to extract a soil block from a soil profile.

usually extracted at various depths in the profile, at various predetermined distances from the plant bases, and in some predetermined time sequence. If depth of extraction is < 1 m, cores often are taken with a hand sampler, but deeper cores frequently require a machine driven sampler. Volume of cores often is much smaller than that of monoliths. Boehm (5) suggests that at least 5 cores be taken at each location to compensate for the smaller core volume.

Time required to extract the core from the soil is only about 20 min. This time is short when compared to the 240 min required to wash out the roots and clean the sample of debris. The core break technique (5) eliminates the wash and clean requirement. The soil core is grasped firmly in both hands and force is applied in such a way as to break the core near some predetermined position (Fig. 4). Roots that project outward from either broken surface are counted. This procedure provides a measure of relative rooting intensity (i.e., cm roots per cm^2 horizontal surface). If a rooting density value (i.e., cm roots per cm^3 soil) is desired, one must obtain a known volume of soil from the core, making sure that both faces are included in that volume. The roots are then washed from the soil and their lengths determined. A relationship is then developed between number of roots protruding from the faces and root length density. Core-break techniques are impractical in stony, gravelly, or low-coherence soils, or in soil containing roots > 2 mm in diameter.

Fig. 4. A soil core is broken to count the number of roots protruding from the broken faces.

Trench profile method

In this method (4), a 100-cm-wide soil profile wall is smoothed with a spade and sharp blades. Roots extending from the prepared wall are cut off with scissors. A fine spray of water at about 0.3 MPa is used to wash away a 5-mm thick layer of soil from the wall. A framed grid is placed against the wall and root length within each square grid is estimated (Fig. 5). Koepke (14) found the trench profile method consistently gave values about 48% to 50% of those determined from a core method (r^2 = 0.88 ± 12% unexplained variation). A conversion factor should be determined for each soil and plant combination if true quantitative values are needed.

NONDESTRUCTIVE METHODS

Minirhizotrons

In 1937, Bates (1) proposed the idea that roots could be observed through the walls of clear cylinders inserted into the soil profile.

Table 1. Comparative information for 5 root sampling methods

Method	Time required for various steps (min)	Plot area destroyed[1] (m^2)	Sampling is destructive of roots?	Literature citation
One framed monolith to 1.8-m depth	Dig a hole (30), refill hole (20), insert rods and place monolith in soaking tank (90), wash soil from root system (180), cut root system into subsamples (90), clean debris, obtain root length and mass (640).	5	Yes	6
One core (washed) to 1.8-m depth	Take core (30), wash roots from core (120), clean debris (120), estimate root length (120), obtain dry weight (60).	2	Yes	6
One core (core-break) to 1.8-m depth	Take core (30), break core and count roots at core faces (30).	2	Yes	5
One trench profile	Dig pit (30), smooth profile wall (90), wash and scrape soil from wall (60), estimate root length (60), refill hole (20).	5	Yes	4
One minirhizotron	Insert TV camera, count roots on monitor, remove TV camera (30)	0.5	No	27, 38

Fig. 5. A thin layer of soil is washed and scraped from the prepared face of an Ida silt loam soil profile. A square grid (left) is then placed on the soil face to allow root location and numbers to be determined in the trench profile method.

Several modifications have been added since then. The light bulb light source (3) has been replaced by fiber optics (28). The vertically oriented tubes have been replaced by tubes angled from 30° (38) to 45° (28) from the vertical. The mirror that reflects the root image has been replaced by a borescope (27) or by a television camera (38) lowered into the cylinder. The television image is viewed on a monitor or recorded on tape.

These changes have drastically improved quality of the minirhizotron results. With the clear vertical tube and mirror technique, roots that followed the soil–tube interface and images of roots that were located deeper than 1 m were difficult to distinguish from other soil features. A television camera, using tubes 30° to 45° from vertical, transmits sharp, clear images of roots located at least 3 m deep. The roots no longer follow the upper soil–tube interface, but may still follow the lower interface if the soil has been smeared during installation of the tubes.

Two experienced people can install one minirhizotron cylinder in about 30 min. These cylinders remain in the soil between measurements. Two experienced people can estimate root length density in another 10 to 15 min per cylinder. The equipment to read the root concentration is lightweight and portable, so it can be carried in a backpack (39) (Fig. 6).

Rhizotrons

Rhizotrons are covered underground cellars of walkways with clear windows on one or both sides (Fig. 7). Soil that contains roots is located behind each window. These rhizotrons can be simple covered pits containing one glass or clear plastic wall, or they may be large installations containing many square meters of viewing surface. Their specific design depends on the research questions to be asked. Rhizotron designs have been published by Fordham (7), Freeman and Smart (8), Glover (9), Hilton et al. (10), Huxley and Turk (12), Rogers (23), Soileau et al. (31), Taylor (32) and Taylor and Willatt (35).

Rhizotrons have several advantages over other root study methods. Successive measurements are made on the same plants each time and estimates of root growth can be made rapidly. These advantages also are true for minirhizotrons. Instruments and sensors can be installed easily in rhizotrons to measure soil conditions and, in some installations, the rooted volume of soil is hydraulically isolated (33).

Rhizotrons also have several disadvantages—one is the cost. The Auburn rhizotron cost about $40,000 when constructed in 1969. Comparable cost would be about $100,000 in 1985 for a well-designed and well-constructed facility. The less versatile Ames rhizotron (35) cost about $20,000 in 1973. For most rhizotrons, the aerial environment is different from field conditions. Rhizotrons require continual maintenance, but are available for many experiments so they are cost effective only if a large number of scientists are located near the facility. Rhizotron construction techniques, their

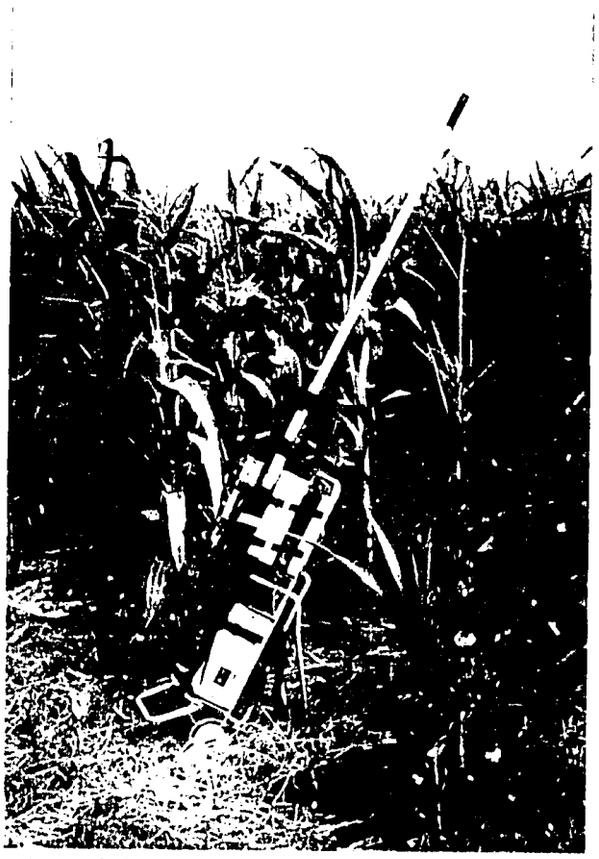

Fig. 6. A television camera is ready to be lowered into a minirhizotron tube to record roots at the soil–tube interface (38).

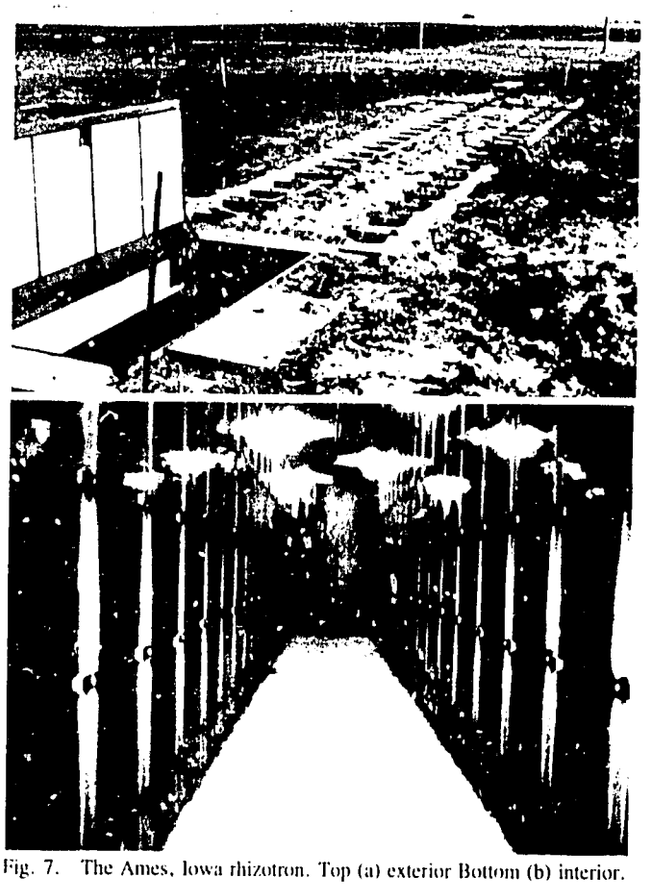

Fig. 7. The Ames, Iowa rhizotron. Top (a) exterior Bottom (b) interior.

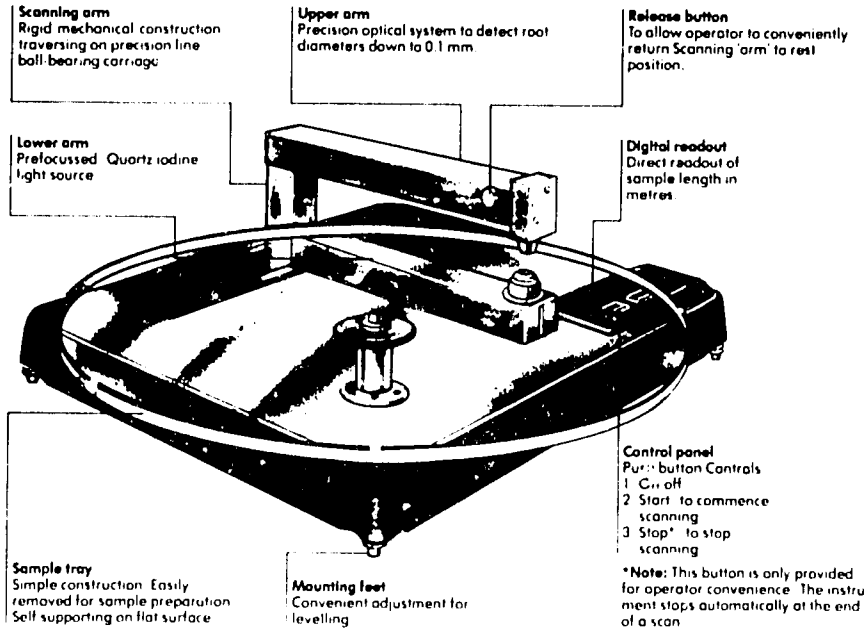

Fig. 8. A root length estimation device that is commercially available. When a root breaks the light beam, the readout counter advances.

operation, and types of experiments to be conducted in them have been reviewed (11, 35).

OTHER CONSIDERATIONS

Measuring root concentration

Many researchers report their results in terms of root mass density, (i.e., grams of root per cm^3 of soil). In those cases, debris is cleaned from the root mass, which is then oven-dried and weighed. This procedure is simple and is sufficiently accurate for many purposes. To increase accuracy, the samples can be ashed after initial weighing so mass of mineral soil clinging to the roots can be subtracted.

Most models of root uptake of water and ions require estimates of root length density (centimeters of root per cm^3 of soil). These estimates, when made on root samples washed from soil, usually are based on the line intercept method of Newman (19) because direct measurement is too tedious and inaccurate. Roots are spread over a flat surface of area (A), then set of randomly placed straight lines of total length (H) is superimposed on the root sample. The number of intersections (N) between the roots and random lines is determined, from which root length in the sample (R) is determined by the formula: $R = \pi NA/2H$.

In Newman's original technique, the straight lines are provided by hairlines in a microscope eyepiece. Newman's technique has been modified by Marsh (15), who superimposed a square grid rather than the eyepiece hairlines. Tennant (36) established the practicality of a square grid concept and Rowse and Philips (26) described an instrument for automating the root-intersection counts. Other root length determination instruments have been developed by Henstridge (LaTrobe Univ., Bundoora, Victoria, Australia), Commonwealth Aircraft, Port Melbourne, Australia (Fig. 8), and by Voorhees et al. (40).

Choosing a method

Root growth and root system architecture studies are so tedious and time-consuming that one should choose the easiest and simplest method that will provide the desired information. All systems where roots are separated from the soil by washing are time-consuming because of the necessity of cleaning debris from the sample. In addition, any of the root-washing techniques is destructive of that part of the soil–root system. For that reason, the minirhizotron technique is being pursued vigorously. D.R. Upchurch (Agricultural Research Service, USDA, Lubbock, Texas) has developed a theoretical basis for determining root length density from the proportionate number of roots striking 2 parallel strips on slanted minirhizotron tubes. In some soils, a nonrepresentative soil layer is created at the tube–soil interface by smearing the soil as a hole is dug for the tube. If the problem of smeared soil (with its altered rooting probabilities) can be solved, the minirhizotron would be the first choice for a field technique. In the meantime, my laboratory will continue to use the soil monolith and core break techniques. All other methods, in any event, will have to be calibrated against some technique involving washing roots from known volumes of soil.

A final caution

A final word of caution seems appropriate. Most workers will conduct whole-plant experiments rather than merely studying root systems as such. Experimental variation will be much greater for roots than for tops. I am asked frequently "How many samples should I take?"; my facetious answer is usually "more". Several years ago, an ARS statistician (C.K. Graham) and I decided to find out how many samples would be required to determine, within 10% error, the true root length density of corn (*Zea mays* L.) growing in Ida silt loam soil of western Iowa. Our answer, never published, was about 40 when the sample volume was 168 cm^3. The Ida silt loam soil developed on a thick loess deposit and is about as uniform a soil as one will find. Few, if any, researchers will take 40 samples to represent one point in space and time. One should be prepared to accept greater sample-to-sample variation in root than in shoot studies. As pointed out by Boehm et al. (6), considerable variation also will occur if methods are changed during the study.

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Rhizogenetics (Root Genetics) of Vegetable Crops

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BACKGROUND

Plants exist as integrations of their many parts and processes. Each part is conditioned by a distinct collection of genes that interact and integrate with the genes that condition other plant parts or processes (44). Root characteristics are conditioned by about 30% of the plant genome, and one-third of these (10% of the total) condition only root characteristics (39). This level of control for a single plant organ is in agreement with that of other plant organs (25) and implies that root characteristics are as amenable to genetic manipulation as the characteristics of any other plant organ or tissue. Root characteristics are not normally emphasized in plant breeding programs because of the difficulty in observing them in situ, rather than because of a reduced potential for improvement. The level of genetic control described (39) should allow the development of isogenic root mutants that have modified physiological and developmental controls to be used for precise experimentation. Data derived from experimentation with these isogenic root mutants would provide a sound basis for developing and testing hypotheses leading, ultimately, to genetic improvement of vegetable root systems.

In most plant species, only 10–20% of mature plant biomass consists of root tissue. Some vegetables, such as beet and carrot, are exceptions. Their extensive primary roots develop prior to flowering. In the plant kingdom as a whole, however, root mass is generally only a fraction of total plant biomass. The root : shoot biomass ratio changes during ontogeny, generally becoming less as the plant approaches flowering, and stabilizing after flowering (40). Genetic variations in the rate of change in biomass ratio as well as final ratio have been demonstrated in nonvegetables (40), and a cursory observation of developing vegetable cultivars (i.e., differing

carrot cultivars) affords the same conclusion for vegetables. Root : shoot ratios are not controlled solely by genotype. Culture of plants in nutrient cultures with differing, though nonlimiting, amounts of N and other inorganic nutrients gives rise to plants with differing root : shoot biomass ratios (14, 15).

With the exception of CO_2, roots are responsible for virtually all nutrient uptake. There has been some demonstration that mineral nutrients can be acquired through the leaves (21), but this is an atypical phenomenon. Roots, through their genetic makeup and/or environment, exert control over whole-plant growth and development by controlling all non-CO_2 nutrient uptake. The effect of environmental parameters on nutrient uptake and translocation within the plant (see ref. 12 for a review of temperature effects) is one aspect of indirect control over whole-plant processes by the root system (11, 18, 28). There is, however, increasing evidence that root environment and/or genotype have a direct effect on plant development and metabolism. Root genotype can dramatically affect or even effect shoot development (39). On the other hand, root gaseous environment can effect changes in net C assimilation rate (2, 3). Soil temperature and moisture content can also dramatically alter photosynthesis (5) and overall crop growth (1). It is not known if these different environmental characteristics obtain their effects through the same physiological pathways, but it is clear that roots exert a measurement of control over C assimilation and whole-plant growth and development.

Finally, the presence of significant amounts of genic duplication in most crop plants is a constraint to the study of genetic control of roots and their effect on the shoot. Even those crop plants considered to be diploid (e.g., corn) have significant amounts of genic duplication other than that commonly associated primarily with polyploidy (41). Research with electrophoresis and molecular techniques has confirmed this conclusion with several vegetables as well as other plant species (4, 19). The presence of significant amounts of duplication (about 80% of the "single copy" DNA in corn and soybean and 60% in pea) severely reduces the likelihood of ever discovering a specific recessive mutant in these species. For example, there is less than a 20% chance of ever finding a corn root mutant that is parallel to the *dgt* (lateral rootless) mutant of tomato. The genes are present, but there is an 80% chance that they are duplicated, and therefore this recessive characteristic will be masked by the dominant normal duplicate alleles. Tomato has been estimated to contain only 20% genic duplication (4). This low amount of genic duplication and the extensive genetic research already established with tomato make it an ideal genetic tool to study the nature of genetic control over roots. Pea, with only 60% duplication (41), is the next most useful species.

CLASSICAL MORPHOLOGY AND DEVELOPMENT

Observational studies with roots have been published for at least 200 years (22, 24, 27, 33). Several excellent recent reviews and texts summarize much of these data and other aspects of roots not covered in this symposium (13, 29, 34, 35). During the past 80 years, there has been an attempt to standardize descriptions of roots so that individuals can clearly understand which part of the root system is being discussed. Terms like primary, secondary, and tertiary are generally used to describe the branching pattern relationship of individual roots or groups of roots to the stem. These are very general terms and provide no insight into the nature of the root itself. In plant anatomy texts (see ref. 13 for an example), 3 types of root characterized by anatomical and developmental differences are discussed: tap root or radicle (the root that is of embryonic origin and constitutes the pole of the embryo opposite to the shoot apex); lateral roots (those roots that arise from pre-existing roots and develop from the pericycle layer); and adventitious roots (those roots that arise from nonroot tissues or nonpericyclic tissues in older roots).

In addition to the classical types of root, there are frequent references to other "types": seminal, transient, proteoid, stress, and "grenzwürzeln" [translated from German as "basal root" or "boundary root" (36)], to name only a few. The first of these, seminal roots, is described by Esau as first appearing in the embryo of some monocots (especially the grasses), but also appearing later in the development of the seedling (13). In most corn cultivars, the radicle degenerates during the development of the embryo and the first root to emerge is one of the seminal roots acting as a replacement for the radicle. Transient, proteoid, and stress roots are normally considered to be environmentally induced morphological variants of lateral roots, while basal roots have been termed adventitious. Relationships between the classical 3 types of root, and seminal roots and basal roots will be discussed in the next section.

Developmental

A brief genetic study described by Zobel (39) clarifies the interrelationships of some of the various types of root. A double homozygote (*dgt/dgt; ro/ro*) was developed from a hybridization between a recessive tomato root mutant that does not develop lateral roots [lateralless, genetic name *diageotropica (dgt)*] and another recessive mutant that does not develop adventitious roots [adventitiousless, genetic name *rosette (ro)*]. Assuming only 3 types of root, hypothetically the double homozygote should have had only a tap root. The resulting double homozygote had up to a dozen roots originating in the hypocotyl and upper portion of the tap root. Zobel concluded that, based on genetic criteria, there are 4 types of root: radicle, lateral, adventitious, and "basal" (39). In unpublished research, Zobel has demonstrated that basal roots originate from the pericycle of the lower hypocotyl and upper tap root. Basal roots clearly are not adventitious in anatomical origin, nor lateral or adventitious in genetic control of their initiation.

In the definitive study on grenzwürzeln (basal roots), Weinhold (36) describes basal roots as arising acropetally (toward the shoot apex) from the germinating seedling, while lateral roots arise basipetally (toward the radicle apex). Weinhold demonstrated this pattern in dicots as well as monocots. This description of basal roots is clearly that of the seminal roots in monocots and hypocotyl adventitious roots in dicots (9). In a series of experiments that were designed to test the effect of several growth-modifying compounds [9-hydroxy-fluorenol-9-carbonic acid-butyl ester (9-OH), 2-chloro-fluorenol-9-carbonic acid-methyl ester (2-CH), benzimidazol (BI), *N*-(phenylmethyl)-1*H*-purin-6-amine (BA), and 1*H*-indole-3-acetic acid (IAA)] on root growth and development, it was found that 3 compounds (IAA, BI, and BA) inhibited or strongly suppressed all root growth. One compound (2-CH) had no effect on the tap root but inhibited both basal and lateral root growth, and the other compound (9-OH) only inhibited lateral root growth (20). Thus, there are distinct physiological differences between roots of different origin. Therefore, based on physiological response, anatomical characteristics of initiation, and genetic control of initiation, there are clearly 4 different types of root (tap, lateral, basal, and adventitious). To understand whole plant root systems adequately, future root studies must take these differences into account when investigating root function, growth, or development (30–32).

Morphological

Lateral roots exist throughout the root system of both monocots and dicots as branches from primary or secondary roots. Large lateral roots are frequently parent roots to the small feeder lateral roots. In dicotyledonous plants, large laterals develop secondary thickening and form a part of the permanent root system structure. Branching laterally from the large lateral, basal, and adventitious roots in both monocots and dicots are the small feeder lateral roots. With diameters in the <0.5–2 mm range, feeder roots provide much of the extensive surface area of a root system, but only a small portion of the total root biomass. As mentioned previously, there appear to be many morphotypes of lateral roots (stress, proteoid, transient, etc.). In the *Graminae*, feeder lateral roots are the predominant root type, branching off of basal and adventitious roots to produce a dense mat of rootlets in the plow layer (sweet corn provides an excellent example of this type of root system in vegetables). In dicotyledonous plants, the root system tends to grow deeper into the soil, with less dense matting near the surface.

Under stress conditions, greater numbers of feeder lateral (stress) roots develop in tomato than under optimum conditions (39). These

stress-related roots are restricted to the plow layer and can easily be observed with minimum excavation. In a given environment, cultivars differ in number of stress roots that develop. Cultivar differences in the quantity of stress roots suggest a fairly strong genetic–environment interaction. In fact, stimulation of feeder lateral roots has been suggested as a simple test for environmental adaptiveness of different tomato cultivars (39). Although small feeder lateral roots are mentioned in relation to most plant species (stress roots, transient roots, fibrous roots, etc.), the observation that they are absent on high-yielding, well-adapted tomatoes (39), suggests that they are not necessary for optimum growth and function of the root system in environments to which the cultivars are optimally adapted.

Differences between small feeder lateral roots and the large lateral roots that develop secondary thickening are not sufficient to classify them as a different type of root at this time. As with basal roots, further study may eventually demonstrate that they are a distinct type of root. In the interim, root studies should very carefully document the developmental and morphological nature of the roots being studied. Data acquired without adequate descriptions may lead to erroneous conclusions by being compared to roots with distinctly different developmental and physiological characteristics. For example, Byrne and Aung (9) adequately described the "adventitious" hypocotyl roots they studied, allowing the conclusions they developed to be correctly applied to basal roots.

Environmental impact on roots, and the resulting interaction with the genotype, require statistical techniques that are capable of separating additive from multiplicative effects. Standard analysis of variance (ANOVA) and linear regression techniques are designed to treat additive effects rather than the multiplicative effects more typical of interactions. As a result, multiplicative effects are not observed, and many significant interactions between the environment and root growth and development are overlooked. Treatment of roots as a single class in experiments is similar to pooling data from leaf, petiole, and stem to determine the function of the shoot. Multivariate techniques allow the separation of roots into classes of different types followed by statistical analysis on the separate classes as well as the pooled data (16). Some multivariate techniques also handle multiplicative effect in least-squares fashion. A hybrid statistical package that uses the best of both the additive procedures and the multiplicative procedures (17) should produce new insights into the genetic nature of vegetable root systems.

A significant obstruction to detailed study of intact root systems always has been the inability to observe the roots nondestructively. Aeroponics, first developed in 1942 (10), has been updated (43) to provide long-term growing conditions for intact plants where the roots are bathed in a nutrient (23) mist of controllable density. This culture technique allows nondestructive observation of intact root systems of all types of plants, even those sensitive to the relative anaerobiosis of highly aerated hydroponics. By manipulation of gases, temperature, and mist density within the aeroponics tank, studies involving very precise environmental–genotype interactions are possible.

Physiological

Genes that control the root system can have their effect either directly or indirectly. Of the 30% of the genome that conditions rooting characteristics, only one-third affect the root system alone. A case in point is the *diageotropica* mutant of tomato. This mutant is without lateral roots (lateralless), but it also has a distinct diageotropic shoot habit. Root characteristics are conditioned by the shoot genotype. Grafting studies have shown that a normal shoot will normalize the root phenotype and, in addition, treatment of the shoot of intact mutant plants with low concentrations of ethylene gas will also normalize the roots (38). The lateralless characteristic is a side effect of the genetic lesion rather than the primary effect.

The root mutants that condition effects that are the reverse of those of *diageotropica* demonstrate an effect roots generally have on the shoot. The *bushy root (brt)* mutant of tomato is characterized by large numbers of roots developing from the basal portion of the hypocotyl and tap root and a small weak shoot. This mutant is characterized physiologically by extensive starch deposition in the basal portion of the shoot and root (37). If the mutant shoot is grafted onto normal roots, the shoot grows normally, while if a normal shoot is grafted onto the mutant roots, the normal shoot takes on the characteristics of a mutant shoot (37). In this instance, the genetic lesion is in the roots, and the shoot characteristics are secondary effects of the mutation.

The 2nd root mutant, dwarf root (this term is used here in a descriptive sense, since it has not been cleared as a name by the tomato genetics nomenclature committee) presents a variation on the phenomenon of root control of shoot growth (39). Although the roots of this mutant are dwarfed under all conditions of culture, high nutrient levels in hydroponics result in a normal shoot rather than the dwarfed shoot typical of a soil-grown mutant. If nutrient levels are reduced to ≤25% of recommended levels (23), the shoot takes on a dwarf-like appearance. The *bushy root* and dwarf root mutants mimic, in tomatoes, dwarfing root stocks of fruit trees. The dwarf root mutant presents a developmental pattern that may be of significant use in commercial tomato production where water is expensive, or in greenhouse production using thin-film hydroponics. The small root system is ideal (for example) for culture under drip irrigation, where water use must be kept to a minimum. The use of highly enriched nutrients will yield normal shoot and fruit development, while root development will be kept to a minimum.

POTENTIAL FOR THE FUTURE

Others in this symposium discuss roots in relation to several different characteristics. The desire for improved nutrient uptake, salt tolerance, drought resistance, etc., all require genetic manipulation of the root system to achieve their end. There is, however, little knowledge about the genetic control of root growth, development, and function. Several reasons for this paucity of information have been advanced here, such as difficulty of study, confounding of results by pooling different root types, inadequate statistical procedures, and the presence of extensive genic duplication in most crops. These problems have not prevented significant advances, and the potential for the future is great (42).

The inherent spatial variability of the soil gives rise to many microenvironments. If data taken from roots grown in these microenvironments are pooled, as is likely with normal experimental plot designs, the effect of these differences will be masked or swamped, concealing potentially significant relationships. Soil science has adopted a group of statistical procedures (called isarithmic mapping) that are capable of treating this microenvironmental variability in a consistent fashion (6–8). Adoption of some of these procedures for field root research will lead to significant advances in knowledge of root growth and development and its interaction with the environment. Vegetable breeding that emphasizes root characteristics would benefit from the use of isarithmic mapping procedures.

SUMMARY

The conclusion that there are 4, rather than 3, distinct types of root leads to the question: Do we really know how many types of root there are in a typical vegetable? With the current paucity of physiological, anatomical, and genetic knowledge of roots, it would be foolish to answer this question in the affirmative. Future root studies, whether they be physiological, anatomical, or genetic, must include detailed descriptions of the morphological characteristics of the roots being used and their relationship to the intact root system. Many past studies have been carried out by pooling physiologically and/or morphologically distinct root types. This pooling leads to data of questionable use at best and invalid or inaccurate conclusions at worst.

It has been shown here that, as with the dwarf root mutant, there is potential for development of root mutants that will improve the efficiency of vegetable production under normal as well as less-than-optimum or novel conditions. Use of the dwarf root mutant in drip or thin film agriculture is only one example of the potential for commercial agriculture. For example, a hypothesis that limiting the numbers of roots on wheat plants will increase yields under

stored soil water conditions has been tested successfully (26). Imagination, not genetics, is the only restriction to using plants with modified roots to improve commercial vegetable culture.

Roots are poorly studied primarily because of their physical location and growth habit. Since 30% of the genome conditions root characteristics, a moderate portion of the "plant" genome remains essentially unknown. Although most crop species have extensive genic duplication, reducing the availability of recessive mutants, 2 vegetables (tomato and pea) have low enough levels of duplication to allow induction of root mutants for development of isogenic lines. These isogenic lines then can be used to study the basic processes in which roots affect and effect plant growth and development. Much greater advances in the knowledge of rhizogenetics of vegetables will be possible if hybrid statistical packages, isarithmic mapping techniques, and aeroponic culture techniques are coupled with these isogenic lines.

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Root System Effects on Lodging of Vegetable Crops

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Lodging may be defined as "the state of permanent displacement of stems from their upright position" (31). Diverse factors are known to bring about lodging. Plants may be inherently weak and susceptible to lodging due to such traits as a low stem lignin content (4, 49) or a small root system (31, 40, 45). Plants may be weakened due to damage by insects or pathogens (24, 31). Cultural practices can increase lodging through increased plant populations (13, 31, 54), high fertilization rates (31, 54), irrigation (31, 54), or damage from cultivation (18). Both stem lodging and root lodging may occur. In stem lodging, the plant bends over or breaks at any point along its stem. In root lodging, straight and intact stems lean over from the ground level due to a disturbed or an inherently weak root system (31).

Lodging investigations have been conducted primarily on field crops, especially those of the family *Gramineae*, reflecting both the morphology of the plants and the early development of mechanical harvesters for them. The continued interest in mechanical harvesting of vegetable crops, combined with a growing recognition of physiological yield losses resulting from lodging (even in hand-harvested crops), leads to a consideration of lodging in vegetable crops. This paper reviews the subject of lodging in vegetable crops with emphasis on the role of the root system in crop anchorage. As much of the research on root lodging has been conducted on agronomic crops, these crops also will be referred to where appropriate.

Relation of root mass to root lodging

Genotypes with inherently large root systems have been associated with reduced lodging in maize (*Zea mays* L.) (45), paprika peppers (*Capsicum annuum* L.) (17), and dry beans (*Phaseolus vulgaris* L.) (40). This association also has been found in several agronomic crops, such as tobacco (*Nicotiana tabacum* L.) (2), oats (*Avena sativa* L.) (36), wheat (*Triticum aestivum* L.) (52), soybeans [*Glycine max* (L.) Merrill] (15, 51), and alfalfa (*Medicago sativa* L.) (48). Uprooting resistance, the amount of force (kg) required to excavate an individual plant, has been used by researchers as an indirect method of evaluating the size of root systems. Significant positive correlations between uprooting resistance and root size have been reported in several crops, including maize (8, 26), dry beans (40, 42), and oats (7, 36). Direct positive correlations between uprooting resistance and lodging resistance were reported in maize (12) and black beans (40).

The association between increased total root mass and root lodging resistance may be better understood if the total root system is partitioned into its morphological components. Descriptions of vegetable crop root systems were developed as early as 1927 by Weaver and Bruner (50). Tanaka (43, 44) classified legume crops into alfalfa, vetch (*Vicia* spp.), and intermediate (soybean) root developmental types based on their elongation, branching, and thickening. Zobel (58) divided tomato root systems into 4 root types based on anatomical and genetic criteria: adventitious roots, basal roots, lateral roots, and radicle (taproot).

Resistance to root lodging may be associated with a particular root morphological characteristic. Stoffella et al. (41) attributed the erect plant type of 4 black-seeded dry bean breeding lines to larger basal roots as compared to 2 standard more prostrate cultivars. Sechler (36) reported that lodging-resistant oat strains had longer rootcrowns, larger culm and root diameters, and lower shoot : root ratios than lodging-susceptible strains. Lodging-resistant genotypes of wheat (30), oats (11), and barley (*Hordeum vulgare* L.) (14) were found to have a wide root-spreading angle. A short basal internode length with a large number of prop roots was proposed to be associated with lodging resistance in maize (53). These findings suggest that individual root mass components may be responsible for the exhibited lodging resistance in cultivars of certain crops. It may be more efficient to screen and select germplasm for a specific root characteristic than for a large total root system.

Lodging in specific vegetable crops

Lodging, whether attributed to the stem or to the roots, has been studied in relatively few vegetable crops. Following are summaries of lodging research on 6 vegetables.

Peas (Pisum sativum *L.*). Samarin (33) studied factors affecting lodging resistance in all the annual *Pisum* species, including 10 cultivars of *P. sativum* and 3 mutants. A 2nd study (34) compared 5 *Pisum* species with *Cicer arietinum* L. and a species of *Lathyrus*. The main factors conditioning lodging susceptibility in pea proved to be low content of mechanical tissue at internodes 5 to 6 and vigorous development of the upper part of the plant. Interspecific differences were observed.

Kaatz and Gritton (16) compared yield and height responses of 5 pea cultivars that were artificially supported or allowed to lodge naturally. Effective support treatments increased shelled pea yields an average of 8%, due primarily to improved light penetration into the plant canopy. Supported plants were taller than unsupported plants during the latter part of the season, when most shading of lower leaves would occur. Unsupported plants sometimes lodged to half their original height. The authors stated that, while some of the shorter and earlier pea cultivars were less prone to lodging, none stood perfectly erect.

Stem lodging appears to be the primary type of lodging in peas. Some modern pea cultivars now possess the *afila* gene, which causes tendrils to be produced rather than leaflets. Plants of such cultivars lock together and become more self-supporting, easing mechanical harvest (3).

Potatoes (Solanum tuberosum *L.*). Large seed pieces, close spacing, irrigation, and high fertilizer rates may increase potato yields either through increased leaf cover or by maintaining leaf cover for longer times, but these practices also result in increased stem lodging (54). In a study with artificial lodging and support of 'Pentland Crown' (54), lodging decreased radiation interception and tuber growth. However, these effects were partially offset by compensatory haulm (vine) growth when lodging occurred early in the season, and the greatest yield loss was about 8%. Compensatory haulm growth did not follow late lodging, but as leaf areas were already declining, the yield loss was even smaller. Thus, lodging had little effect on this cultivar, which produces large haulms and has a long growing season. The authors suggested that lodging might be a problem with earlier cultivars or those with small haulms (55).

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Tomatoes (Lycopersicon esculentum *Mill.*). Adelana (1) found that lodging in tomato was positively correlated with plant height, leaf area per plant, number of branches per plant, and fruit yield. Tall, indeterminate cultivars were vulnerable to wind-induced lodging due to heavy branching and the production of fruit trusses high in the plant profile. However, indeterminate cultivars also tended to produce more fruits than determinate cultivars. Staking was useful to prevent lodging and maximize yields, but was expensive. Adelana (1) suggested breeding for increased yields on shorter plants.

Maize (Zea mays *L.*). Almost all of the lodging research on this crop has been conducted on field corn. However, sweet corn belongs to the same species, so results may be applicable.

In an early report, a lodging resistant inbred strain of 'Yellow Dent' maize had more main roots and lateral roots per plant, a greater total length of lateral roots, and a greater uprooting resistance than a lodging-susceptible strain (12).

Wilson (53) stated that extensive development of prop roots and a short length of the 3 most basal internodes were important aspects of maize lodging resistance.

Phosphorus and K increased maize root anchorage to a greater degree than did N in deficient soils (29). In addition, the amount and distribution of rainfall had more influence on maize lodging than wind velocity. The greatest lodging occurred when rainfall was accompanied by high winds. Root lodging was much more common than stem lodging in this study (29).

Hall (10) studied selfed lines of maize and their F_1 hybrids. Correlation coefficients showed little or no relationship between the amount of lodging and ear height, length of underground stem, stalk cross-section, stalk disease, size of brace roots, number of suckers, and ear weight. Significant negative correlations were obtained between the amount of lodging and the depth, width, and volume of the root clump; the length and angle of brace roots; and pressure required for uprooting for the selfed lines. It was concluded that lodging was determined by a complex of characters and these characters were inherited separately.

Craig (8) observed that mass selection for root strength (in terms of uprooting resistance) seemed to be a practical means of increasing root strength and root lodging resistance in maize populations having sufficient variability for this trait. Selection for root strength did not affect yield of the maize synthetic.

Thompson (45) extracted maize root clumps from the soil with a potato digger. Significant negative correlations were obtained between root clump size and root, stalk, and total lodging.

Nass and Zuber (26) grew maize in sand cultures and evaluated roots at 28 and 35 days after planting. Total root weight, root volume, and weight of nodal roots were positively correlated with root clump weight and root pulling resistance of mature plants under field conditions, while the percentage of seminal roots was negatively correlated with these 2 field measurements.

Thompson (46) used recurrent selection in 2 maize synthetics for lodging susceptibility and resistance. As the percentage of erect plants increased, stem tissue became stronger and denser, the rind thickened and became more resistant to puncture, roots proliferated, and grain yield decreased. However, a subsequent study (47) showed that the yield reduction was minimized in hybrid combination with unrelated testers. In the 1972 study (46), stem lodging accounted for 89% of the total lodging in the cross of the original synthetics. Little change occurred for root lodging resistance until stalk strength was improved.

Potassium fertilization reduced stem lodging of maize in one study (22). The main benefit of K was said to be maintenance of the stalk tissue.

Zuber and Kang (59) reported that stalk lodging causes an annual yield loss of 5–25% in United States' field corn. Stalk strength was evaluated by the stalk-crushing and rind-puncture techniques. High stalk crushing strength was associated with an increased lignin content of the rind and with reduced stalk lodging. They stated that maize hybrids in the 1970s had 2 to 3 times greater stalk strength than strains grown in the 1940s.

In a Nigerian study, lodging in maize was positively correlated with plant height, ear height, and length of the basal internode, and negatively correlated with yield. Earliness, stem diameter, and leaf area were not related to lodging. Stem lodging was more common than root lodging (32).

Inoue and Okabe (13) found that, in lines of maize grown at 88,800 plants per ha and sown in early June or at 44,000 plants per ha and sown in mid-May, root lodging was 2.5 times more frequent with the high density–late planting combination. Low temperature and dry conditions during early growth and heavy rainfall at or soon after tasseling were thought to be related to root lodging.

Root lodging was positively correlated with stalk rot rating and negatively correlated with stalk strength per area and rind strength in a study of a maize synthetic subjected to recurrent selection for stalk quality (24). Many stalk-rotting organisms enter the plant through the roots, which helps explain the positive association between stalk and root quality (38). These results contrast with those of Mohamad (25), who found that 4 cycles of selection for high stalk crushing strength decreased resistance to root lodging.

In summary, it appears that root lodging received more attention than stem lodging in the decades before the development of hybrid maize. The nodal or brace roots seem to be most important in conferring root-lodging resistance through their contribution to a deep, spreading, voluminous root clump. Stem lodging is a primary concern today. Although maize breeders have greatly improved stem lodging resistance, their gains have been partially offset by increased fertilization and higher plant populations (59). Interrelationships between root and stem lodging in maize are not clear-cut. Colbert et al. (6) have stated that the simultaneous selection for maximum yield and stalk and root lodging resistance by maize breeders has resulted in a favorable partitioning of the available photosynthate into the ear, stalk, and roots. A disproportionate positive emphasis on any one of these 3 components seems to produce a negative response in the other 2. They suggested this dilemma may be solved if the amount of photosynthate produced per plant can be increased.

Peppers (Capsicum annuum *L.*). Observations have shown that lodging often is a problem in pepper fields. Some of the specialty types, such as paprika, are mechanically harvested, and there is interest in development of a mechanical bell pepper harvester (19). Tall, upright plants are important for mechanical harvest of peppers (19), but little information is available on lodging differences in this crop.

Kahn (17) compared 3 lodging-resistant and 3 lodging-susceptible paprika pepper lines. Root lodging was more common than stem lodging in this study. On the average, lodging-resistant plants had large stem diameters at soil level, greater total root weights, and lower shoot : root ratios than lodging-susceptible plants but did not differ from lodging-susceptible plants in shoot weight, number of marketable red pods, and cellulose and lignin content in the lowermost 8 cm of central axis stem tissue. Thus, a thick stem and large root system relative to the above-ground parts seemed to explain the lodging resistance of the upright lines.

Dry beans (Phaseolus vulgaris *L.*). Erect bean plants with pods high off the ground at maturity dry more rapidly, which can result in lower harvest losses and improved seed quality (35). Stoffella et al. (40) found 4 blackseeded dry bean breeding lines lodged less than 2 cultivars. The difference can be pronounced, as shown in Fig. 1. The lines were found to have larger total root masses, greater uprooting resistance, lower shoot : root ratios, and greater seed yields than the 2 cultivars under field conditions. Lodging generally began after the seed initiation stage and progressed until final harvest. Root weight during full pod fill and lodging were negatively correlated.

Stoffella et al. (41) also partitioned the root systems of the 6 bean genotypes. Basal roots comprised the bulk of the total root mass under field conditions. The 4 upright lines had greater stem, hypocotyl, and taproot diameters than the 2 cultivars. These traits provided the plants with a solid base of support and may have allowed a greater portion of photosynthates to be translocated to the root system. Genotypes did not differ for basal root number in the field, but basal root diameters and weights were highest in the 4 upright lines. Apparently, basal root thickening, rather than an increase in number, provided greater lodging resistance. Most root parameters increased up to the seed initiation stage, followed by a

Fig. 1. Plants of the black-seeded dry bean cultivar 'Black Turtle Soup' (foreground) and the breeding line '70001' (background) at harvest near Aurora, N.Y. Note the upright habit of '70001' and the lodging susceptibility of 'Black Turtle Soup'.

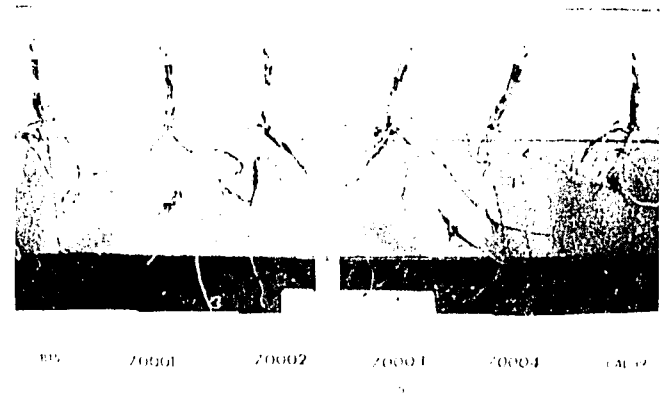

Fig. 2. Root systems of 4 black-seeded dry bean breeding lines ('70001', '70002', '70003', and '70004') and 2 cultivars ('Black Turtle Soup'-BTS and 'Strain 39'-CAL39) excavated from the field at the full pod fill growth stage. The breeding lines are greater in total root mass, basal root diameter and weight, and lodging resistance than the cultivars.

significant decrease or no further increase at the full pod fill stage. Thus, root senescence may have begun before physiological maturity, which could contribute to lodging before harvest. Root systems at the full pod fill stage are illustrated in Fig. 2.

Root weight, shoot weight, and shoot : root ratio of black beans decreased linearly as between-row spacing decreased from 76 to 61 to 46 cm in one study (18). However, lodging ratings and seed yield were not significantly affected.

Barriers to maximum yield attributed to plant lodging

Yield losses attributed to plant lodging may result from physiological, physical, or mechanical harvesting barriers. Examples are given in Table 1.

It is well-documented that lodging causes physiological yield reductions. An important cause for this may be reduced carbohydrate levels due to decreased light interception by lodged plants (15, 16, 23, 54). Lodging also exposes fruits or seeds to bare soil, making cleaning more difficult and promoting attack by pathogens, insects, or slugs (1). The reduced air circulation in a lodged canopy may also promote disease (16). Thus lodging is a concern even in crops that are not mechanically harvested.

SUMMARY

The capability to support or anchor the above ground shoot properly is a vital function of the root system. Root lodging can be a major yield barrier in certain vegetable and agronomic crops. An upright plant habit is desirable for ease of mechanical harvesting and to reduce or avoid physical and physiological yield losses. Significant gains have been made in the development of lodging-resistant cultivars. Future research needs to be directed toward a fundamental as well as an applied approach to reducing root lodging. There is considerable information on root lodging for several agronomic crops. Additional research is needed on the relationship of root systems to lodging and yield reduction in many vegetable crops.

Table 1. Causes of yield losses attributed to plant lodging.

Barriers	Results from plant lodging	Crops	Literature cited
Physiological	Reduction in fruit or seed yield when comparing lodged plants with erect plants of the same genotypes	Barley	9, 37
		Dry beans	5, 39
		Oats	28
		Peas	16
		Potatoes	54
		Soybeans	15, 23, 57
		Wheat	20, 52
Physical	Reduced air circulation and increased exposure of fruits or seeds to bare soil, promoting attach by pathogens, insects, or slugs	Peas	16
		Tomatoes	1
Mechanical harvesting	Inability of a machine to harvest all of marketable fruits or seeds	Dry beans	40
		Maize	56
		Peas	16
		Peppers	17
		Soybeans	21, 27, 57

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Root Systems in Relation to Stress Tolerance

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Roots anchor the plant in the soil, absorb and translocate water and nutrients, synthesize and transport growth regulators and other organic compounds, provide a sink for carbohydrates from the shoots, and in some species act as storage organs. Most research on roots has dealt with their role in absorption. Root characteristics that affect the area of absorbing surface are important, i.e., root length density, number and type of root hairs, and mycorrhizal relations. With nutrients that diffuse slowly in the soil, such as P and K, root density is especially important. Factors that reduce root growth may injure the plant by reducing the volume and intensity of soil exploration. Fortunately, plants produce more roots than are needed for normal growth—insurance that the plant can survive stresses, purchased at a cost of the increased photosynthate and other materials required for the extra root production.

The root environment is seldom optimum for extensive, effective growth. Adverse conditions include deficient water and O_2, deficient or imbalanced nutrients, non-optimum soil temperatures, mechanical impedance, adverse chemical environment, and pathogen and insect problems. Most of these factors interact.

Canopy conditions that limit photosynthesis reduce shoot growth and limit assimilate translocation to the roots, thus reducing root growth. If root growth declines due to stress, the supply of water

and nutrients to the shoot is reduced, with subsequent reduced shoot growth. Thus, stress originating in either the shoots or roots affects the rest of the plant (10, 36).

Roots synthesize hormones such as ethylene, cytokinins, gibberellins, and abscisic acid. These affect root : shoot ratios, leaf senescence and abscission, root initiation and branching, root permeability, and stomatal behavior (35). Root stresses affect plant reaction to disease and may predispose the host tissue to pathogen invasion (40).

Root systems in response to 4 stresses (water, O_2, mechanical impedance, and temperature) will be discussed in this review. Stresses due to nutrients (5, 48, 83), toxic compounds (1, 71), salinity (34), and pathogens (31, 58) are discussed in recent reviews.

WATER STRESS

Probably the most common plant stress is lack of water (35, 39, 69, 96, 97). Water is needed as a) a constituent of protoplasm; b) an essential reagent in photosynthesis and in hydrolytic processes such as conversion of starches to sugar; c) a solvent in which salts and gases enter and move through the plant; and d) an essential factor in maintaining turgidity for growth, form, and position of shoots and opening of stomata (46). Many species show decreased root growth as soil water potential (Ψ_s) decreases (88).

Most water absorbed is transported through the plant and lost to transpiration. If transpiration exceeds intake, internal water stress develops quickly and physiological activities are adversely affected. Continued failure to replace transpired water will result in death from dehydration.

Mechanisms have evolved in higher plants that favor survival and growth with inadequate or irregular water supplies. These mechanisms have been classified as drought-escape, avoidance, and tolerance (51, 52, 69).

Drought-escape. Plants are able to complete their life cycle during periods when water is available. Short life cycles are characteristic.

Drought-avoidance. Plants are able to maintain a favorable water status by increasing water uptake or decreasing water loss in the presence of high evaporative demand. Inasmuch as drought is an environmental condition, the plants do not actually avoid it but rather avoid the low tissue water potentials associated with drought.

Drought-tolerance. Plants are able to maintain turgor pressure and near normal functions despite low Ψ_s. The term drought-resistance is used to include both avoidance and tolerance.

Drought-avoidance

Maintaining a water supply. Some species avoid or reduce drought damage by continued expansion of the root system into moist soil. For most species of interest, this provides only supplemental water that may be minimal for survival. If the soil water content is low enough that flow to the roots is negligible, available water also will be quite low. Water needed to sustain active transpiration cannot be supplied by root expansion only (97). The benefit of deep root systems in reducing water stress with limited water has been documented by several studies (42, 82).

Many plants can develop compensating roots in favorable soil zones when normal root growth is restricted elsewhere. Roots usually proliferate in moist soil, especially near the surface, partly because moist soil offers low resistance to root expansion and allows for a steep water gradient into expanding root cells. Root : shoot ratios usually increase with water stress (35, 63) as plant response mechanisms increase the water supply relative to demand. Jordan (39) reported regulating systems within young seedlings altered the flow of seed reserves among expanding organs so that as Ψ_s decreased roots grew relatively faster than the shoots. Sorghum (*Sorghum bicolor* L.) cultivars have been selected for differences in root : shoot ratios with the idea that plants with higher ratios should be more drought resistant (82).

Increased root resistance to water flow may reduce rates of water absorption early in a season so that more would be available at later critical growth stages (39, 86). Reduced root penetration rates of soybeans (*Glycine max* L.) may be beneficial (86). If root growth were slowed so that maximum depth was achieved in about 100 days, water use would be effectively deferred until the critical maturation time.

An extensive root system is not necessary for optimum plant growth if a plant can obtain adequate water and nutrients from a restricted zone. The lack of response to subsoiling in the coastal plains states (70) in years with adequate rainfall shows this. We have found little response to subsoiling a restrictive sand soil when we irrigated daily but did find a benefit when the irrigation interval was extended to 4 or 5 days (38). With trickle irrigation, roots grow in clusters in the moist soil around the emitters and thrive as long as nutrients are also supplied (33). However, crops with restricted root systems are vulnerable to water stress should rainfall or an irrigation system fail. Deep root systems reduce this possibility.

Reducing water loss. Some plants reduce water loss through reduced leaf expansion, leaf curling, and leaf orientation to minimize radiation interception, leaf shedding, radiation reflection, and increased water-flow resistance through the plant. Closing of stomata is a common mechanism to reduce water demand. This closing also results in restricted CO_2 diffusion into the leaves, reduced photosynthesis, and reduced evaporative cooling.

Drought-tolerance

Water uptake is a passive process with water flowing into the root down a water potential gradient from the soil, into and through the root and shoot, and into the atmosphere (35). The capacity to develop low osmotic potentials (Ψ_π) and thus maintain turgor is essential to survival and growth when Ψ_s is low. Cary (16) observed that drought-tolerant plants can grow and exchange air with the atmosphere even with very low Ψ_π. Ruf et al. (74) showed that species vary in the degree of adaptation to low Ψ_s. In both crested wheatgrass [*Agropyron desertorum* (Fisch.) Schult.] and potatoes (*Solanum tuberosum* L.), Ψ_π decreased as Ψ_s decreased, but wheatgrass Ψ_π was always about 0.7 MPa lower than that in potatoes. Top growth in both species was reduced much more than root growth as Ψ_π decreased. Tomatoes (*Lycopersicon esculentum* Mill.) have an adaptive feature for osmotic adjustment during water stress (85). Raden (69) indicated a limit of about 0.5–0.7 MPa osmotic adjustment, but some plants can adjust to much lower values.

With the exception of escaping water stress by rapid maturation, increased rooting volume and turgor maintenance are the only processes that allow plants to withstand drought without a reduction in photosynthesis and crop growth (96).

OXYGEN STRESS

Roots require O_2 for respiration, water and mineral absorption, and other metabolic activities. The O_2 used by roots is replaced largely by molecular diffusion between soil air and the above-ground atmosphere (43). Oxygen diffuses through the soil in air-filled pore spaces to the water films surrounding roots and then through these films into the roots. Carbon dioxide and other volatile compounds given off by the root follow the reverse route. Inasmuch as diffusion of O_2 through water is only about 10^{-4} as fast as through air, water within soil pores or covering a root surface often determines the aeration status. Although low O_2 contents in the rhizosphere will reduce root growth (84), recent literature has focused on oxygen diffusion rate (ODR) as a better measure of soil aeration. Large, air-filled pores are much more effective in O_2 diffusion than small pores (21, 76). Moist aggregates can have anaerobic zones within them, due to water interfering with diffusion, when air between aggregates contains adequate O_2. Although soil compaction reduces total porosity and pore size, compact dry soil is rarely poorly aerated. Only when many of the air passages become blocked with water do aeration problems occur, and such blockage is more likely in compact than in loose soil (21).

Grable and Siemer (29) showed that ODR approached 0 at about 10–12% air-filled porosities. They also demonstrated the combined effect of soil water and compaction in reducing air porosity (Fig. 1). There is much evidence that ODR values of about 0.20 $\mu g \cdot cm^{-2} \cdot min^{-1}$ are needed for normal growth (25, 80, 81). Prolonged periods of low ODR are unusual unless the soil is kept wet,

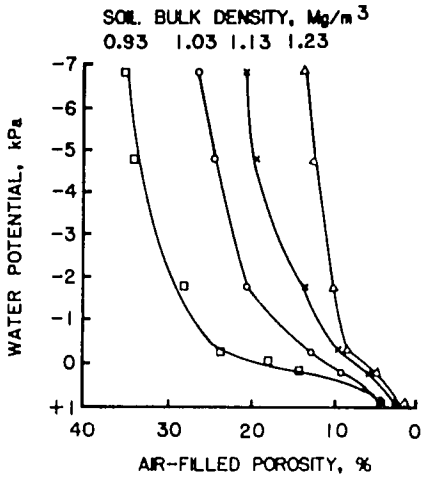

Fig. 1. Influence of soil bulk density and soil water potential on air-filled porosity of a silty clay loam (redrawn from 29).

but short periods of low ODR that occur after rain or irrigation can be detrimental. Temporary low ODR affected growth of peas (*Pisum sativum* L.), tomatoes, sugarbeets (*Beta vulgaris* L.), and corn (*Zea mays* L.) (26). Peas were severely injured by 24 hr of low ODR just prior to blossom. Tomato growth was reduced 50% by low ODR in early growth stages.

Increased air porosities are needed to maintain an adequate ODR when respiration rates are high (29, 62). Soil microflora represent an important O_2 sink comparable in magnitude to a crop (9). Low ODR is more detrimental to plant growth at high than at low root temperatures, probably because respiration increases with temperature (49, 50).

Internal aeration

Roots obtain most of their O_2 from the soil air, but O_2 can diffuse through the shoots to the roots of some species in amounts sufficient to prolong life. Oxygen diffusion through pea radicles in O_2-free air allowed 20% of normal elongation rates (23). The models of Luxmoore et al. (53) for sweet corn indicate that internal aeration was 34% of the total in well-aerated soil and 42% in O_2-deficient soil. Sunflower (*Helianthus annus* L.) tolerates low aeration because of internal oxygen diffusion (104). In this latter research, flooding caused less damage to corn, sunflower, and wheat (*Triticum aestivum* L.) than to barley (*Hordeum vulgare* L.) and tomato, and this reduced damage was associated with the large increase in root porosity of the first 3 species under flooding conditions compared with normal aeration (Fig. 2).

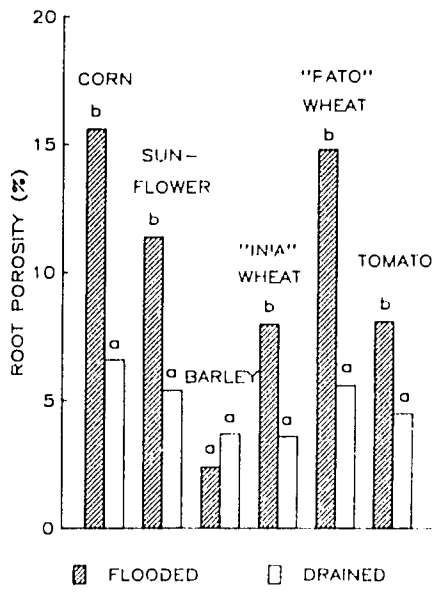

Fig. 2. Root porosity of 5 species as affected by flooding induced low soil oxygen. Bars within a species with different letters are significantly different at $P = 0.05$ (adapted from 104).

Adventitious roots

Development of adventitious roots in some crops is related to plant tolerance of excess soil water, i.e., low C_2. Such roots developed by corn after one day of flooding were short and porous enough to allow significant O_2 movement from the shoots to the root meristems (102). Development of adventitious roots in zones favorable to growth is beneficial to plants but it requires expenditure of C resources and may result in reduced top growth (78). Adventitious root formation and increased root porosity are temporary plant responses that aid recovery from waterlogging, but most crop plants will soon perish under such conditions. Internal gas transfer is probably a survival mechanism at best, and does not supply adequate root oxygen for most crop species.

Toxic materials produced under low O_2

When roots are deprived of O_2, respiration becomes anaerobic, and organic compounds are produced that may be toxic (76, ref. 20 cited in 78). Stresses other than low O_2 may result in production of some of these compounds (44). For example, ethylene production is a general response of plant tissues to environmental stress, including deficient water (35).

Probably the most-studied compound associated with poor soil aeration is ethylene, a naturally occurring plant hormone. It is produced in low-O_2 conditions by plant roots, shoots, and soil microorganisms. Precursers of ethylene may be produced in anaerobic roots and transported to the shoots for conversion to ethylene (8). Ethylene suppresses potato tuber initiation and increases tuber respiration rates (18), and encourages adventitious rooting of tomato, sunflower, and corn (14). It affects germination and root growth at concentrations <1 ppm (77). Concentrations of 1–20 ppm have been measured in water-logged soil (37). The influence of ethylene on root growth of cereals is illustrated by Table 1. Differences among species in sensitivity to ethylene are correlated to sensitivities to excess soil water (77). In addition to toxic organic compounds that result from anaerobic respiration, toxic inorganic products also may be formed (14).

Aeration and root disease

Low soil O_2 may cause conditions conducive to root diseases such as the attracting and stimulating effect of C lost from roots on soil pathogens (78). Smucker and Erickson (79) observed rapid growth of *Fusarium solani* f. sp. *pisi* (F.R. Jones) Snyd. & Hans. on pea roots in a N_2 atmosphere. This rapid growth apparently was due to the C compounds exuded by the roots. With the low root energy accompanying low soil O_2, nutrients can be lost from the roots into the soil (14), further encouraging microbiological activity in the rhizosphere.

We found that poor aeration markedly aggravated injury to beans (*Phaseolus vulgaris* L.) caused by *Fusarium solani* f. sp. *phaseoli* (Burk.) Snyd. & Hans., but bean growth was not affected by temporary low O_2 levels in fusarium-free soil (55, 56). This injury aggravation may have been due to low O_2-induced root exudates that stimulated the pathogen activity, as suggested by Smucker and Erickson (79). Low soil O_2 predisposed bean roots to attack by

Table 1. Effect of ethylene concentration on root extension of 3 crops (77).

Ethylene (ppm)	Root extension (% of control)		
	Barley[z]	Rye[y]	Rice[x]
0.5	57	81	105
1.0	42	72	90
10.0	20	62	75
100.0	15	61	73

[z]*Hordeum vulgare* L.
[y]*Secale cereale* L.
[x]*Oryza sativa* L.

Fusarium solani f. sp. *pisi*, which is normally not pathogenic to beans (57).

Low soil O_2 and soil compaction

Root growth rates are affected more by low soil O_2 and soil compaction occurring together than separately (75, 84) and O_2 requirements for root penetration of a compact soil are higher than for a loose soil. As shown by Fig. 3, roots do not penetrate very dense soil, regardless of soil O_2 levels. They can easily penetrate loose soil, even with low O_2 levels. Both O_2 levels and compaction affect root growth when they are at intermediate levels. Impedance due to soil compaction results in compressed root cells, reducing internal porosity and increasing root diameter (12), thus reducing the O_2 supply to internal root cells. The combined reduction of O_2 supply and increased O_2 demand could result in anoxic conditions earlier than if either condition were absent (75).

Compact subsoils may restrict water movement out of the surface soil following a rain or irrigation and thus cause temporary poor aeration, as is illustrated for a Charity Clay in Table 2. If 0.35 $\mu g \cdot cm^{-2} \cdot min^{-1}$ is taken as a critical level, O_2 was deficient for 2, 5, and about 7 days in the deep-chiseled, plowed, and compact soils, respectively.

STRESS DUE TO MECHANICAL IMPEDANCE

Root elongation rates >12 cm per day have been observed (94), and many fine roots and rootlets develop daily. These absorb water and nutrients for a few days, then die and disintegrate, and are replaced by new roots (95). Rapid growth takes place as new cells are formed and elongate in the root tips. As a root grows through the soil, it must pass through a pore that is larger than it is or it must enlarge a smaller pore (103). Root cell expansion can be reduced or stopped either by the failure to adjust osmotically to the lowering Ψ_s of a drying soil and to absorb the water needed for expansion, or by the failure to develop enough hydrostatic pressure within the cell to overcome the resistance of the soil matrix.

Reduced rooting volume is the main detrimental effect of soil compaction except for quality factors such as the shape of roots or tubers. Rooting volume has little significance as long as the water and nutrient needs are met. Inasmuch as nutrients can usually be supplied from a small soil volume, reduced water supply is likely to be the most serious effect of reduced root volume (70, 87, 94), especially when the crop is dependent on stored soil water for an extended period. With modern irrigation and chemigation techniques, the root volume is only important to physically support the crop because adequate water and nutrients can be absorbed under almost optimum conditions. Deep root systems may be undesirable with frequent irrigation and fertilization because of the extra demand

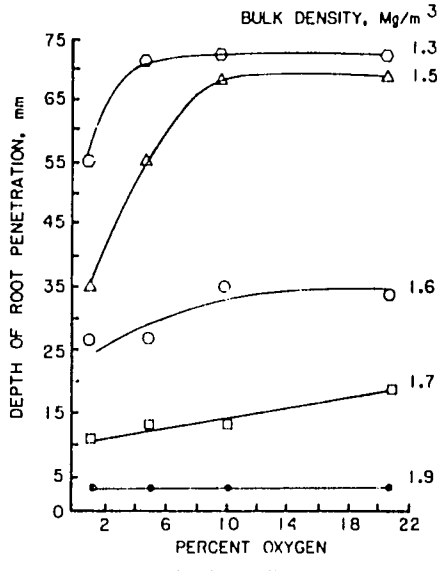

Fig. 3. Cotton taproot penetration into soil as affected by soil bulk density and soil oxygen content (redrawn from 84).

Table 2. Oxygen diffusion rates (ODR) in a clay soil as affected by tillage and time after a 7-cm rain on 27 July (25).

	ODR ($\mu g \cdot cm^{-2} \cdot min^{-1}$)		
Date	Deep-chiseled (50 cm)	Plowed	Compact
28 July	0.32	0.29	0.18
29 July	0.34	0.30	0.15
30 July	0.40	0.31	0.22
1 Aug.	0.43	0.35	0.31

on photosynthate supply for the extra root growth (64). Plants with a restricted root system are vulnerable to water stress should the water supply be temporarily curtailed. A shallow root system is also exposed to the extreme temperature changes in the surface soil. Two commonly used indices of the soils' resistance to root growth are bulk density and strength (17).

Bulk density

Some general bulk densities ($Mg \cdot m^{-3}$) that will impede root growth in moist soil are 1.55 for clay loams, 1.65 for silt loams, 1.80 for sandy loams, and 1.85 for loamy fine sands (7). However, mechanical impedance is a function of both bulk density and water content and the concept of a critical bulk density for root penetration is not acceptable (7, 63). A density that restricts root growth at a low water content may offer negligible impedance if the soil is wet. Coarse-textured soils have much higher bulk densities and lower porosities than fine-textured soils, and a bulk density representing low impedance in a sand would completely restrict root growth in a clay loam.

Thin, restrictive layers often occur in otherwise unrestrictive soil. Camp and Lund (12) found a compacted traffic pan of 1.9 $Mg \cdot m^{-3}$ at the 18 to 19 cm depth in a Norfolk sandy loam. Very thin layers in a silt loam in the Columbia Basin of Washington restricted potato roots (73). These layers probably would be overlooked by usual bulk density sampling. Although bulk densities provide a measure of compaction for a given soil, they are not good indices of root penetration resistance for that soil.

Soil strength

The capability of roots to penetrate a soil is related to the soil's resistance to deformation—referred to as mechanical impedance or soil strength. This characteristic is commonly measured as the force required to press a penetrometer into the soil (22). Various types of penetrometers have been used, ranging from needles that approach root size (66) to those that are several centimeters in diameter, with blunt or pointed tips. A lubricated penetrometer that exudes polymers from the tip has been used (93). The American Society of Agricultural Engineers has adopted design and use standards to help reduce the confusion due to the variation in penetrometers (3).

Soil strength is the critical value in determining root penetration and is dominated by bulk density and water content. This is illustrated by the results of Taylor and co-workers (90, 92). Cotton (*Gossypium hirsutum* L.) root penetration into Amarillo fine sandy loam was linearly related to soil strength regardless of whether it was due to high bulk density or low water content (Fig. 4). Roots did not penetrate a soil in which penetrometer resistance was more than 3 MPa. The soil strength–root penetration relation was similar for 4 soils ranging in texture from loamy fine sand to loam (92). Soil strength increases with decreasing water content much more rapidly at high than at low bulk densities (13).

Some workers have criticized the use of rigid soil probes to characterize the resistance of soil to root penetration (30). Penetrometers are much larger than roots, are rigid and unable to find zones of weakness, and penetrate into the soil much faster than roots (17). Regardless of the theoretical deficiencies, penetrometer measurements do give a useful measure of soil strength. It is recommended that soil water and bulk density samples also be taken to help interpret the penetrometer results (17).

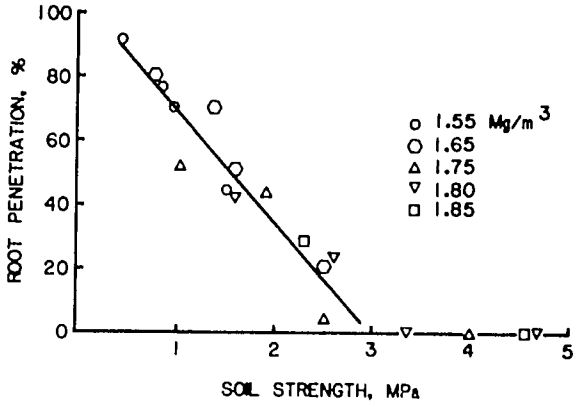

Fig. 4. Root penetration into Amarillo fine sandy loam soil as influenced by soil strength. Soil strength was varied through combinations of soil bulk density and water content (redrawn from 90).

Effects of compaction on plant growth

Many studies have shown crop yields to decrease as soil strength increases. Examples are cotton (15), sorghum (91), sugarbeets (89), and potatoes (11, 27). Large roots and tubers must displace considerable volumes of soil in order to expand to full size and this expansion is against the surrounding soil resistance. Flocker et al. (27) reported a 50% decrease in potato yields due to compaction, while tomatoes were unaffected. Reductions are often attributed to water stress, in turn caused by soil compaction-reduced root volume.

Soil compaction is less likely to reduce yields of perennials than annuals (7, 88) because roots of perennials have an opportunity to grow through old root channels or through layers at times of the year when strength is reduced. Some plants seem to be able to penetrate and disrupt hard soil, i.e., alfalfa (*Medicago sativa* L.) and sweet clover (*Melilotus alba* Medik) (7). Bahia grass (*Paspalum notatum* Flugge) penetrated soil layers that excluded cotton roots and cotton following the Bahia grass had increased rooting to at least 60 cm compared to where the grass had not been grown (see 24 cited in ref. 7).

Compensatory growth may occur whenever a portion of the root system is inhibited (41). Roots that are restricted by hard soil usually show increased branching and density in less-restrictive zones. As cited previously, this compensatory growth represents an increased demand for photosynthate in root production.

Interactions

As indicated previously, if high soil strength results from soil compaction, porosity and pore sizes have been reduced also. If a compact soil is also wet, there may be poor aeration.

Higher corn yields were obtained from rows between traveled furrows than from between nontraveled ones (98). This difference was attributed to compaction due to travel, which increased water content and accelerated P diffusion to the roots. With P fertilization, the effect disappeared.

Cotton tap root growth was evaluated under various combinations of soil strength, temperature, and aluminum activity (65). Any of the 3 variables exerted the greatest effect when the other 2 were at optimum. When any variable was near a critical point, the other variables had only a slight effect on the elongation rate.

Work conducted in the coastal plains of the southeastern United States (see ref. 70) has shown that the major benefit in increasing root depth through disrupting a hard subsoil layer was an increased volume of soil to supply water during dry periods. As shown in Table 3 (38), potato tuber yield was not affected by subsoiling with daily sprinkler irrigation. When the irrigation interval was extended to 4 to 5 days, subsoiling improved yield and grade compared to not subsoiling. It is probable that deeper rooting due to subsoiling would reduce severity of temporary water stress in case of an irrigation system failure.

Table 3. Yield and percentage of No. 1 'Russet Burbank' tubers as affected by subsoiling and irrigation interval on Quincy sand (38).

	Irrigation interval			
	Daily		4 to 5 days	
	Not SS	SS[z]	Not SS	SS[z]
Total yield, ($Mg \cdot ha^{-1}$)	55.8	56.5	50.0*	58.6*
No. 1 yield, ($Mg \cdot ha^{-1}$)	42.9	46.3*	17.0*	35.3*
Percentage no. 1	77.0	82.0*	34.0*	60.0*

[z]SS = subsoiled to depth of 85 cm.
*Significantly different from daily, not SS at P = 0.05.

A hard soil layer aggravates fusarium root rot of beans, especially when soil water is marginal. In low-strength soil infested with *F. solani* f. sp. *phaseoli*, bean roots can penetrate deeper than the *Fusarium* infestation, so that healthy roots can absorb water and nutrients and partially compensate for the ineffective diseased roots near the surface. Water and nutrient absorption may be inadequate to sustain growth if rooting is restricted to infested soil (54).

ROOT TEMPERATURE STRESS

Temperature is a major factor in determining adaptation of various plant species to given locations. Most physiological functions are controlled to some extent by temperature-dependent mechanisms. All root functions are highly temperature-dependent. Soil temperature influences plant growth indirectly through its effect on nutrient availability and residue decomposition and directly through its effect on seed germination, seedling emergence, and root temperature. A number of excellent reviews of soil temperature and plant growth have been written (19, 59, 60, 72, 99).

Only the effects of low soil temperatures on plant performance will be discussed here. Langridge (47) reviewed general physiological responses to high temperatures.

Much of the research related to root zone temperatures has been conducted under controlled conditions so as to define optimum ranges. A generalized root growth–temperature response curve for temperate zone crops is given in Fig. 5. Root growth is low at about 5°C, and increases nearly linearly with increased temperature up to a maximum at about 25°. Further increases in root zone temperature cause rapid decline in root production. However, there is much variation among species and cultivars as to optimum root zone temperatures, as illustrated by the following values selected from reviews of Nielsen (59) and Voorhees et al. (99): Beans (*Phaseolus vulgaris* L.) 28°; potato (*Solanum tuberosum* L.) 20° to 23°; corn (*Zea mays* L.) 25° to 30°; squash (*Cucurbita* sp.) 27°; onion (*Allium*

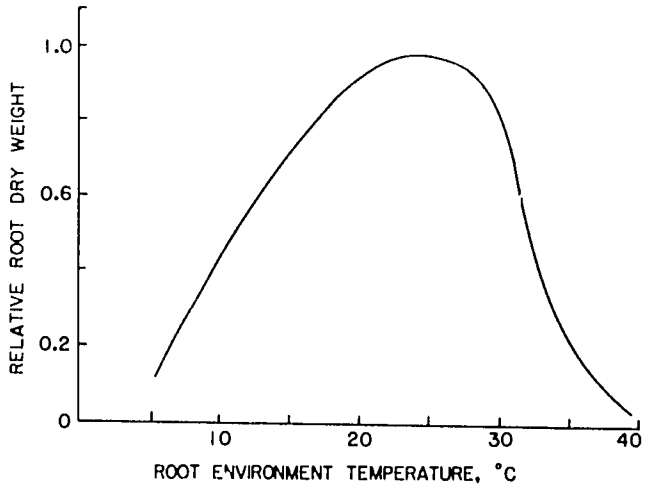

Fig. 5. Generalized root growth response curve to root zones temperatures (redrawn from 99).

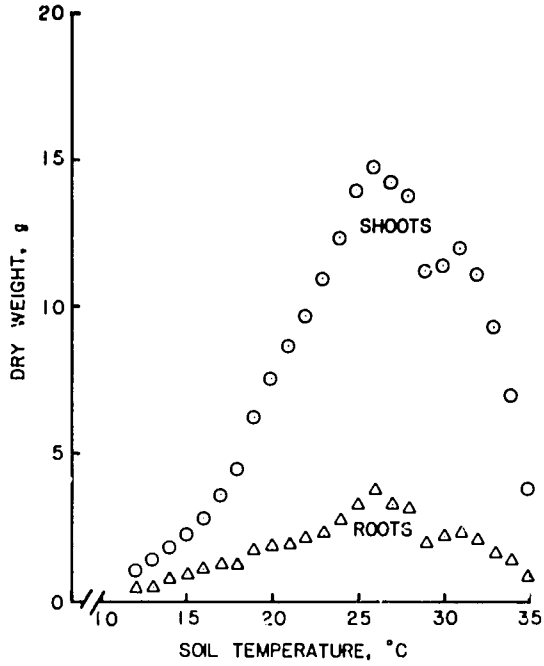

Fig. 6. Shoot and root weights of 23-day-old corn seedlings as influenced by 1°C increment changes in soil temperature (redrawn from 100).

cepa L.) 18° to 22°; sugarbeet (*Beta vulgaris* L.) 20° to 24°; pea (*Pisum sativum* L.) 18° to 22°; and tomato (*Lycopersicon esculentum* Mill) 26° to 34°. Cool-season crops are generally less sensitive to low soil temperatures than warm-season crops (45).

Optimum soil temperatures for maximum root growth are generally lower than the optimum soil temperature for maximum shoot growth. Optimum soil temperatures usually are highest at germination and decrease with time. For example, turnips (*Brassica rapa* L.) have an optimum root temperature of 27°C in the spring and 19° in the fall (4). The optimum root temperature for top growth of sugarbeets progressively decreases from 26° at 6 weeks after emergence to 23° at 13 weeks (68). Similar shifts have been shown in corn (2) and barley (67). Temperatures in the field are never constant but vary diurnally, seasonally, and with depth. Thus, it is difficult to use plant responses to constant temperatures to estimate responses in the field except in a general way. Some crops grow better with fluctuating than with constant root temperatures [e.g., peas (32) and corn (101)].

The sensitivity of shoot and root growth of corn to soil temperature changes is illustrated in Fig. 6. Total seedling weight markedly increased as temperature increased from 12° to 26°C, and then decreased with higher temperatures. Roots increased less rapidly than the shoots, so that the root : shoot ratio decreased up to about 33°. Such results indicate that at high temperatures, a relatively small root system can take up and transport adequate water and nutrients for vigorous growth.

Effect of low temperatures on root functions

Root morphology. Cell division is more rapid at optimum root temperatures but for a shorter time than at cooler temperatures, and root cell maturation is delayed by cool temperatures (59). Root branching increases with resulting increased root–soil contact as root temperature increases. The normal decrease in temperature with soil depth during the growth season encourages root branching near the surface (28).

Root temperature also affects the growth and anatomy of shoots. This effect is to be expected because of the root's influence on nutrient and water uptake and production of growth regulators and other organic compounds.

Water uptake. It has been known for many years that low root temperatures reduce water and nutrient uptake (59). Root temperatures can be low without a concurrent reduction in atmospheric demand for water, which results in water stress in the shoots. Some of the reasons for low water absorption by cold roots are: a) retardation of root elongation, thus reducing exploitation of new soil water supplies; b) decreased movement of soil water to roots; c) decreased root permeability to water; d) increased viscosity of root cell protoplasm; e) increased viscosity of water; and f) decreased metabolism, in turn affecting the permeability of root membranes. The principal cause of reduced water uptake is the combined effects of reduced membrane permeability and increased viscosity of water and protoplasm (45).

The rate of change of root temperature may be as important as the absolute temperature. Nielsen et al. (61) found that cooling corn roots from 20° to 5°C in 3 hr caused permanent shoot wilting. Similar observations were made with kidney beans. Sunflower and tomato recovered from such treatment (6).

Nutrient uptake. Because of the large influence of soil temperature on root growth and density, uptake of nutrients of low mobility (such as P) is reduced by low root temperatures (60). Uptake of mobile nutrients (such as N and S) is much less affected by root temperatures than relatively immobile ones. Soil temperature also affects plant nutrition indirectly through influencing the rate of release of nutrients from inorganic and organic forms, the synthesis of nutrients into complex organic compounds, and their transport to the shoots.

The detrimental effects of low soil temperatures on plant growth are complex (60) and are due to a combination of reduced water and nutrient uptake, reduced nutrient assimilation and transport of the products, and reduced production and transport of growth regulators required by shoots and/or roots. Because root growth is reduced by low temperatures, root capacity to act as a sink for carbohydrates produced in the shoots also is reduced.

SUMMARY

Roots absorb and translocate water and nutrients, synthesize and transport organic compounds, are a sink for carbohydrates, and support the plant. These functions are affected by stresses to which the roots may be subjected—inadequate or excess water, deficient O_2, deficient or imbalanced nutrients, adverse temperatures, mechanical impedance, toxic chemicals, and attack by pathogens and insects. Many of these factors interact, and an adverse condition in any one factor may affect the plant response to several other factors. Higher plants have mechanisms to cope with the various stresses. These mechanisms include such things as an expanding root system, change in root : shoot ratio, development of additional adventitious roots and internal pore space, stomata opening control, adjustment of Ψ_π, and changes in morphology. Most of these adaptations allow plant survival under adverse conditions, but yield or quality is reduced compared to what would occur under optimum conditions.

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Genetic Variability in Root Systems Associated with Nutrient Acquisition and Use

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Variability within the plant kingdom for nutrient acquisition and use reflects differences in root morphology and differences in mechanisms that either aid or prevent ion movement into the root. This variability implies genetic variance, yet few genetic studies have been completed. Methods of studying acquisition and their application to genetic research and interpretation are presented for K, Ca, and P.

The means by which plants acquire and use essential mineral elements from the soil are complex. Many different interactive processes are involved. Different organs, tissues, cells, and cellular components are used. A significant amount of variation exists, both within and among species. Although certain processes of mineral nutrition are common to many species of plants, this variation reflects genetic differences that may be used both in the development of low-input cultivars and in studies of comparative processes by which mineral element acquisition and use occur. This paper summarizes methodology, interpretation, and use of information derived from studies intended to identify intraspecific, phenotypic differences in plant growth under stress levels (low) of essential elements. Emphasis will be placed on genetic interpretation of differences in root systems associated with acquisition and use of P, K, and Ca.

To assume that roots "acquire" mineral element nutrients from the soil implies that movement of these nutrients from the rhizosphere into the root is the entire story of acquisition. But acquisition may involve mycorrhizae, root hairs, and proton pumps. Transpiration, energy sources, and growth regulators each impact on the amount and rate of nutrient acquisition and internal movement within plants. Research on acquisition and use needs to recognize these complexities.

SOURCES OF PHENOTYPIC VARIATION

Plant variability in acquisition and use of essential elements is common (6, 12). Species evolving in an environment low in one or more of the essential elements will reflect recombination of genes that enhance various aspects of acquisition and use of these marginal resources. Among self-pollinating economic species, weedy relatives would be prime sources of genetic variation. Landraces selected to produce food in soils of limited fertilization are also excellent sources. Among cross-pollinating species, genetic variation is often masked; here inbred strains developed artificially may prove very useful (8–11).

IDENTIFYING PHENOTYPIC VARIABILITY

The method of assaying germplasm must be determined carefully. Assays should be accurate and repeatable. More important, the assay should be meaningful.

Growing plants in a deficient soil is preferred by some who want to use the isolates for developing low-input cultivars. Soils deficient in K, P, and Ca are not easily found in agricultural areas of developed countries. Even if found, research workers must recognize the lack of uniformity and reproducibility of assays on natural soil sites. Aeration, compaction, and moisture are important variables in addition to the non-uniform distribution of the element under study. Environmental variables limit the opportunity to find unique individual plant phenotypes on element-deficient soils with precision.

Solution-culture assays

The most uniform assay medium is a solution culture that continuously bathes the roots of plants. Solution cultures can be adapted readily to single-plant evaluations. The use of aerated solution cultures for growing plants has been highly standardized. However, maintaining an element at a concentration approximating soil solution concentration is difficult. Likewise, the pH will change rapidly in solution cultures and may not be uniform between individual cultures.

Solution-culture techniques seldom discriminate differences in acquisition of an element. Strain differences in acquisition have been found only for Ca (7) out of the 4 elements studied in solution cultures in our program. If elements are maintained at a low concentration, continuous bubbling of the culture over plant roots makes the limited element far more available than desired and differences in growth due to low-mineral stress difficult to identify. In contrast, if a minimal level of the element is provided at the beginning of the growth period (without subsequent replenishment of the element) all or much of the element will be absorbed and growth will continue only until all of the element is used. This pattern of acquisition and use with a "batch" culture is not comparable to deficiency-stress under field conditions, where the amount of the nutrient available for absorption will continue to be marginal throughout the life of the plant.

The batch-solution culture technique permits full recovery of root systems and does discriminate differences in conversion of the absorbed stressed element into dry matter. Differences in partitioning growth and ion distribution can be measured with precision.

Plant isolates varying in response to low-element environment should be studied eventually in an element-deficient field in order to accept or reject the solution culture as a meaningful medium for screening. The solution culture technique can then be used as an assay of phenotypic variability.

Differences in response of tomatoes to low-Ca stress have been measured using a solution culture (7). Tomatoes were grown in 2 liters of Hoagland's solution modified to contain 5 ppm Ca. The pH was 4.7 at the start of the experiment. Differences among plant strains were found in capacity to remove Ca from the solution (36–81%), total dry weight (1.35–3.63 g) and CaER (milligrams of dry matter produced per milligram of Ca absorbed by the plant). Six families were created, and genetic analyses were made without difficulty.

MEASURING DIFFERENCES IN ROOT GROWTH AND NUTRIENT ACQUISITION UNDER MINERAL ELEMENT STRESS

Solution-culture measurement of beans grown under low-P stress

Differences in dry matter production of beans grown in a Hoagland's solution modified to a low-P level have been identified (13) and shown to be highly heritable (5). The amount of root growth, as well as the proportion of total dry matter allocated to roots also varied (Table 1) and was highly heritable among the bean strains

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Table 1. Variation in dry weight of tops, roots, and total plants and shoot : root ratio among 6 bean lines when grown at low P (3 mg per plant) and adequate P (31 mg per plant) (5).

	Low P				Adequate P			
Line	Shoot dry wt (g)	Root dry wt (g)	Total dry wt (g)	Shoot : root ratio	Shoot dry wt (g)	Root dry wt (g)	Total dry wt (g)	Shoot : root ratio
3	0.72 a[z]	0.55 a	1.27 a	1.31	1.08 a	0.58 a	1.66 a	1.86
9	1.05 b	0.46 a	1.51 ab	2.28	3.03 b	0.72 a	3.75 b	4.21
6	1.07 b	0.52 a	1.59 b	2.06	3.43 b	0.76 ab	4.19 b	4.51
12	1.13 b	0.47 a	1.60 bc	2.40	3.37 b	0.90 b	4.27 b	3.74
1	1.23 bc	0.55 a	1.76 c	2.24	3.33 b	0.64 a	3.97 b	5.20
11	1.48 c	1.03 b	2.51 d	1.44	4.23 c	1.48 c	5.71 c	2.86

[z]Mean separation within columns by Duncan's multiple range test, 5% level.

(5, 13). PI 206002 (Line 11) produced nearly 100% more dry matter of roots when grown under low-P stress than the other 5 lines tested. A lower shoot : root ratio was characteristic of PI 206002 also when grown under an adequate P level (Table 1).

PI 206002 appears to be a unique genotype when measured in solution culture media. Families created by hybridizing PI 206002 to other bean strains demonstrated genetic recombination for P-use efficiency. Two of 20 plants exceeded the mean of the efficient parent (+1 SE) for root dry weight in the population derived by backcrossing the F_1 to the efficient parent. Three of the 55 F_2 progeny similarly exceeded PI 206002 (Table 2). Broad sense heritability values (H_{BS}) of 79% (5) indicate the usefulness of the procedure in identifying useful variation controlling root growth using solution culture technique.

In order to evaluate, under field conditions, the genetic variation measured in solution culture, the next step was to introduce the genes for extensive root development under P stress into cultivars adapted to our area. PI 206002 is a late-flowering, large-seeded bean poorly adapted to bean production in Wisconsin. The genes for P efficiency in the exotic PI 206002 were transferred into the adapted cultivar Sanilac by a modified backcross breeding method. Testing near-isogenic lines for performance separately in solution culture and under field conditions was performed in order to obtain data on the correlation of responses to P stress in the laboratory and in an agriculturally related growth situation.

Solution culture measurement of tomatoes grown under low-Ca stress

Two lines with similar CaER values differed from 36% to 81% in absorbed Ca. Reciprocal grafts between these 2 lines clearly showed differences in acquisition to be controlled by the plant top and transpiration differences were not the control mechanism as might be suspected for an element presumed to move passively from root to shoot. Subsequent efforts, however, showed that other factors, e.g., a slight increase in pH or an increase in Ca concentration of the solution culture to 10 ppm without changing the total Ca in the medium (reduce culture from 2 liters to 1 liter) changed the measured plant responses completely. The basis of selecting nutritional variants using solution culture must be studied with great care, and interpretation of the data must be made carefully.

Assay for P acquisition in sand culture

Movement of P (in particular) of the nutrients arriving at root surfaces is diffusion-limited. An ideal medium for determining strain differences in P acquisition would use a particle to which the ion to be studied can be adsorbed and later released in a nutrient culture. The "loaded" particle would be mixed with sand, and plants would be grown in the well-aerated medium. Limitation in growth either would reflect differential ability to acquire the diffusion-limited ion, a difference in internal use of the ion, or both. Resins have been proposed as carriers (4). Resins specific for most of the essential elements for plant growth are available. In a similar way, a system using activated alumina as a carrier for absorbed P has been developed (1). The sand-alumina system has been used successfully to measure differences in acquisition and use of P by tomatoes (2).

Transfer of "large root" trait from PI 206002 to 'Sanilac'

An inbred-backcross method of breeding was used to transfer the beneficial root growth in PI 206002 to an adapted cultivar ('Sanilac'). In this method, 44 plants of the first backcross (F_1 × 'Sanilac') were backcrossed to 'Sanilac' to give rise to 44 BC_2 progeny, each of which was self-pollinated for 3 generations using single-seed descent, which provided 44 BC_2S_4 progeny. Each of these progeny would be 87.5% 'Sanilac' and 12.5% donor (PI 206002) germplasm. Each line would be about 97% homozygous. The 12.5% donor germplasm is adequate to ensure occasional transfer of desired genes to the recurrent parent. The 87.5% recurrent parent germplasm ensures the general similarity of all lines to 'Sanilac', including adaptation. The 97% homozygosity ensures a homogeneous response of plants within each line.

Field and solution culture testing of BC_2S_3 and BC_2S_4 progeny

The 44 lines derived from the inbred-backcross program tested in solution culture confirmed the similarity of each line to 'Sanilac' for morphological traits and flowering dates. As expected, some of the derived lines performed poorly in solution culture for total dry matter production and total root dry matter production. However, a small group (3–5) approached the PI 206002 parent for total plant dry matter and root dry matter.

The same 44 lines also were grown on a Plano silt loam soil with 22 kg·ha^{-1} of P (Bray 1 test). Several lines that had large root systems in solution culture also had high total dry weight at R1 (date on which 50% of plants had at least one flower). The larger root system and higher PER (milligrams of dry matter produced per milligram of P absorbed by the plant) identified in solution culture were associated with increased P uptake in a soil marginally deficient of P.

Table 2. Frequency distribution of root dry weight (g) for populations derived from the cross of Lines 11 and 6, plants grown with 3 mg P per plant (5).

	Root dry wt														
Pedigree	0.25g	0.35	0.45	0.55	0.65	0.75	0.85	0.95	1.05	1.15	1.25	N	Mean	SE	CV (%)
	No. plants per class midpoint														
11(E)[z]						3	6	6				15	0.875	0.101	11.54
6(MI)	2	5	4	4								15	0.432	0.098	22.69
F_1		1	2	5	6	1						15	0.577	0.099	17.16
11 × F_1	1		2	9	4	2			1		1	20	0.531	0.179	33.90
6 × F_1	4	1	3	5	5	1	1					20	0.505	0.160	31.68
F_2	4	4	7	7	10	9	9	2	1	1	1	55	0.553	0.218	39.78

[z]E = efficient; MI = moderately inefficient.

Table 3. Genetic recombination for enhanced vegetative dry weights in F_2 and BC progenies. All plants grown under stress level for single element.

Element	Crop	No. of families	Proportion of segregants[z] exceeding better parent by 10%	50%
K	Bean	6	0	0
K	Tomato	6	1	0
Ca	Tomato[y]	6	7	0.2
P	Bean	15	15	1
P	Tomato[y]	1	15	6

[z](Mean of better parent + SE) × 1.10 and × 1.50, respectively.
[y]Reflects acquisition and use.

Sand–alumina as a culture medium for measuring differences in P acquisition and differences in root length of tomatoes under low-P stress

A sand medium to which activated alumina loaded with P has been added provides a range of stable, reproducible P concentrations for plant cultures (1). The lowest P levels compare favorably to concentrations found in soils. Diffusion of P to root surfaces appears to be the primary factor limiting P availability in this system as in soils.

Tomato strains tested at low P in the sand–alumina system varied by 73% in the amount of vegetative growth (2). Strains differed in a) total P uptake and b) P use within plants after absorption. Total P uptake was associated with differences in total root length, as expected, and the P uptake rate per unit of root length. At higher levels of P these same strains did not differ in vegetative growth and P acquisition.

In a subsequent experiment concerned with the inheritance of P acquisition and growth 2 tomato lines, 55 (PI 102886) and 214 (PI 126409), varied by about 100% in dry matter production, with line 55 being more efficient (3). The F_1 showed significant heterosis (112% above the midparent mean). Individuals in the BC of the F_1 to the efficient parent exceeded the midparent mean by 150% to 200%. Broad sense heritability ranged between 0.6 and 0.7 for shoot dry weight. Root length differences correlated with total growth. P uptake, as milligrams per plant, ranged from about 2 mg for line 214 (inefficent parent) to about 6 mg for line 55, 6–8 mg in the F_1 and 7–9 mg in the backcross of the F_1 to line 55. Two exceptional BCP_1 plants acquired 13.95 mg and 15.63 mg P under low-P stress, compared to 19.44 mg for mean of 2 parents grown with adequate P. Increased root length (which enhanced P acquisition), an increased uptake per unit of root, and a high efficiency in internal P use were associated with superior performance under P-limiting conditions.

POTENTIAL GENETIC RECOMBINATION FOR ROOT GROWTH CONTRIBUTING TO ENHANCED ACQUISITION AND USE BY PLANTS GROWING UNDER LOW-NUTRIENT STRESS

Data obtained in a series of studies on K, P, and Ca uptake and use indicate that genetic recombinants exist that are superior to the best of the parents isolated from exotic material (Table 3). More potential progress was found in the studies on Ca and P than on K. Segregants exceeding the better parent by 10% would be extremely valuable; by 50%, totally unanticipated. The apparent ease of recovering recombinants for P uptake and use is particularly significant. Root extension differences in tomatoes and beans are not only expressed morphologically; the P uptake capacity of these recombinants from low-P soil and sand–alumina provides new biological materials for research on the processes by which P moves from the soil into the plant. Certainly breeders should heed the sand–alumina system as a useful method for selecting uniquely efficient root systems.

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Vesicular–Arbuscular Mycorrhizae in Vegetable Crops

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Mycorrhiza refers to a mutualistic, symbiotic relationship formed between fungi (Gr. *mukes*) and living roots (Gr. *rhiza*) of higher plants. These associations are prevalent among most plant species and have been observed in most vegetables except the Cruciferae and Chenopodiaceae. In fact, some vegetables do not appear to grow or develop normally without mycorrhizae. In addition to their wide distribution in the plant kingdom, these nonpathogenic relationships are geographically ubiquitous. Thus, the mycorrhizal condition is the rule, as both host plant and fungus specificity is minimal and usually not observed.

Interactions between host plant and fungus are complex and include reciprocal relationships. The host plant supplies carbohydrates to the mycorrhizal fungi, while benefitting from the fungal relationship primarily through enhanced uptake of immobile, inorganic nutrients. Secondary benefits of the mycorrhizal relationship also can include increased resistance to diseases, drought, and salinity and enhanced N_2 fixation in legumes.

HISTORY AND CLASSIFICATION OF MYCORRHIZAE

History

Frank first described mycorrhizal relationships about 100 years ago, but it is only during the past 20 years that horticulturists have begun to understand and appreciate their importance, especially in vegetable crops. Even before Frank coined the term "mycorrhiza," it was known that microorganisms (including fungi) lived in association with plant roots (rhizosphere population). Research interest in mycorrhizae started with pine trees after morphologically different, bifurcate, short roots were observed. Early work was conducted almost exclusively by mycologists, who acquired an interest in the identification and classification of different types of mycorrhizae and the various endophytes involved. Modern mycorrhizal research began in the 1950s; however, intensive research on mycorrhizae was not conducted until the 1960s, with major activity from 1970 to the present. Once different responses to inoculation with mycorrhizal fungi were observed, research interest shifted to the physiological basis for these responses and other detailed studies.

Classification of mycorrhizae

Originally, mycorrhizae were grouped into ecto-, endo-, and ectendomycorrhizae, based on the type of fungus–root structures formed (40). In ectomycorrhizae, the fungus forms a structure (called a mantle or sheath) that encloses the rootlet. Hyphae also penetrate between root cells to form an intercellular network known as the Hartig net. There is no intracellular penetration. In ericomycorrhizae, there are no discernible morphological changes in the external root structure of the host. A fungal mantle is not present, but hyphae enter root cortical cells without causing visible damage to the invaded root. Ectendomycorrhizae exhibit characteristics of both ecto- and endomycorrhizae.

This original breakdown emphasized only fungal penetration of the host cells and formation of various fungal structures. A recent classification by Harley and Smith (41) stresses these factors, as well as the host and endophyte involved. They described 7 types of mycorrhizae, namely vesicular–arbuscular, ecto-, ectendo-, arbutoid, ericoid, monotropoid, and orchid. Each mycorrhiza forms a different type or combination of structures. Vesicular–arbuscular mycorrhizae (VAM) are the only type observed in vegetables. VAM have all the characteristics described for endomycorrhizae in the earlier classification.

THE VA MYCORRHIZAL SYMBIOSIS

Vesicular–arbuscular mycorrhizae refers to those mycorrhizal associations formed with fungi in the family Endogonaceae. Vesicular–arbuscular mycorrhizal fungi are aseptate phycomycetes. The fungi cannot be cultured on synthetic media, so they must be multiplied in association with a host plant.

Vesicular–arbuscular mycorrhizal fungi produce structures known as vesicles and arbuscules, in addition to hyphae and spores. Arbuscules are intracellular, haustoria-like structures that develop by repeated, dichotomous branching of hyphae. Arbuscules can be seen with a light microscope and are short-lived; varying from one to 3 weeks. They can form very soon after the roots become colonized. Vesicles are sac-like, usually terminal swellings at the tip of hyphae. They are primarily storage organs of the fungus and contain lipid droplets. Usually, vesicles form after arbuscules and become more numerous as the plants mature.

Hyphae of VAM fungi can be formed both within the root and externally. These hyphae mediate the transfer of mineral nutrients and other material from the soil to the host plant. Hyphae have a very large surface to volume ratio and thus constitute an extra, efficient, well-distributed absorbing surface. Vesicular–arbuscular mycorrhizal fungi also produce morphologically distinct, resting spores in the soil that can be recovered using wet-sieving techniques.

PLANT RESPONSE TO COLONIZATION

Phosphorus

Phosphorus uptake and growth. The earliest studies of VAM of vegetables crops were those examining growth response and nutrient uptake in inoculated plants compared to noninoculated controls. A majority of these studies were done with onions, since onions were known to be highly dependent on mycorrhizal fungi for normal growth and development. Hayman and Mosse (46) compared the responses of onions to VAM and to phosphate in 10 sterilized, P-deficient soils in a pot experiment. Mycorrhizal plants grew as well in 3 soils, in one they grew better, and in 6 worse than those given phosphate. However, in 8 of 10 soils, mycorrhizal plants possessed significantly higher shoot dry weights than control plants receiving neither phosphate nor mycorrhizal inoculum. Mosse et al. (64) found that dry weight of onion plants was significantly increased by mycorrhizal infection in 3 British soils tested. Rhodes and Gerdemann (86) found onion plants inoculated with *Glomus fasciculatum* (Thaxter sensu Gerd.) Gerdemann & Trappe had significantly greater mean heights and mean dry weights than noninoculated control plants. Ten weeks after transplanting, ^{32}P-labeled phosphate solution was injected into each individual growth chamber at the midsoil level. Plants were harvested 3 days later, dried, and assayed for radioactivity. Root segments of mycorrhizal plants contained high levels of ^{32}P. Uptake of ^{32}P by mycorrhizal plants was greatest about 3 to 6 cm from the root surface. Leaf segments of mycorrhizal plants also contained relatively high levels of radioactivity, indicating ^{32}P had been released rapidly to the mycorrhizal host and translocated to aerial portions of the plant. Gray and Gerdemann (37) also added labeled phosphoric acid solution to pots containing 110-day-old onion plants. After 43 hr, there was significantly greater radioactivity in tops and roots of mycorrhizal plants than in those of nonmycorrhizal plants. Relatively high levels of radioactivity in uninfected segments of mycorrhizal roots suggested phosphate had moved from the mycorrhizae into portions of the uninfected root system. Mosse (61) conducted an experiment in which 0, 0.2, 0.5, 1.0, or 1.5 g monocalcium phosphate [$Ca(H_2PO_4)_2$] per kg of soil was added to mycorrhizal and nonmycorrhizal onion plants in 4 sterilized soils. Mycorrhizal plants in all soils without added phosphate were several times larger than nonmycorrhizal plants. Nonmycorrhizal plants

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reached dry weights comparable to mycorrhizal plants when 0.5 or 1.0 g of $Ca(H_2PO_4)_2$ was added to each pot. Daft and Nicholson (26) examined the effect of different amounts and times of application of potassium dihydrogen phosphate (KH_2PO_4) on growth of mycorrhizal maize in sand. Nonmycorrhizal plants grew as well as mycorrhizal plants at all levels of KH_2PO_4 added, but without it less growth occurred. Gerdemann (34) also obtained similar results when comparing mycorrhizal and nonmycorrhizal corn seedlings. Gaunt (33) determined dry weights of onion and tomato plants inoculated with a mixture of *Glomus microcarpum* Tul. & Tul. and *G. mosseae* (Nichol. & Gerd.) Gerdemann & Trappe spores were significantly greater than the nonmycorrhizal controls in a range of sterilized soil–vermiculite mixtures. He found no significant differences between dry weights when inoculum was pelleted onto the seed or added to the soil.

Sanni (97) determined that 80-day-old cowpea plants that had been inoculated with *Gigaspora gilmorei* Trappe & Gerdemann had significantly greater amounts of P in both roots and shoots than did noninoculated control plants. Dry weight of inoculated plants at harvest was higher than that of control plants; however, differences were not significant. Sanni obtained similar results with 111-day-old tomato seedlings and 59-day-old maize plants, respectively, inoculated with *Gigaspora coralloidea* Trappe, Gerdemann and Ho and *G. gigantea* (Nichol. & Gerd.) Gerdemann & Trappe. Rajapakse and Miller (80) observed increased shoot P percentages in 2 cowpea cultivars inoculated with *Glomus mosseae* or *G. fasciculatum* and *Rhizobium* than in plants inoculated with *Rhizobium* alone.

Yost and Fox (107) discerned that the growth rate of cowpea plants in P-deficient soils without mycorrhizae was one-half or less than that of mycorrhizal plants. Phosphorus accumulation rates were highly correlated with plant growth rates, and increased P uptake very likely contributed to increased growth.

Mycorrhizal researchers agree that increases in plant growth observed in mycorrhizal plants are due primarily to improved uptake of P. Percentage of increase in concentration is usually the largest in mycorrhizal plants; similar growth responses can, however, be obtained by supplying soluble P to nonmycorrhizal plants. This theory is further supported by the fact that response to VAM colonization is minimal or absent at high soil P levels.

Source of P used. Several studies have suggested that mycorrhizal plants are capable of solubilizing and using unavailable forms of P in the soil. Daft and Nicholson (25) found that mycorrhizal tomatoes responded quite well to small additions of relatively insoluble bone meal. Only when 16 times as much bone meal was given to nonmycorrhizal plants did their growth and P uptake approach that of mycorrhizal plants.

Murdoch et al. (65) demonstrated that mycorrhizal maize plants were larger and had higher P contents than nonmycorrhizal plants when P sources of low availability, such as rock phosphate, were added to the soil. Mycorrhizal and nonmycorrhizal plants grew equally well when supplied with readily available P. Jackson et al. (52) also found that mycorrhizal maize plants responded markedly to addition of rock phosphate. Similar results have been obtained with a variety of host plants, usually in soils of low pH. Results such as these promoted the theory that mycorrhizae have the capability of absorbing normally insoluble P through the presence of phosphate enzymes on mycorrhizal surfaces. Mosse (61) and Mosse et al. (64) realized that the solubility of rock phosphate increases considerably in acid soils and conducted similar experiments with onion and maize seedlings. They found uptake and use of added rock phosphate was greatly increased in acid soils by mycorrhizal colonization. Rock phosphate remained unavailable, however, to both mycorrhizal and nonmycorrhizal plants in alkaline or neutral soils. There was little indication in the latter experiments that VAM inoculation increased solubility or improved phosphate availability. Mycorrhizal colonization, however, did improve use of available P.

Hayman and Mosse (47) tested the concept that mycorrhizae might use organic forms of phosphate. They determined that most of the organic phosphates tested were equally available to mycorrhizal and nonmycorrhizal onion plants, although the P content was quite often higher in mycorrhizal plants.

Sanders and Tinker (96) labeled soils low in available P with ^{32}P and then measured specific activities (ratios of labeled to unlabeled P) of the soil solution and of onion roots with and without mycorrhizal colonization. Specific activities of the mycorrhizal and nonmycorrhizal roots, as well as of the surrounding soil, were similar, indicating that similar sources of P were used. Mycorrhizal plants, however, demonstrated P influx rates 3 to 16 times greater, indicating the same source of P was used, but there was increased efficiency of uptake in the mycorrhizal system. Experimental results of Powell (78) confirmed those of Sanders and Tinker (96). The former also concluded that mycorrhizal and nonmycorrhizal onion plants absorbed P from the same or similarly labeled fractions of soil P. Owusu-Bennoah and Wild (72) also determined specific activities of P absorbed by mycorrhizal and nonmycorrhizal onion and lettuce plants were about the same, although mycorrhizal plants absorbed a larger quantity of P. They concluded that mycorrhizal plants did not significantly increase the size of the labile pool of soil phosphate.

Contradictory results were reported by Swaminathan and Verma (105), who found P absorbed by mycorrhizal potato plants did indeed have a lower specific activity than that absorbed by nonmycorrhizal plants. Researchers generally agree that VAM plants use the same sources of soil P as do nonmycorrhizal plants. Nonetheless, results are conflicting and the evidence is not conclusive.

Mechanisms responsible for increasing P uptake. Several studies were undertaken to clarify how VAM fungi increase the efficiency of P uptake. Rhodes and Gerdemann (86) reported that uptake of ^{32}P by mycorrhizal onion plants was greatest at injection points about 3–6 cm from the root surface. Radioactivity generally was not detected in root segments of nonmycorrhizal plants adjacent to any of the tracer injection points. Hattingh et al. (42) determined that onion roots inoculated with *Glomus mosseae* and *G. fasciculatum* had considerably higher uptakes of ^{32}P introduced 27 mm away from the root surface than did roots of nonmycorrhizal plants. Diffusion could not account for the increased uptake, as its effect was found to extend only 7.5 mm from the point of injection and the nonmycorrhizal root surface was a minimum of 15 mm away. These results suggest the existence of an active transport mechanism in the fungus, which extends beyond the immediate vicinity of the root surface. When hyphae growing from the mycorrhizae were severed, ^{32}P uptake between mycorrhizal and nonmycorrhizal plants differed only slightly. This observation supports the hypothesis that fungal hyphae do play an active role in P uptake.

Cress et al. (21) determined increased absorption of P by mycorrhizal tomato roots in the higher concentration range of P (>30 μM KH_2PO_4) appeared to be related mainly to an increased number of absorbing sites contributed by the added fungal surface area. However, the increased number of absorbing sites did not appear to be a major factor in increased absorption in the lower concentration range of P (<20 μM KH_2PO_4). The increased absorption rate observed was due primarily to increased absorption site affinity, as indicated by the lower K_m value for mycorrhizae. Splittstoesser (104) supports this conclusion and states that mycorrhizal fungi have an absorption K_m for P that is 10 times lower than that observed in most plant roots.

Results of research conducted to date indicate that mycorrhizae can increase uptake of P by hyphal extension (which greatly increases the number of absorption sites) and also by increased affinity for available soil P. Thus, mycorrhizae allow far more efficient absorption of P from low-concentration pools in the soil.

Physiological pathways involved in the mycorrhizal symbiosis. In the late 1970s, emphasis began to shift from studies concerning mycorrhizal effects on growth and nutrient uptake to studies whose objective was to identify physiological pathways involved in the mycorrhizal symbiosis. The first type of experiments to be discussed are those that identified physiological mechanisms involved in the transfer of P from fungal hyphae into the host root and to determine the form of P transferred.

Cox et al. (19) found that onion roots colonized by *Glomus mosseae* had fungal vacuoles containing metachromatic lead-staining bodies that appeared to be polyphosphate granules. Callow et al. (14) later confirmed that polyphosphates comprise at least 40% of

the total P present in the fungal component of the mycorrhizal onion root. Parish et al. (75) determined that polyphosphates accumulate rapidly in the external hyphae and later also appear in the internal mycelium of colonized roots when phosphate is applied to phosphate-starved mycorrhizal plants. These results were substantiated by others who also found that mycorrhizal fungi accumulate P in the vacuoles in the form of polyphosphates (19, 104, 106).

Movement of inorganic P in fungal hyphae has been shown to occur at rates 10 times faster than it does in plant roots (56). This suggests the presence of an active transport mechanism. Sanders and Tinker (96) derived theoretical phosphate translocation rates in hyphae of *Glomus mosseae*, and Person and Tinker (76) and Cooper and Tinker (17) subsequently measured phosphate translocation rates directly. Their results indicated that phosphate translocation does occur at high rates ranging from 0.1 to 3.8×10^{-9} mol·cm^{-2}·s^{-1}. All of these investigators concluded that phosphate translocation within hyphae of *Glomus mosseae* is driven by metabolically dependent active processes. The most acceptable hypothesis to explain rapid phosphate translocation in VA mycorrhizal fungi is still that of Tinker (106), who proposed that the transport mechanism is cyclosis, plus bulk flow, with loading and unloading of polyphosphates into vacuoles as the method of varying P concentration of the streaming protoplasm.

Capaccio and Callow (15) and Cox et al. (19) demonstrated that polyphosphate activity is only associated with internal mycelia and that polyphosphate granules disappear from vacuoles in the fine arbuscular branches. This finding suggests unloading of polyphosphates from VAM fungi occurs within host plant cells. Unloading of polyphosphate could be a rate-limiting step in the phosphate nutrition of mycorrhizal plants and its retention in the fungal tissue may contribute to the greater P concentrations sometimes found in roots of mycorrhizal plants. Results of several studies (10, 90, 105) indicate that the preferential site for phosphate transfer from fungus to host plant is across the living interface in the intracellular arbuscules. Cox and Tinker (18) found evidence indicating that phosphate released by the fungus into the interfacial matrix is actively transported across the host plasmalemma. ATPase activities bound by this membrane are specifically concentrated around the fine, living arbuscular hyphae (59).

Biochemical studies of VAM fungi have shown that they have the enzymes necessary for polyphosphate synthesis and degradation. The accumulation of polyphosphates in VAM roots transferred from phosphate-deficient conditions to a sufficient phosphate supply is accompanied by large increases in polyphosphate kinase activity (15), suggesting that this enzyme is inducible in VAM systems. The necessity for induction of this enzyme to prime the phosphate transport system in the fungal hyphae could explain the initial lag period in phosphate transport observed in many translocation experiments.

Discovery of another enzyme, alkaline phosphatase, by Gianinazzi-Pearson and Gianinazzi (35, 36), has spearheaded a 2nd area of physiological studies, notably those involved in identifying physiological mechanisms responsible for P inhibition of mycorrhizal colonization. These researchers have shown that activity of this mycorrhizae-specific phosphatase (MSP) is closely linked to the development of both the mycorrhizal colonization and the colonized host plant. Enzyme concentration reached a maximum when the colonized root length was 50% and contained only well-developed arbuscles. Maximum MSP activity also coincided with the beginning of plant growth stimulation due to mycorrhizal formation. Once the initial growth response had occurred, the level of mycorrhizal colonization reached a maximum and then remained constant as it followed root development. The close correlation between MSP activity, the morphological and physiological stage of the colonization, and the mycorrhizal growth response suggest that MSP may be involved in the assimilation of P in the mycorrhizal system.

Orthophosphate ions inhibited MSP activity and thus, final product formation. This inhibition could be of great importance when considering the implication of the enzyme's activity. Soil solutions of P typically range from 2×10^{-6} M to 1×10^{-5} M (9). MSP activity was greatest at these concentrations, but it became markedly inhibited in the presence of increasing phosphate concentrations from added fertilizers. The observations of Gianinazzi-Pearson and Gianinazzi (35, 36) indicated that inhibition of mycorrhizal-specific alkaline phosphate by high concentrations of P in plant roots is one possible explanation for inhibition of mycorrhizal colonization. Other theories, however, do exist. It is known that plants grown under low phosphate conditions demonstrate an increase in permeability of the cell membranes due to decreased phospholipid content and the resulting irregular distribution pattern of available phospholipids within the membrane structure. Ratnayake et al. (85) have hypothesized that the much greater leakage of sugars and amino acids occurring from this type of root might stimulate the growth of fungus and the development of mycorrhizal colonization. Increased P nutrition usually reduces membrane permeability, which would curtail exudation of these substances from plant roots. However, exudation of sugars and amino acids from plant roots can also stimulate growth of bacteria and fungi other than VAM fungi.

Other elements

VAM have also been implicated in increased uptake of elements other than phosphorus. Ames et al. (1) determined celery plants inoculated with *Glomus mosseae* derived significantly more ^{15}N from organic and inorganic sources of N than did nonmycorrhizal plants. An average of 25% of ^{15}N enriched ammonium sulfate [$(NH_4)_2SO_4$] appeared in mycorrhizal plants over a 30-day period. Control plants accumulated an average of only 3.4% during the same time period. Rhodes and Gerdemann (86–88) demonstrated that VAM hyphae were involved in transfer of radioactive sulfur to plant roots when it was injected 4.5 cm from the root surface. Rhodes and Gerdemann (89) proved that phosphate fertilization, as well as mycorrhizal colonization, increased S and Ca uptake from the soil. They suggested that improved phosphate nutrition mediated by mycorrhizal colonization was the most likely explanation of their results. Very little work has been done on the uptake of nutrients other than P in vegetable crops; however, 2 micronutrients, Zn and Cu, have been found consistently at increased concentrations in mycorrhizal plants in general.

Carbohydrate physiology

Several studies conducted on VAM deal with the carbohydrate physiology of the symbiosis. This topic has not been studied in great detail, but there is clear experimental evidence that the C requirements of VAM fungi are supplied by the host plant. Snellgrove et al. (103) used ^{14}C-labeling techniques to investigate C distribution and use in mycorrhizal and nonmycorrhizal leek plants. *Glomus mosseae* colonized 60% to 70% of the root length and resulted in about 7% more of the total fixed C being translocated from the shoots to roots as compared to nonmycorrhizal plants. This additional translocated C could be accounted for by increased root respiration rates and increased loss of C in the form of root exudates to the soil. The results of Pang and Paul (74) agree closely with those of Snellgrove et al. (103). They measured the photosynthetic incorporation of $^{14}CO_2$ into *Vicia faba* plants inoculated with VAM fungi. Roots of mycorrhizal plants respired 30% of the incorporated $^{14}CO_2$, while nonmycorrhizal plants respired only 18%. The work of Bevege et al. (8) and of Cox et al. (20) also indicated that there is rapid translocation of photosynthates to root systems of mycorrhizal plants. They have shown by autoradiography that photosynthate passes into both intracellular fungal structures and hyphae outside roots.

Cooper and Losel (16) determined that mycorrhizal onion roots contained significantly more total lipids than nonmycorrhizal roots and proposed that host plant photosynthates were largely incorporated into the lipid fraction of mycorrhizal roots. They suggested that a significant lipid sink is necessary for the growth of fungal hyphae, and later confirmed their hypothesis by proving mycorrhizal onion roots incorporated significantly more ^{14}C from photosynthate into lipids than did nonmycorrhizal roots (57).

Nitrogen fixation

The importance of P nutrition in efficient N_2 fixation has long been recognized. The N_2 fixation process is dependent on adenosine

triphosphate (ATP) as an energy source. Phosphorus, as a major constituent of ATP, is an essential element required for biological N_2 fixation.

The great majority of studies concerning the effect of VAM on biological N_2 fixation have involved forage legumes rather than vegetable or grain legumes. Nonetheless, the results from these studies are strikingly similar. Daft and El-Giahmi (22) found that colonization of French bean with mycorrhizal fungi and *Rhizobium* compared with *Rhizobium* alone resulted in increased growth, nodulation, rates of N_2 fixation, leghemoglobin, P, and total protein content. Application of soluble phosphate to nonmycorrhizal plants duplicated the effects of mycorrhizal colonization. Manjunath and Bagyaraj (58) found that cowpea and pigeon pea inoculated with both *Rhizobium* and *Glomus fasciculatum* possessed greater shoot, root, and nodule dry weights, as well as higher N and P contents of shoots, roots, and nodules than did plants inoculated with either organism alone. Islam and Ayanaba (51) found that inoculation of the cowpea 'Pale Green' with *Glomus macrocarpum* Tul. & Tul. var. *macrocarpum* resulted in increased nodulation and N_2 fixation. Rajapakse and Miller (83) studied the effects of inoculation with *Glomus mosseae*, *G. fasciculatum*, and *Rhizobium* on plant growth and N_2 fixation variables using 2 different cowpea cultivars, 'Brown Crowder' and 'Bush Purple Hull'. Inoculation with mycorrhizal fungi significantly increased the percentage of colonized roots and plant heights while root length was decreased. Interaction between VAM colonization and cowpea genotype was significant for nitrogenase activity. Inoculation with *G. fasciculatum* increased nitrogenase activity of 'Brown Crowder' compared with the nonmycorrhizal control, whereas *G. mosseae* reduced the activity and neither fungi affected nitrogenase activity of 'Bush Purple Hull'. Nodule number and weight were not affected by inoculation with VAM fungi. In this study, increased nitrogenase activity was not attributed directly to P concentration of roots or shoots.

Although mycorrhizal colonization generally has been found to increase N_2 fixation rates and plant growth, one study clearly indicated inoculation of vegetable legumes with VAM and *Rhizobium* does not always result in a favorable plant response. Bethlenfalvay et al. (7) indicated that bean plants (*Phaseolus vulgaris* L. cv Dwarf) inoculated with both *Rhizobium* and VAM demonstrated a depression in growth, as compared to noninoculated controls, when a majority of the days during the growing season were overcast. Colonization of nodulated host plants by VAM fungi resulted in significantly smaller nodule numbers, nodule dry weights, and shoot weights. Increased demand for carbohydrates by both VAM and *Rhizobium* could not be met when photosynthetic efficiency was reduced by low light intensity.

Disease resistance

Interactions between VAM and plant disease in vegetable crops have received only minimal experimental consideration; therefore, this discussion will also include findings where other horticultural or agronomic crops have been used. Most reports in the literature indicate that colonization by VA mycorrhizal fungi reduces the severity of plant disease, particularly diseases caused by soil-borne pathogens.

Mycorrhizal onion roots have been shown to be less susceptible to pink root disease caused by *Pyrenochaeta terrestris* (Hans.) Gorena, Walker and Larson (6, 92). Only the mycorrhizal segments of the root system were more resistant to the pathogen. Safir (92) found larger amounts of reducing sugars in mycorrhizal plants and suggested this as a possible explanation for decreased root infection in onion by *Pyrenochaeta terrestris*.

Dehne and Schönbeck (30) found that prior colonization by *Glomus mosseae* reduced damage to tomato plants by *Fusarium oxysporum* Schlet. f. sp. *lycopersicae* (Sacc.) Snyd. and Hans. The number of yellow leaves and the amount of electrolyte leakage from leaf and stem tissues were reduced in mycorrhizal plants. Sikora and Schönbeck (102) found that colonization of tomato plant roots by *G. mosseae* significantly reduced the number of nematode larvae (*Meloidogyne incognita* Kofoid & White) that developed into adults. They also determined that carrot root colonization by *G. mosseae* suppressed the population of the nematode *Meloidogyne hapla* for up to 18 weeks.

Kellam and Schenck (53) studied the development of VAM and a root-knot nematode on soybean plants. At the end of the growing season, the presence of *Glomus macrocarpum* on soybean roots significantly increased seed yield and significantly reduced the number of *Meloidogyne incognita* galls. Paget (73) observed that root colonization of strawberry plants by *Cylindrocarpon destructans* (Zins.) Schol., a mild pathogen of strawberry, was greatly reduced and plants demonstrated less stunting when roots were also colonized by *Glomus fasciculatum*. Schenck et al. (98) reported that prior root colonization by *Gigaspora margarita* or *Glomus macrocarpum* reduced the damage caused by *Phytophthora parasitica* Dast. to 2 citrus rootstocks, Carrizo citrange and sour orange.

Schönbeck and Dehne (99) found cotton plants colonized with *Glomus mosseae* and nonmycorrhizal cotton plants were colonized with *Thielaviopsis basicola* (Berk. and Br.) Ferraris to the same degree. Shoot weights of mycorrhizal plants were significantly greater than nonmycorrhizal plants, although root weights did not differ significantly. Mycorrhizal plants tolerated infection by *T. basicola* better than nonmycorrhizal plants. Baltruschat and Schönbeck (4) reported that the chlamydospore production of *T. basicola* was negatively correlated with mycorrhizal colonization of tobacco and alfalfa roots. Reduction in chlamydospore production was attributed to high levels of free amino acids in the roots, notably arginine and citrulline. The addition of synthetic arginine to nonmycorrhizal root extracts inhibited chlamydospore production on agar, confirming its prohibitive effect.

Some reports, however, indicate no difference or even an increase in disease severity when plant roots are nonmycorrhizal. Baath and Hayman (3) found no difference in the severity of verticillium wilt or the subsequent decrease in plant growth between mycorrhizal and nonmycorrhizal tomato plants.

Menge et al. (60) found that prior root colonization of *Citrus sinensis* (L.) Osbeck 'Pineapple' by *Glomus fasciculatum* provided no protection against root infection by *Phytophthora parasitica*. Plants colonized by the mycorrhizal fungus alone had a 3-fold increase in plant height and a 65% increase in dry weight compared to nonmycorrhizal plants, but these benefits were negated by infection with the pathogen. Ross (91) was the first to report a VA mycorrhizal fungus (*Glomus macrocarpum* var. *geosporus*.) that increased the severity of a plant disease. Nearly 90% of the susceptible soybean plants with VAM demonstrated internal stem discoloration symptoms of phytophthora root rot (*P. megasperma* Drechs. var. *sojae* Hildeb.), while 20% of the nonmycorrhizal plants developed these symptoms. Davis et al. (27) discovered that cotton plants colonized by *Glomus fasciculatum* had a higher incidence of verticillium wilt than did nonmycorrhizal plants.

Schönbeck and Schinzer (101) inoculated mycorrhizal (*Glomus mosseae*) and nonmycorrhizal tobacco plants with tobacco mosaic virus. They observed an increase in the number of lesions on leaves of mycorrhizal plants. Daft and Okusanya (24) discovered that the multiplication rate of the aucuba mosaic virus was highly correlated with the percentage of colonization of tomato roots by *Glomus macrocarpum* var. *geosporus*. Greater colonization by the fungal endophyte always accelerated multiplication of the virus. Viral diseases seem to be particularly enhanced by the mycorrhizal symbiosis. Experimental evidence indicates increased virulence and enhanced reproductive rate of a virus may be due to the improved nutrient status of mycorrhizal plants. Electron microscopy has revealed tobacco mosaic virus was intensively concentrated in cells that contained arbuscular stages with rather fine branches (100), indicating that the accumulation of virus particles was favored in regions of high phosphate metabolism and high concentrations of nucleic acids and proteins.

Interactions among symbiont–pathogen–host combinations appear complex and seem to vary with each combination. Nonetheless, generalizations can be made from research results of the past 2 decades. Diseases caused by soil-borne fungi can be influenced by the formation of mycorrhizae in the root system. In general, mycorrhizal plants suffer less damage and the incidence of disease is decreased or pathogen development is inhibited (29). The retar-

dation of pathogen development in the root system is restricted to the site of mycorrhizal establishment. This retardation of pathogen development may be due to VA mycorrhizal fungi physically limiting the number of available colonization sites in the roots.

VA mycorrhizal fungi are also known to alter host plant physiology. Mycorrhizal roots are more lignified than nonmycorrhizal roots (28). This effect may be responsible for the restriction of the endophyte to the root cortex. The same mechanism of resistance may be effective against parasitic soil-borne organisms invading the host root. Host plants contain chitinolytic enyzmes that successively degrade aging arbuscules of the endophyte. These enzymes could be effective against fungal pathogens as well. Host plant physiology can also be altered to produce substances inhibitory to sporulation or development of pathogens. This particular effect can be demonstrated in the case of sporulation of *Thielaviopsis basicola* on mycorrhizal roots, which was inhibited by high levels of arginine (4). In addition, the accumulation of reducing sugars in mycorrhizal roots may inhibit root infection by *Pyrenochaeta terrestris* (92).

Improved nutrition of mycorrhizal plants usually enhances plant development and vigor. This increase in plant vigor may lead to disease escape or to higher tolerance toward soil-borne pathogens in some instances. However, improved nutrition of mycorrhizal plants in nutrient-deficient soils often enhances vulnerability of those plants to shoot and leaf pathogens. The general rule "what is good for the plant is also good for the pathogen" is applicable under these circumstances. From this point of view, vigorous mycorrhizal plants should be more susceptible to shoot and leaf pathogens than less-healthy nonmycorrhizal plants.

It is important to note that the effectiveness of VAM in combating soil pathogens is also dependent on the virulence of the pathogen. Highly virulent pathogens or increased inoculum levels of less virulent pathogens tend to decrease the positive influence of the mycorrhizal symbiosis (31). Increased resistance, when it occurs, requires optimum conditions for the development of the mycorrhizal symbiosis before the attack of the pathogen.

Plant water status

Very little research has been conducted concerning the water relations of plants colonized by VAM fungi, but the limited research completed is encouraging. Safir et al. (93), working with mycorrhizal and nonmycorrhizal soybeans, found that the presence of mycorrhizae formed with *Glomus mosseae* decreased the plants' resistance to water transport considerably compared to nonmycorrhizal controls. In a subsequent study (94), they confirmed decreases in resistance to water transport of about 40% in mycorrhizal soybeans compared to the nonmycorrhizal controls. Differences in resistance to water transport were found to occur in the roots, but there were no significant differences in stem and leaf resistance between mycorrhizal and nonmycorrhizal plants. Addition of nutrients to nonmycorrhizal plants growing in low nutrient-status soils lowered the resistance to water transport to the same level as mycorrhizal plants, suggesting lowered resistance in mycorrhizal plants was due to enhanced nutrient status brought about by the fungus.

Olson et al. (70) determined that P uptake is greatly reduced in plants subject to drought due to slower diffusion of P through the soil and impaired root uptake capacity. In addition to its direct effect on plant growth, water stress indirectly affects plant growth through repressed P nutrition. Nelsen and Safir (67) found that mycorrhizal onion plants had higher leaf water potentials, leaf transpiration rates, hydraulic conductivities, and lower leaf resistances than did nonmycorrhizal plants grown under low soil P conditions. All 4 parameters were not different from those of mycorrhizal plants when nonmycorrhizal controls were grown under high soil P conditions.

Bolgiano et al. (11) found that colonization of onion plants inoculated with *Glomus etunicatum* Becker & Gerdemann decreased more sharply with increasing P levels in irrigated plots than it did in nonirrigated plots. Colonization remained high in nonirrigated onions but decreased exponentially with increasing extractable P concentrations in irrigated onion plants. These results substantiated a previous report that claimed mycorrhizal dependency of onions increased under drought stress (66). Yield of nonirrigated onion plants at lower levels of added P exceeded that of irrigated onion plants receiving the same P levels, indicating the effectiveness of VAM in increasing P uptake. Maximum yield and high colonization occurred simultaneously in nonirrigated treatments, but irrigation significantly decreased mean colonization rates. Much higher soil P levels and irrigation were required to exceed yields of the highly colonized nonirrigated treatments. They concluded that the magnitude of the effect of mycorrhizal fungi on the water relations of the host is most likely a function of improved P nutrition, rather than water stress alone.

FACTORS AFFECTING ROOT COLONIZATION AND PLANT GROWTH RESPONSE

Host variability

Plant response in terms of root colonization and growth varies considerably from host to host, indicating that the host plant plays an important role in the VAM symbiosis.

Interspecific. Some vegetables do not form mycorrhizae when inoculated with VAM fungi (e.g., Cruciferae and Chenopodiaceae) (Fig. 1). Chemical inhibition and intrinsic resistance of the epidermis and cortex have been attributed to the lack of mycorrhizae formation in these plants. However, most vegetable species do form mycorrhizae.

Interspecific variability has been observed among those vegetables that form mycorrhizae. Onions are found to be much more responsive to inoculation with VAM fungi than other vegetables. Yost and Fox (107) reported that cowpea is more dependent on mycorrhizal association than soybean.

Harley and Smith (41), inferring from the results of Baylis (5), reported that, generally, plants with thick, unbranched roots and few root hairs (e.g., citrus and onions) are more dependent on mycorrhizae than those with finely branched roots with numerous long root hairs. Long root hairs and well-branched root systems of Cruciferae may be a reason for the lack of mycorrhizae in this family.

Intraspecific. Recent evidence indicates that considerable variability exists among cultivars in their response to the same mycorrhizal endophyte and among the responses of the same cultivar to different mycorrhizal endophytes. Ollivier et al. (69) reported that *G. mosseae* and *G. E3* Gilmore stimulated the growth of 2 cowpea cultivars, while *G. epigaeum* Daniels & Trappe gave a positive growth effect with only one cultivar, 58-185. Infection levels were lower and growth effects less with *G. epigaeum* than with other VAM fungi. Rajapakse and Miller (83) inoculated 2 cowpea cultivars with *G. mosseae*, *G. fasciculatum*, and *Rhizobium*. Influence of inoculation with VAM fungi on shoot dry weight and nitrogenase activity was dependent on the species of fungi as well as the host cultivar. 'Brown Crowder' showed a significant increase in shoot dry weight and nitrogenase activity when inoculated with *G. fasciculatum*, while 'Bush Purple Hull' did not show a significant response to either VAM fungi in terms of shoot dry weight or nitrogenase activity. Therefore, it appears that the 'Brown Crowder' and *G. fasciculatum* host endophyte combination is preferable to the other combinations.

Rajapakse and Miller (81) conducted an experiment to study the variation in mycorrhizal colonization with time. 'Brown Crowder' had a significantly higher percentage of root colonization than 'Bush Purple Hull' 4 weeks after inoculation; however, the developmental pattern for hyphae, vesicles, and arbuscules was not significantly different between the 2 cowpea cultivars or the 2 VAM fungi used. In a subsequent investigation, they screened 19 cowpea cultivars under field conditions with 3 soil treatments (82). Treatments included fumigation with methyl bromide, inoculation with *G. fasciculatum* after fumigation, and no fumigation or inoculation. Fumigation reduced dry matter in shoots, leaf growth, nodule weight, and nitrogenase activity in most cultivars. Cowpea cultivars showed a differential response to inoculation with VAM fungi. A number of cultivars showed a response to natural inoculation, but only a few benefitted from inoculation with *G. fasciculatum* after fumigation. Percentage of and intensity of root colonization at harvest were not significantly affected by cultivar. Total mycorrhizal root

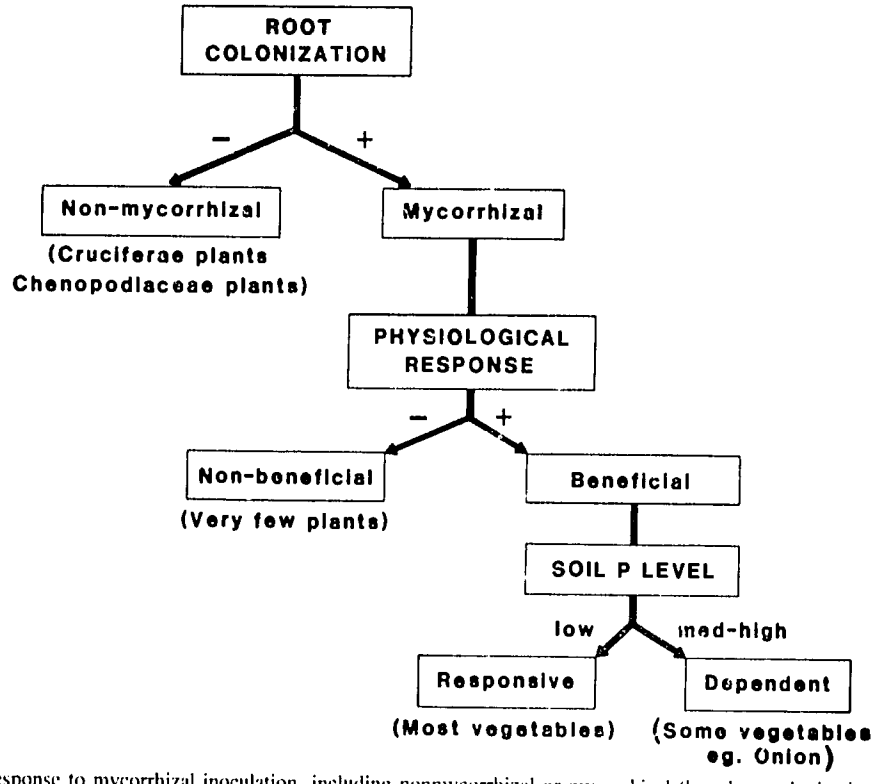

Fig. 1. Types of host response to mycorrhizal inoculation, including nonmycorrhizal or mycorrhizal (based on colonization), nonbeneficial or beneficial (based on plant or physiological response), and responsive or dependent (based on soil P level).

length (percentage of infection × root length) was different between cultivars. This measure appears to be more appropriate than percentage of root colonization for selecting cultivars that show an inoculation response to VAM fungi.

Powell et al. (79) determined that indigenous mycorrhizal fungi increased P uptake and plant growth of onion cultivars 'Takai Top Keeper' (TTK) and 'White Barletta' (WB), but failed to do so in 'Pukekohe Longkeeper' (PKL) or 'Dragon Eye' (DE). In separate experiments, PLK, TTK, and WB were grown in unsterilized native soils and inoculated with *Glomus* sp., *Gigaspora margarita* Becker & Hall, F4, F20, NP9 (VA mycorrhizal fungal selections from field soils), or the indigenous mycorrhizal fungi. Inoculation with *Glomus* sp. significantly increased bulb weights and P uptake in all 3 cultivars. *Gigaspora margarita* significantly increased bulb dry weights and P uptake in TTK, but was far less effective with PLK and WB. Endophytes F4 and F20 increased bulb dry weights and P uptake in TTK, but were less effective with WB, and demonstrated no significant increases in bulb yields or P uptake in PLK. NP9 depressed bulb yield and P uptake in PLK and WB, while it increased bulb yield by 67% and P uptake by 57% in TTK.

Highly significant fungal inoculant–cultivar interactions were observed in these onion experiments. Inoculation with different fungal endophytes resulted in almost identical levels of colonization in host plant roots within specific cultivars. However, significant differences in plant growth response and nutrient uptake were observed. There were also clear cases of identical VAM endophytes heavily colonizing plant roots and significantly increasing plant growth and nutrition in a particular cultivar and not in another. Even though the same fungal species from the same pure culture was used, low plant growth response was associated with very little or no colonization of host plant roots. Significant differences in plant growth response and nutrient uptake, despite nearly identical root colonization levels, also have been found among cultivars inoculated with identical mycorrhizal fungi from the same pure culture.

Many physiological mechanisms, each governed by specific genes, are responsible for the successful interaction of fungi and plant roots. Undoubtedly, differences in the genetic makeup of host plants and of the different fungal endophytes involved are a component of the variability in plant growth responses observed. Plant hosts and mycorrhizal fungi with synergistic genes should result in the greatest stimulation of plant growth.

Unlike the legume–*Rhizobium* symbiosis, there is no evidence supporting a well-defined host specificity for VA mycorrhizae. Nonetheless, the genotype of both symbionts has been known to influence the degree of root colonization and growth response. Therefore, host preference, in contrast to host specificity, usually is observed in the VAM symbiosis. In addition, other differences between the legume–VAM and the legume–*Rhizobium* symbioses have been observed (Table 1).

Endophyte variability

Once it was discovered that mycorrhizal fungi are present in most soils and colonization by these fungi is the rule rather than the exception, experiments were designed to compare the effectiveness of introduced isolates of mycorrhizal fungi with those indigenous to native soils. This work was necessary to determine if field inoculation using selected species of mycorrhizal fungi was feasible.

Mosse and Hayman (63) investigated the effect of inoculation with *G. mosseae* on growth of onion seedlings in 4 different soils. Soil treatments consisted of sterilization to eliminate indigenous mycorrhizal fungi and nonsterilization. Dry shoot weights of previously inoculated transplants harvested after 11 weeks of growth averaged 4.85, 4.58, 1.87, and 24 times greater than plants colonized by indigenous mycorrhizal fungi in each of the 4 soils tested. Average shoot dry weights of seed-inoculated plants harvested after 11 weeks of growth were 3 times greater than those of plants colonized by indigenous mycorrhizal fungi in 3 of the 4 soils tested. In one soil, however, shoot dry weight of plants colonized by indigenous mycorrhizal fungi was 1.7 times greater than shoot dry weight of plants inoculated with *G. mosseae*.

Owusu-Bennoah and Mosse (71) found clear differences in growth between onion seedlings inoculated with either *Glomus caledonicum* (Nichol. & Gerd.) Trappe & Gerdemann or a mixture of *Glomus* endophytes and noninoculated onion plants grown in the field as early as 4 weeks after emergence. At harvest, it was found that inoculation with the mixture of *Glomus* species improved growth by 77% (shoot dry weights) and inoculation with *G. caledonicum*

Table 1. Comparison of the vesicular-arbusculaar mycorrhizal symbiosis and the legume-*Rhizobium* symbiosis.

VAM	Legume-*Rhizobium*
Fungi + plant	Bacteria + plant
No broad specificity	Specific (cross-inoculation groups)
Fungi-obligate symbionts	Bacteria-facultative symbionts
Inoculum production outside the host not possible	Inoculum production outside the host feasible
Cannot fix atmospheric N_2 but helps the process through improved P nutrition	Fix atmospheric N_2
Five genera involved, (e.g., *Acaulospora, Entrophospora, Gigaspora, Glomus, Sclerocystis*)	Two genera involved (*Bradyrhizobium* and *Rhizobium*)
No special structures formed by host	Highly visible structure formed by the host (nodules)

improved growth 6 times over plants infected by indigenous mycorrhizal fungi despite the fact these noninoculated plants were well-colonized. Percentage of colonization was less, however, than in inoculated plants. Owusu-Bennoah and Wild (72) determined that 42-day-old onion plants that had been inoculated with *Glomus mosseae* possessed significantly higher total plant dry weights than did noninoculated seedlings in either sterilized or unsterilized treatments of 3 separate soils. Improved growth was always associated with a significantly higher rate of colonization than that of noninoculated seedlings colonized with indigenous endophytes.

Results with lettuce plants were more variable. In 2 soils, inoculation with *G. mosseae* resulted in significantly higher plant dry weights than did colonization by indigenous mycorrhizal fungi. Inoculation in the 3rd soil did not significantly increase plant weights compared to noninoculated controls in either sterilized or unsterilized soils. Mycorrhizal colonization was absent or very low in all treatments.

Plenchette et al. (77) inoculated leek plants with 4 different species of mycorrhizal fungi and asparagus plants with 2 different mycorrhizal endophytes. Leek and asparagus plants were harvested 4.5 and 3.5 months after initial establishments, respectively. Regardless of the mycorrhizal strain used, all of the inoculated plants exhibited growth superior to that of the control plants. Roots of control plants were not colonized by indigenous mycorrhizal fungi in any of the control treatments. Dry weight of leek tops and stem diameters was significantly increased by all species of VAM fungi used; however, *G. epigaeum* and *G. monosporum* Gerdemann & Trappe were more effective than *G. macrocarpum* or *Gigaspora calospora* (Nichol. & Gerd.) Gerdemann & Trappe. The dry weight of asparagus tops and roots was significantly increased by *Glomus epigaeum* and *G. monosporum*, but there were no significant differences between the 2 fungi. Significant correlations were found between the magnitude of colonization and shoot dry weight for both leek and asparagus.

Hussey et al. (49) found similar results with asparagus inoculated with *Glomus versiforme* (Karsten) Berch grown in this same clay soil. Inoculation resulted in greater root fresh weights, shoot dry weights, number of shoots, and shoot heights. Indigenous VAM fungi had no significant effect on these growth parameters. They concluded the suppression of growth in plants infected by indigenous endophytes may be due to the ineffectiveness of the particular indigenous fungi associated with asparagus.

Islam and Ayanaba (51) compared the effect of indigenous VAM fungi to the effect of inoculation with *Glomus mosseae* on growth and nutrient uptake of cowpea and maize plants. Colonization by indigenous endophytes significantly increased shoot dry weights and the total plant N and P content of cowpea plants compared to non-colonized control plants. Inoculation with *G. mosseae* in sterilized soil significantly increased growth, nutrient uptake, and yield compared to colonization with indigenous endophytes. It was concluded that *G. mosseae* was superior to indigenous endophytes in improving cowpea yield in this sterilized field soil. Growth and yield of maize plants were significantly increased as a result of inoculation in both sterilized and nonsterilized soils, again indicating the superiority of an introduced, effective endophyte over indigenous mycorrhizal fungi.

Similar results were found by Mosse (62) in maize transplants inoculated with *Glomus fasciculatum* and grown in unsterilized field soils. She discovered that colonization by indigenous endophytes was sparse in maize and only slightly increased by added phosphate. She theorized that the low level of colonization by indigenous fungi may denote host specificity of the indigenous endophytes or differences in response to mycorrhizal colonization among maize cultivars. Khan (54) also determined that inoculated maize seedlings planted in a field containing indigenous mycorrhizal fungi had greater plant weights, percentage of P, and ear size than noninoculated control plants.

Powell et al. (79) inoculated 4 different cultivars of onions with a mixture of *Glomus fasciculatum* and *G. tenue* (Greenall) Hall, F4, F11, F20, NP9 (VA mycorrhizal fungi selections from field soils), the indigenous mycorrhizal fungi, plus a control with no mycorrhizal fungi. They found that 4 of the 5 introduced fungi significantly increased plant growth and P uptake compared to the indigenous mycorrhizal fungi, which failed to colonize plant roots. Although F11 colonized plant roots, it was ineffective in increasing P uptake or plant growth.

Research efforts currently indicate that field inoculation of vegetable crops, using carefully selected species of mycorrhizal fungi, is usually superior to using indigenous mycorrhizal fungi present in native soils. Significantly improved plant nutrient uptake rates and consequent growth stimulation should result from this practice in a majority of cases. A great deal more research needs to be completed before identification of the most effective endophyte for each vegetable cultivar grown in a particular soil is accomplished.

Soil fertility

The majority of mycorrhizal plants benefit from the symbiosis and show increased growth, nutrient uptake, N_2 fixation, etc. However, most vegetable plants show these physiological responses to VAM fungi only under low soil P levels.

Daft and Nicholson (26) tested the effect of cumulative P application on growth and mycorrhizal colonization rates of maize seedlings. They found that endophyte activity, estimated both by numbers of spores and percentage of colonization, was progressively depressed when soluble phosphate was applied over extended periods. The same was true when the maximum quantity of phosphate was added early during growth of the host. Buwalda et al. (13) grew leek plants inoculated with *Glomus mosseae* in pots to which P at 0, 30, 120, and 480 $mg \cdot kg^{-1}$ of soil had been added. The level of

VAM colonization decreased noticeably as the amount of P added increased. Decrease in colonization was also correlated with increased levels of P in plant tissue. Nelsen et al. (68) sowed onion seeds in 2 soils that were high and low in available P and that contained an indigenous population of mycorrhizal fungi. They added P at 0, 30, 97, and 193 kg·ha^{-1} and inoculum of *Glomus etunicatum* Becker & Gerdemann. Root colonization and mycorrhizal spore numbers were negatively correlated with added P in soil that was low in available P (3 kg·ha^{-1}). Root colonization and spore numbers were not influenced by added P or mycorrhizal inoculum in soil that was high in available P (97 kg·ha^{-1}). Mycorrhizal colonization ratings in the latter soil remained very low throughout the growth period of the plants. Interpretation of these results suggested a threshold level of soil P below which mycorrhizal colonization was high and above which colonization was low. Rajapakse and Miller (84) found that addition of soluble phosphate to the sand growth medium reduced cowpea root colonization by *Glomus fasciculatum*. Mycorrhizal influence on certain growth parameters was observed under all P levels used (i.e., 13, 23, 33, and 43 ppm); however, maximum growth response was observed at 23 ppm P. Azcon et al. (2) and Khan (54) also discovered that high soil P levels suppressed mycorrhizal development in lettuce and corn seedlings, respectively. Sanders (95) applied phosphate solution directly to the leaves of onion plants. He determined that P application reduced the intensity and rate of spread of the mycorrhizal colonization, reduced the weight of external mycelium associated with each centimeter of colonized root, and depressed the supply of P to the host via the mycorrhizae. It was concluded that reduction in numbers of external hyphae, arbuscules, and chlamydospores was more closely related to the phosphate concentration in the roots than to that in the soil.

Nitrogen fertilization has also been shown to affect mycorrhizal formation negatively. Hayman (43) found application of NH_4NO_3 to heavy clay loam soil significantly reduced growth and spore formation of VAM endophytes. Similar results were observed in light sandy soil. Kruckelmann (55) also found N fertilization equivalent to 224 kg·ha^{-1} inhibited mycorrhizal spore formation in a heavy clay loam soil at the Rothamsted Station. However, addition of N at 40 kg·ha^{-1} increased spore numbers in a soil at Braunschweig, Federal Republic of Germany. Opposite effects in these 2 soils were attributed to differences in basic fertility as well as to the amount of N applied.

The soil fertility picture becomes considerably more complicated when interactions between P and N are taken into account. Hepper (48) also found that increasing the amount of phosphate applied to lettuce plants inoculated with *Glomus moseae* depressed mycorrhizal colonization. At all phosphate levels, however, mycorrhizal colonization increased as more nitrate was supplied to the host plants. The extent to which mycorrhizal colonization was depressed depended on the N : P ratio rather than phosphate concentration alone. Mosse (61) also noted that increased N tended to counteract the inhibitory effect of high phosphate.

Research results all clearly indicate that high levels of P and N in the soil inhibit colonization of plant roots by mycorrhizal fungi. The extent to which colonization is inhibited, however, does vary with plant species. It appears that internal P level in the root, resulting from high soil P levels, inhibits mycorrhizal formation. Mechanisms for this inhibition of colonization were discussed previously in this paper. Mechanisms involved in N inhibition of colonization have not yet been identified.

Generally, high soil fertility results in minimal VA mycorrhizal colonization, so that much mycorrhizae is unlikely to be found in intensively cultivated soils. However, maize in the midwestern United States is heavily mycorrhizal (45). Since VAM fungi are often abundant in both poor and rich soils, low soil fertility is not always a prerequisite for extensive mycorrhizal development. Certain endophytes will undoubtedly perform well within a broad range of soil textures and soil fertility levels. Others will prove more effective in soils of low fertility in which they are better adapted. Plants that show physiological response to VAM fungi only under low soil P levels are termed "responsive". Other plants that benefit from VAM regardless of soil P level are "dependent" on VAM fungi (e.g., onion and casava) (Fig. 1).

Soil temperature

Most mycorrhizal fungi have an optimum temperature for establishment of the symbiotic relationship and survival of the mycorrhizae. There is, however, considerable variation in the temperature range tolerance of individual fungi. For example, *Gigaspora coralloidea* and *Gigaspora heterogama* (Nichol. & Gerd.) Gerdemann & Trappe have an optimum temperature for spore germination and fungal growth at 30°C, considerably higher than that for *Gigaspora calospora* (26°) or *Glomus mosseae* (20°) (97). In general, there is an increase in the percentage of colonization up to about 30° (37). A great deal of work remains to be done in identifying temperature optima of the many different species of VAM endophytes.

Light Intensity

Light intensity is believed to influence mycorrhizal colonization. Daft and El Giahmi (23) found that shading reduced colonization by *Glomus macrocarpum* var. Geosporum Tul. & Tul. or *G. mosseae* in a variety of plant hosts. Gunze and Hennssey (38) recorded increases in the numbers of arbuscules in roots of shaded cowpeas, while the number of vesicles decreased. Hayman (44) reported that mycorrhizal development was best in onions colonized with *Glomus mosseae* at high light intensities. The number of arbuscules was particularly increased at high light intensities. Increased levels of colonization were correlated with high sugar concentrations in the roots. Greater mycorrhizal development at high light intensities appears to be linked to increased photosynthetic activity and subsequent carbohydrate translocation to the roots. Unfortunately, conflicting research data suggest that this relationship is not clear. For example, Furlan and Fortin (32) found that onion plants inoculated with *Gigaspora calospora* showed more extensive and rapid mycorrhizal colonization at low light intensities than at high light intensities.

LIMITATIONS OF CURRENT VA MYCORRHIZAL TECHNOLOGY

Scarcity of VAM inoculum has limited the broad use of VAM fungi. This scarcity is due to the inability to culture VAM fungi axenically, which makes use of a host plant essential for multiplication of the endophyte. To ensure quality, inoculum must be produced under controlled conditions, including freedom from contaminating pathogens. Presently, 2 types of inocula are feasible—VAM-colonized roots and VAM-infected soil carrying chlamydospores. It has been found that an inoculum of root segments caused more rapid growth stimulation than spores (39). As little as 10 g of infected soil per plant proved to be sufficient inoculum for field-grown cowpeas and corn (50, 71).

Different methods of inoculum application could be used with vegetable crops, depending on whether the crop is transplanted or seeded directly. Inoculation of transplanted crops is less difficult, since it simply involves an incorporation of the inoculum into the medium and it occurs within a relatively small area. For seeded crops, a more difficult situation, with several options, is presented. Inoculum can be applied to the seeds using a sticker or by pelleting, drilling with the seed, layering, or banding. Additionally, broadcasting and incorporation could be used in conjunction with a conventional planter; however, this method is an inefficient use of available inoculum.

A recent approach is fluid-drilling (12). This process has not been totally successful on a commercial basis due to several problems. The problems include the need for a large volume of inoculum carrier gel and frequently encountered unfavorable planting conditions (such as drought or heat), which limit its effectiveness.

In addition, there are post-application problems and constraints that must be overcome, including lack of competitiveness and survivability of the introduced VAM fungi as well as the effect of pesticide application on the endophyte. VAM fungal species and

strains differ in their capacity to compete with indigenous fungi and survive in the new environment. Additionally, application of fungicides and other chemicals to the fields can selectively or completely destroy the VAM propagules.

Viability of VAM inoculum during storage and transportation is another problem. Mycorrhizal inoculum can be stored for relatively short periods as compared to *Rhizobium* inoculants. Pelleting and lyophilization of VAM inoculum increase storage life; however, lyophilization can lead to a marked reduction in infectivity. It is also necessary to multiply VAM pot cultures routinely. As stated previously, there are many limitations to the application of VAM technology to vegetable crops. However, the inability to culture VAM endophytes axenically is certainly the major obstacle to large-scale inoculation.

There are other constraints specific to vegetable crops. Most vegetables have a relatively short growing season and subsequent rapid crop turnover, requiring the production and application of large quantities of inoculum, which may not be economically feasible. The short growing season has made it less appealing to develop the technology when compared to perennials (such as forest trees or nursery crops), where one inoculation may suffice for a period of 20 or more years. However, this line of reasoning is shortsighted, since certain vegetable crops benefit greatly from mycorrhizal relationships.

Mycorrhizal benefits are greatest and most obvious under low-input growing conditions (e.g., those found in developing countries). Vegetable production in developed countries usually occurs under conditions of intensive cultivation, where optimum inputs are usually provided for crop growth. Currently, it is much simpler to apply high N and P fertilizers rather than to use mycorrhizal fungi. This situation, undoubtedly, will not change until mycorrhizal inoculation procedures are perfected and inoculum can be mass-produced, so that it is less expensive to use than fertilizers.

In general, recognition of the mycorrhizal phenomenon is relatively recent. It is still very much a new and emerging field, whose workers only recently were given a recognized title—"mycorrhizasts". Relatively little applied research has been conducted thus far on vegetables due to the reasons previously discussed.

FUTURE RESEARCH NEEDS

First, it is necessary to make the transition from basic to applied research in order to develop the necessary technology for application to vegetable crops. Most of the work with vegetable crops—for that matter all crops—has involved pot experiments. What is needed now is thorough testing of the value of inoculation of different vegetable species over a wide range of field conditions. How well these experiments are conducted and the extent to which they are carried out will of course depend on continuing research and development efforts in inoculum production and methods of application including quantity, quality, and frequency of application.

Identification of efficient VAM endophyte species for symbiotic effectiveness, competitiveness against indigenous VAM fungi, tolerance to environmental extremes such as drought and salinity, tolerance to mineral deficiencies and toxicities, and tolerance to a broad range of pesticides are needed. Improved use of indigenous VAM fungi also requires attention, as does the role of host plants in determining benefits of the VAM symbiosis. Finally, no discussion of the need for future mycorrhizal research would be complete without underscoring the necessity and importance of additional research on the axenic culture of VAM endophytes.

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