Chapter 5

ROOT EXUDATES AND EXUDATION

M. G. HALE, L. D. MOORE AND G. J. GRIFFIN

1. HISTORY AND INTRODUCTION

1.1. What are exudates?

Water soluble organic molecules synthesized in the plant may make their way to the surface of the root and be lost into the surrounding medium. Photosynthates from leaves are translocated to the root via the phloem and a portion can be exuded. Movement across the tissues of the root may occur entirely in the symplast through the interconnecting plasmodesmata, or the molecules may leave the symplast at any point along the pathway and enter the apoplast and be leached or exchanged for charged ions in the soil solution. In most plant species the root cap cells actively secrete organic molecules. For example, corn secretes a polysaccharide through the activity of the dictyosomes in the root cap cells. In many other plants a mucilaginous material may cover the surface of the roots.

Cells and tissue fragments from the root cap, epidermis, and cortex are lost as the root grows. Some of this material may continue to live for some time after it is sloughed. Upon death, contents of these cells and tissue fragments can be released into the rooting medium and contribute to root exudates.

Loss of solutes from roots occurs as a result of mechanical injury from cultivation, insects, nematodes, or by the growth of secondary or lateral roots. Contents of injured cells along this pathway add to the root exudates.

Various environmental factors affect the exudation processes by altering the cell membrane permeability and flux ratios or by changing source to sink relationships within the plant. In this manner, composition of exudates is affected.

As a consequence of the complexity of sources and the factors affecting exudation, just about any soluble compound found within the plant can also be found in exudates from the roots depending upon the plant species, growth conditions, rooting medium, and stage of plant development. Thus, amino acids, sugars, organic acids, proteins, polysaccharides, growth substances, growth inhibitors, attractants, and repellants have been reported as root exudates.

1.2. What are the roles of exudates?

The subject of root exudation has been reviewed many times (i.e., Lyon and Wilson, 1921; Clark, 1949; Bonner, 1950; Borner, 1960; Woods, 1960; Evanari, 1961; Garb, 1961; Schroth and Hildebrand, 1964; Grodzinsky, 1965; Samtsevich, 1965; Rovira, 1969; Hale et al., 1971). De Candolle (1832) ascribed an important role in the "soil sickness" problem to excretion from roots. Agronomists have since become aware of the "soil sickness" problems in the rotation of crops which require the postulation of a chemical effect of compounds from previous crops as residues in the soil (Muller, 1966).

Chemical interaction between organisms is well-known. Whittaker and Feeny (1971) have classified the roles of chemicals in these interactions into the three general categories of nutrients, foods and allelochemics. The devices of chemical interactions appear in all the major groups of organisms and are a part of the adaptation of one species with another. Ecologically, the intricate pattern of exchanges of materials relates the organisms of a community to the environment and to one another. Such interactions occur in the rhizosphere of plants between roots and soil inhabiting organisms and a part of this ecological pattern involves exudates from roots.

Chemicals synthesized and released by an organism affect the physical, chemical, and biotic environment. Whittaker and Feeny (1971) have coined the term "allelochemics" to describe interorganismic chemical effects. Allelopathy describes the effects of allelochemicals that inhibit organisms other than the producer. Allelochemical effects between organisms range from inhibition to stimulation, from repellants to attractants, and from nutrients to toxins.

In the aforementioned concepts the range of effects on the physical environment are omitted. Perhaps these should be referred to as "allelophysics". The role of exudates in chelation of nutrients, pH of the soil solution, solubilizing nutrients, or effects on aggregation of soil particles, are examples of the role of root exudates affecting the abiotic physical environment of roots.

In the sphere of influence of the root in soil, the rhizosphere (a region which exists in concept but defies accurate definition in absolute terms), a complex of reactions and interactions occurs between roots and soil inhabiting organisms. Concentrations of exudates at the surface of the root and a millimeter or two from the surface are much greater than in non-rhizosphere soil. How much greater are these concentrations? Attempts to measure them are subject to many kinds of criticisms because they usually involve use of artificial systems. One must agree in part with Holm (1971): "To gather substances from roots placed in a sterile, artificial system is not much help in understanding what takes place in the microsites of the soil. It is possible that adsorption, chemical activity from solution, or degradation

by microorganisms may be the fate of any substance coming out of a root. On the inside of the plant there is an equally complex chemical milieu, and it is here that the chemical maintains its integrity prior to its exit to the soil. Theories and experiments showing that complex molecules are produced inside the cell, are maintained in very low concentration, and may participate in one or several reactions, are common place today. Why is it not also possible for production (exudation) and loss to reach a steady state outside the cell, and thus make a constant supply of a metabolite available to other roots or organisms? Until the techniques for such studies are known, the fate of exudates in natural sites cannot be understood".

1.3. Evolution of concepts

Soil microbiologists were the first to draw attention to the fact that there is a difference in environment between an area of soil close to the roots, and that at some distance from the root surface. Hiltner (1904) coined the term "rhizosphere" for this area in which the population of microorganisms was different from that in "non-rhizosphere" soil. Plant pathologists became interested in the rhizosphere and root exudation in relation to colonization of roots by soil-borne plant pathogens. A comprehensive, world-wide conference on the ecology of soil-borne plant pathogens and publication of the proceedings (Baker and Snyder, 1965) served to stimulate thinking and research. An international conference on the plant root and its environment in 1971 (Carson, 1974) again focused attention on the many different aspects of the root as it lives, grows, and develops in various kinds of environments.

The evolving concepts of the absorbing system of a plant involve not only the root tissues, but associated microorganisms which may form mantles around the root surface, exist inside the root, or both; or which may live and die in a region in close proximity to the root but still influence root exudation and uptake. Preoccupation by plant physiologists with absorption of nutrients has led them, by and large, to overlook the importance of the reverse processes which result in exudation. Many of the principles which apply to absorption and other functions of the plant can be of help in making significant contributions to exudation studies and rhizosphere ecology. Much of the discussion which follows centers around such applications.

2. THE PHYSIOLOGY OF EXUDATION

2.1. Sources of naturally occurring exudates

Photosynthates may appear as exudates in the rhizosphere either in their original form, which is usually sucrose, or may be altered metabolically

between sites of synthesis and exudation (Rovira, 1969; Hale et al., 1971). Once in the roots photosynthates may be exuded, incorporated into a soluble pool, metabolized, or stored as insoluble substances.

2.1.1. Phloem translocation and the source to sink effect

Mechanisms of phloem translocation can be divided into two broad groups: (1) Systems that require the energy from respiration to direct the transport of photosynthates and in which sources and sinks have only regulatory roles, and (2) processes that do not require respiratory energy, but the movement is controlled by the sources and sinks and metabolic energy is needed only for the maintenance of the conducting tissue (Wardlaw, 1974). Both these groups may be further subdivided based on a requirement for accompanying water movement. Movement involving mass flow (pressure flow), electroosmosis, or tubular peristaltic flow requires accompanying water movement, while movement involving interfacial flow or cytoplasmic streaming acts independently of water movement. To explain the translocation of photosynthates, one can readily accept a modified mass flow concept involving a requirement for adenosine triphosphate (ATP) in which cytoplasmic streaming and diffusion also may be involved. Phloem translocation may involve different mechanisms operating at different times or in different tissues in the same plant (Bidwell, 1974). Soybean plants, for example, have two distinct patterns of translocation (Blomquist and Kust, 1971). Prior to podfilling, translocation occurred from a given leaf to meristematic areas above the leaf but as the leaf aged and its position changed relative to the stem apex, progressively more of its photosynthate was translocated directly to the roots. In 8 day old axenic wheat seedlings, within 2 hours ^{14}C photosynthate reached the root apices and a portion was exuded in both volatile and non-volatile forms (McDougall and Rovira, 1965; McDougall, 1970). In ponderosa pine seedlings the maximum exudation of ^{14}C compounds occurred 72 hours after exposure of the leaves to $^{14}CO_2$ (Reid, 1974). Sugars, amino acids, and organic acids in the exudates contained ^{14}C.

The commonly observed downward movement in the phloem is from regions of synthesis (source) to regions of utilization (sink) such as roots or underground storage organs (Beevers, 1969). In young plants, foliage often constitutes the major source and roots the major sink. In older plants, more complex situations exist. Shoot tips, fruits, parenchyma of the bark, phloem, and xylem can serve as sinks. Sinks may also become sources. Underground storage organs, seeds, and storage cells of xylem which were at one time sinks, become sources for newly formed sinks in structures such as sprouts and in seedlings.

Environmental factors that affect photosynthetic activity have comparable effects on the photosynthetic source to sink ratio and so may affect root exudation. Photosynthetic rate is controlled by light, temperature,

carbon dioxide concentration, wind velocity, water supply, plant nutrition, age, chlorophyll content, enzyme factors, and leaf structure. For example, Lawn and Brun (1974) employed excess lighting, shading, depodding, and defoliation to alter the source to sink ratio in soybean plants. Supplemental light and depodding enhanced the photosynthetic source to sink ratio, while shading and defoliation reduced that phenomenon.

Factors that primarily affect root systems have also been shown to alter the assimilation of $^{14}CO_2$ and, subsequently, translocation of ^{14}C-labeled materials to roots (see also Section 3, this Chapter). Reid (1974) reported that the ^{14}C-labeled sugars, amino acids, and organic acids content of ponderosa pine roots was altered by inducing water stress. Linder et al. (1957) demonstrated that the exudation of foliar applied α-methoxyphenylacetic acid (MOPA) was greatly reduced by subjecting the roots of bean plants to a lower oxygen supply in the water surrounding roots. Decreased oxygen supply reduced the rate of respiration in phloem causing a subsequent reduction in the rate of translocation.

2.1.2. Apoplastic and symplastic movement

Only mass flow in the phloem can account for the large amounts of photosynthate translocated from leaves to roots in higher plants. It has been suggested that movement to and from this vascular tissue across the root occurs in the apoplast and/or symplast (Arisz, 1956). The apoplast consists of the cell wall, intercellular spaces, and the tissues of the stele. It is therefore discontinuous and consists of two regions: (1) the cortex and all the tissue external to the endodermis, and (2) the tissues of the stele internal to the endodermis, including the xylem vessels and tracheids. Modifications of the concept have included the protoplasts of all cells and their plasmodesmata in the symplast. Movement of compounds from cell to cell without leaving the symplast is possible (Arisz, 1956; Helder and Boerma, 1969). Movement of photosynthate from the cells of the leaf into the phloem and translocation in the phloem may occur in the symplast. Whether movement from the phloem in the roots to sites of exudation is symplastic is not clear because materials may leave the symplast anywhere along the pathway and enter the apoplast. Conversely, materials in the apoplast would be subject to the mass flow caused by transpiration and move predominantly upward in the plant. Therefore, organic exudates probably arrive at the root surface primarily via the symplast, but exudation of ions and low molecular weight compounds may involve leakage from the apoplast (Krichbaum et al., 1967) at times when the transpiration rate is low or none is occurring.

2.1.3. The soluble pools

The principle cause for the exudation of compounds from root tissue is the existence of a concentration gradient of these compounds from the root tissue to the surrounding medium. The higher concentrations in the root

tissue may be due to its role as a sink for photosynthates, or because insoluble materials are hydrolyzed to soluble materials. In either case, substances can continuously accumulate in soluble pools and leak into the soil. The presence of microbes in the rhizosphere also creates a sink. Leakage of substances from roots is often enhanced by the presence of microorganisms.

There is ample experimental evidence that soluble pools are sources of root exudates. Mitchell et al. (1961) found that relatively little MOPA was exuded from roots of bean plants until the roots became saturated with the compound. Following saturation, there was a marked increase in the rate of exudation. They concluded that the phloem was the path of translocation and that a pool had to be formed in the root system prior to any release of the compound. McDougall (1968, 1970) discovered that photosynthetically fixed carbon appeared to be translocated as ^{14}C sucrose. Once in the roots, ^{14}C sucrose entered a pool with unlabeled sucrose. After a period of 10 hours, nearly 50% of the ^{14}C in this soluble pool was still present as sucrose. The rest was incorporated into glucose, fructose, raffinose, glutamine, glutamic acid, aspartic acid, and several unidentified substances. Approximately 33% of the ^{14}C in the soluble pool appeared as exudates after 24 hours. Soluble pools of amino acids in roots have also been reported (Oaks, 1965).

2.1.4. Seed exudates contrasted with root exudates

Both seeds and roots have been reported to exude a vast group of compounds such as aromatic and aliphatic acids, amino acids, sugars, phenols, and proteins. Vancura and Hanzlikova (1972) showed that there was a direct correlation between seed size (the amount of storage material in the seeds of different plant species) and the amount of exudates from the seeds. No such correlation existed with seedlings; the amount of root exudates from seedlings was governed by many plant properties including the number and size of the cotyledons and photosynthetic efficiency.

Not only does the composition of exudates from seeds differ with species but it also differs when seed and seedling root exudates of the same species are compared. Kovacs (1971), for example, found larger quantities of free and polymeric aromatic acids in seed exudates of barley, cotton, and pea compared to seedling root exudates. He found appreciable levels of *para*-hydroxybenzoic, protocatechic, and vanillic acids in seed exudates, but only trace amounts of these acids in seedling root exudates. Cotton and pea seed exudates alone contained salicylic and *para*-coumaric acids.

Vancura and Hanzlikova (1972) observed that more reducing compounds (recorded as mg g^{-1} of seed and root exudate of barley, bean, cucumber, and wheat) were exuded from seedling roots than from the seeds. Little difference was found in amino acids and organic acids of seed and seedling root exudates. The difference in the organic acid exudate among species was

greater compared to seeds and seedling roots of the same species. Exudates of seeds and seedling roots of barley, bean, and wheat contained malic, glycolic, and fumaric acids but those of cucumber did not. Although no oligosaccharides were exuded by wheat seeds, six oligosaccharides were exuded by its seedling roots. Seed exudates of bean contained five keto sugars while seedling root exudates contained only fructose. Galactose was the predominant monsaccharide in seed exudates of bean, whereas glucose, arabinose, fructose, and other monosaccharides were present in seedling root exudates. Oligosaccharides constitute 45% of the reducing sugars in cucumber seedling root exudates but only 17% in seed exudates.

2.1.5. Sites of exudation along roots

Many different plant structures produce exudates. Specialized structures such as glands and hydathodes are active in exudation from above ground plant parts. Comparable structures do not occur on roots but the root cap is a region of active secretion and exudation may also occur all along the root.

In a series of experiments (McDougall and Rovira, 1965, 1970; McDougall, 1968; Rovira, 1973) involving pulse labelling of the photosynthate with ^{14}C and subsequent autoradiographic scanning of roots, sites of root exudation in wheat seedlings have been identified. Autoradiographs made 24 hours after the pulse labelling demonstrated that ^{14}C accumulated in large amounts in the growing tips of primary and secondary roots while the rest of the root was uniformly labelled. Exudation occurred, however, mainly from the basal region of roots and represented approximately 33% of the ^{14}C in the soluble pool in the roots. The site of exudation at the basal region was correlated with the number of lateral roots developing in the region. It was originally suggested that the release of ^{14}C-labelled compounds might be related to the number of points of rupture of the tissues of the main root by the laterals as they grew from the pericycle to the surface (McDougall, 1968). This was later discarded, based on the evidence that most of the radioactivity came from the tips of the developing laterals (McDougall and Rovira, 1970).

The pattern of exudation appeared to be of two types (McDougall and Rovira, 1970; Rovira, 1973) resulting in: (1) an intense, discrete release of nondiffusable labelled material from the apices of lateral roots possibly composed of root cap cells, mucilaginous material, or sloughed root caps, and (2) a diffuse pattern associated with the main root axis and probably consisting of soluble, diffusible compounds. According to Rovira (1973) the major zone of release of diffusible exudates is the zone of elongation.

Bowen (1968) determined the distribution pattern for the efflux of chloride ions. The exudation of previously absorbed radioactive chloride ions from the apical portion of *Pinus radiata* roots was 18.3% of the total present as exudate while that from the basal portion was 8.2%. This greater efflux from the apical portion of the root was probably due to the accumulation of

chloride in cytoplasmic pools rather than in the vascular pools of older root parts.

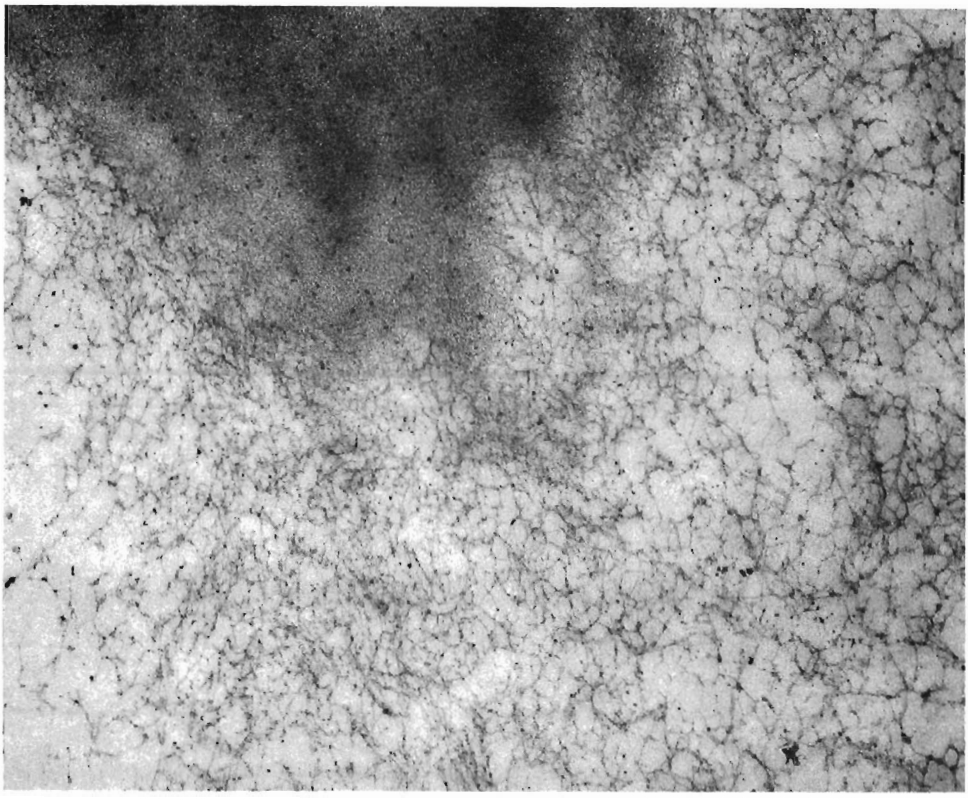
Pearson and Parkinson (1961) tested broad bean seedling exudates and observed ninhydrin-positive substances around emerging roots. As the roots grew, most of these compounds appeared in a limited region behind the root tip and microquantities were released from all other regions of the root surface, particularly where the root was wounded. Frenzel (1960) has also reported that different amino acids may be exuded from the various regions of sunflower roots. Threonine and asparagine originated from the meristematic and elongation regions while leucine, valine, and phenylalanine were exuded in greater amounts from the root hair region. Aspartic acid and glutamic acid were not exuded from any particular region of the root.

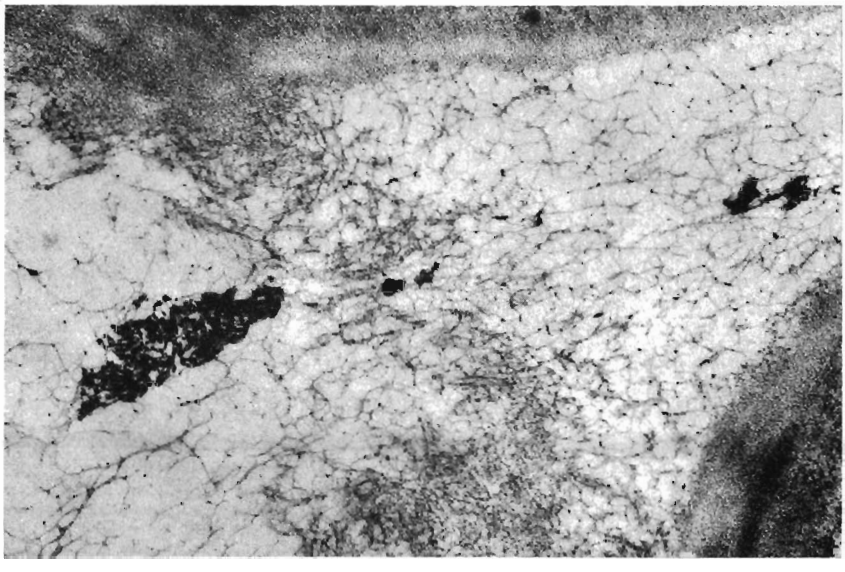
Sloughed root cap cells and mucilaginous materials have been reported as exudates of barley (Jenny and Grossenbacher, 1963; Juniper and Roberts, 1966), citrus (Brams, 1969), maize (Samtsevich, 1965; Jones and Morré, 1967; Morré et al., 1967; Juniper and Roberts, 1966), peanuts (Hale and Griffin, 1974), and wheat (Northcote and Pickett-Heaps, 1966). Mucilage sometimes appears as unevenly distributed layers of granular and fibrillar material covering the outer surface of axenic roots and root hairs with the greatest quantity around the root cap (Greaves and Darbyshire, 1972). Larger quantities of mucilage developed on roots of the same species, when microorganisms were present.

Leppard (1974) has reported a diffuse network of electron-opaque fibrils on the root tips of both axenic and non-axenic wheat roots (Fig. 1). These fibrils have not been observed previously in other electron microscopy investigations. This may be due to the lack of contrast enhancement of most staining procedures. These fibrils were revealed by a combination of electron stains used to identify fibrillar polygalacturonic acids (Leppard, 1974).

Exudation from hypocotyls has not been studied extensively. Recently exudation of organic compounds, particularly amino acids and sugars from squash hypocotyls, has been documented by Magyarosy and Hancock (1974). Although conducted under non-axenic conditions, their investigation demonstrated that the quantities of ^{14}C assimilates exuded from the hypocotyl increased progressively toward the basipetal end. The greatest amount of exudation was observed in the zone of transition between the hypocotyl and root. The relative importance of this portion of the plant as a source of exudates has been emphasized by Schroth and Hildebrand (1964).

Fig. 1. Above. Electron micrograph of a diffuse tuft of fibrils projecting from the wall of a cell in the elongation zone of *Triticum aestivum* (x 60,000). Below. Fibrils projecting into a gap between cells of the root cap (x 60,000). Electron micrographs furnished by G. G. Leppard.





2.2. *Mechanisms of exudation*

2.2.1. *Secretion processes as contrasted with leakage*

Both secretion and leakage have significant roles in the release of exudates. Secretion is a process involving metabolic energy in the transport of compounds through membranes and is selective with respect to the compounds transported. It can take place against electrochemical potential and chemical potential gradients. Leakage, on the other hand, is the loss of compounds along electrochemical potential gradients by simple diffusion.

Secretion is a fundamental process in all living cells, but is most often observed from specialized glandular cells such as salt glands, nectaries, hydathodes and wax glands. In addition, secretion from root cap cells has been reported for many different plant species. The Golgi apparatus of outer root cap cells secretes polysaccharides which form viscous droplets at the root tips. These droplets may be formed on both axenic and non-axenic roots (Mollenhauer and Morré, 1966; Morré and Mollenhauer, 1973). Secretory vesicles containing the polysaccharides are released from dictyosomes in the cytoplasm and migrate to the plasmalemma where they fuse with the membrane and release the contents into the free space of the cell wall region (Morré et al., 1967). The polysaccharides move through the cell walls to the surface of the root cap where the slime droplets eventually appear. This movement is considered by Morré et al. (1967) to be passive since it is not affected by metabolic inhibitors and is suppressed by osmotic agents. The synthesis and deposition of polysaccharides in the root cap region, therefore, occurs as a result of both secretion and leakage.

Vesicles produced by the Golgi apparatus also give rise to cell wall materials. Autoradiography experiments (Northcote and Pickett-Heaps, 1966) demonstrated that high molecular weight, nondiffusible polysaccharides carrying the label from D-(6^3H) glucose could be isolated from the cells in both the hemicellulose and the α-cellulose fractions. Over a 3 hour period, a large amount of radioactive label accumulated in the walls of the root cap cells and in the external mucilaginous layer.

The exudation of ^{14}C-labelled photosynthates from root systems is most likely the result of leakage. McDougall (1970) reported that the metabolic inhibitors dinitrophenol and potassium cyanide, stimulated exudation from wheat roots while active uptake was blocked. Several Russian scientists believe that the main cause of root exudation is the difference in the concentration of dissolved substances in the root tissues and in the medium surrounding them (Samtsevich, 1967). Rovira (1973) suggested that most of the photosynthetically assimilated materials released from the zone of elongation in wheat roots involved a "leakiness" in that area.

Exudation from hypocotyl tissue is also most likely the result of leakage along an electrochemical potential gradient. Factors which stimulated an increased level of soluble metabolites in hypocotyl tissues also increased

exudation (Magyarosy and Hancock, 1974). Increase in soluble substances may have resulted in higher respiration and in turn the quantity of ATP available for the secretion process.

2.2.2. Membrane permeability changes

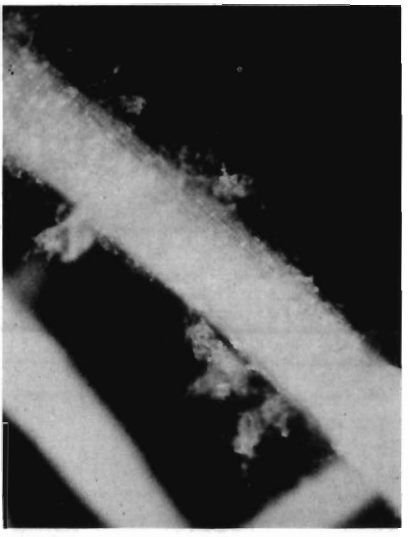
The plasmalemma probably has a significant role in the exudation process although most of the evidence implicating the membrane in exudation is circumstantial. A number of factors affect membrane permeability and may in turn affect the kinds and quantities of exudates. Among such factors are: (1) ionic concentration in the rooting medium, (2) pH of the rooting medium, (3) ATP levels in root cells, (4) oxygen concentration and availability to roots, (5) concentration of growth regulators in roots, (6) temperature, (7) light, (8) moisture stress, and (9) certain biotic factors including viruses.

2.2.3. Sloughed cells and tissues

The importance of sloughed cells as a source of organic carbon and nitrogen in the rhizosphere has been recognized for a long time. Rovira (1969) considers these cells as an important component of the insoluble exudate. There have been only a few studies concerned with measuring the quantities of sloughed cells produced by roots. Rovira (1956) attempted to determine the amount of cell debris, exclusive of root fragments, for pea and oat plants grown in quartz sand. The highest yield obtained was 0.63 mg/plant for 21 day old pea plants (0.21 mg/plant/week). In recent investigations by Griffin et al. (1976), root caps and sheets and fragments of cortical cells comprised the bulk of sloughed material produced by Argentine peanut plants grown in solution culture, as indicated by microscopic observation of roots and centrifuged sloughed material (Fig. 2). Organic matter yields of 0.26 to 0.73 mg/plant/week and 1.5 mg/g root dry wt/week were obtained. Based on the percentage content of carbon, nitrogen, and hydrogen of sloughed cells and peanut root tissue, it was concluded that approximately 0.15% of the root tissue was sloughed per week. Yields of total cell debris were much higher, but microscopic and chemical analysis indicated that this was due to the association of inorganic precipitate with sloughed cells. Bowen and Rovira (1973) have indicated that the insoluble mucilaginous exudate of wheat roots (including sloughed root cap cells) accounted for 0.8 to 1.6% of the root carbon and 80% of the total carbon released into the soil.

2.2.4. Injury

As Schroth and Hildebrand (1964) stated, "injury can result from mechanical abrasion, physiological disorders, as well as entomological, nematological, fungal, bacterial, and viral invasions, and also from toxins from decomposing residues of plants, and the microflora. In their natural



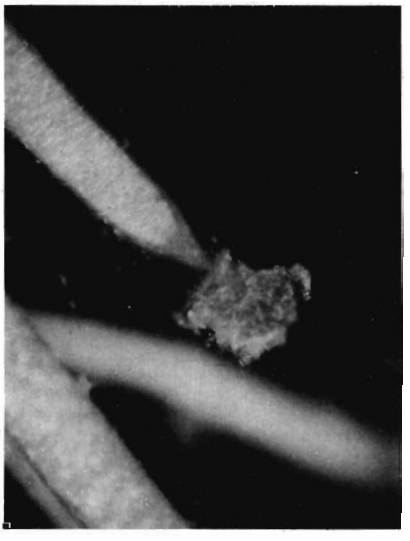


TABLE I

Sources and causes of injury

Source	Cause
Microfloral and microfaunal	Permeability changes, dissolution by enzymes or lysis, puncture, toxins, growth factors
Cultural practices	Pesticides, cultivation, fertilization, water stress, mineral nutrient deficiency and toxicity
Growth	Lateral root eruption, abrasion by soil particles, sloughing of tissues and root caps, pressure from cambial activity, permeability changes, regrowth of mechanically injured roots
Environmental stress	Water stress, O_2 tension, CO_2 tension, temperature extremes, pH, salt concentrations

environment, plants are subject to all these factors in varying degrees and presumably the composition and quantity of exudates could be affected depending upon which tissue sustained the injury". The discussion here will be restricted to mechanical injury of underground plant parts whether as a result of external forces or as a result of internal forces of growth (Table I).

The zones of lateral root and adventitious root development have been associated with high levels of exudation (Schroth and Snyder, 1961; McDougall, 1968; McDougall and Rovira, 1970). There may be injury to cortical cells by mechanical forces or digestion as lateral roots emerge from internal portions of mature roots (Esau, 1953), but this may not result in high levels of exudation. McDougall and Rovira (1970) reported that the lateral root zone of wheat roots was the major region of exudation, mainly from the apices of emerging laterals, and not from the point of rupture where the laterals emerged from the main root. Microscopic observation and the careful handling of roots during assays on moist filter paper suggested that this exudation by apices was not because of injury to the root tips.

Ayers and Thornton (1968) have made a case for injury being responsible for exudation from root tips. They reported that wheat roots grown in sand consistently gave dense ninhydrin reacting areas corresponding to the root

Fig. 2. Roots of peanut, *Arachis hypogaea* L. grown in nutrient solution. Above left. Branching of root showing possible injury at point where laterals have broken through surface. Note discontinuity of tissue of main root at point of emergence of the laterals. Above right. Loose cortical fragments being sloughed along the root surface. Below left. A sloughing root cap. Below right. A root cap which has been sloughed photographed with interference contrast microscopy.

TABLE II

Sugar exudates from injured and non-injured peanut fruits (mg per g dry weight of fruits); 24 h in ¼ strength Hoaglands solution after scarification over one fourth of the surface

	Immature fruits		Mature fruits	
Sugar	Non-injured	Injured	Non-injured	Injured
Fructose	0.169	1.079	0.034	0.227
Glucose	0.119	0.475	—	0.136
Galactose	0.024	0.075	—	0.023
Sucrose	0.012	1.275	0.046	1.091
Inositol	+	++++	+	+++
Totals	0.322+	2.904+	0.080+	1.477+

tip region whereas roots removed from nutrient solution and placed in contact with filter paper did not. No microscopic observations or other proof of injury were made.

There is little quantitative information concerning the effects of injury. Hale and Griffin (1974) attempted to quantify injury effects. Underground peanut fruits in various stages of development were collected aseptically from axenic plants and separated into mature and immature groups. One half of each group was scarified over a quarter of the surface of each fruit and then placed in nutrient solution. In 24 hours over 100 times more sucrose was exuded from injured immature fruits and 24 times more from injured mature fruits than from uninjured fruits (Table II).

2.3 Plant factors affecting exudation

Few studies have been specifically designed to determine differences in exudation between plants with fibrous roots and those with tap roots. A number of studies, however, have attempted to elucidate the role of age, stage of development, and species in exudation.

2.3.1. Root growth and type of root system

Most dicotyledonous plants and gymnosperms possess root systems consisting of a tap root with branches. On the other hand monocotyledonous plants most often have fibrous root systems. Adventitious roots arising from the stem are often present in all these classes. Plants used in root exudation studies encompass dicots, monocots and gymnosperms (Table III).

Root secretion as a result of the activity of the Golgi apparatus occurs in monocots (Floyd and Ohlrogge, 1970; Greaves and Darbyshire, 1972), dicots

TABLE III

Common names, scientific names and references for some plants used in root exudation studies

Common name	Scientific name	Reference
Dicotyledons		
Alfalfa	*Medicago sativa* L.	Hamlen et al. (1972) Richter et al. (1968)
Apple	*Pyrus malus* L.	Head (1964)
Bean	*Phaseolus vulgaris* L.	Linder et al. (1957) Miller and Schmidt (1965) Mitchell et al. (1961) Schroth et al. (1966) Vancura and Hanzlikova (1972)
Broad bean	*Vicia faba* L.	Pearson and Parkinson (1961)
Citrus	*Citrus* sp. var Sour Orange	Brams (1969)
Clover	*Trifolium subterraneum* L. *T. pratense* L.	Rovira (1959) Bonish (1973)
Cotton	*Gossypium hirsutum*	Kovacs (1971) Schroth et al. (1966)
Cucumber	*Cucumis sativus* L.	Nezgovarov et al. (1970) Vancura (1967) Vancura and Hanzlikova (1972)
Flax	*Linum usitatissimum* L.	West (1939)
Maple	*Acer saccharum* Marsh.	Smith (1970, 1972)
Pea	*Pisum sativum* L.	Ayers and Thornton (1968) Juo and Stotzky (1970) Kraft (1974) Kovacs (1971) Rovira (1956) Schroth et al. (1966)
Peanut	*Arachis hypogea* L.	Hale (1969) Hale and Griffin (1974) Shay and Hale (1973)
Soybean	*Glycine max* (L.) Merr.	Blomquist and Kust (1971) Keeling (1974) Shapovalov (1972)
Squash	*Cucurbita maxima*	Magyarosy and Hancock (1974)
Strawberry	*Fragaria chiloensis* (Dcne.)	Hussain and McKeen (1963)
Sunflower	*Helianthus annuus* L.	Juo and Stotzky (1970)
Sunnhemp	*Crotalaria juncea* L.	Balasubramanian and Rangaswami (1969, 1973)
Tomato	*Lycopersicon esculentum* Mill.	Balasubramanian and Rangaswami (1969) Rovira (1959) Subba-Rao et al. (1961) Vancura and Hovadik (1965)

TABLE III Continued

Common name	Scientific name	Reference
Monocotyledons		
Barley	*Hordeum vulgare* L.	Hiatt and Lowe (1967)
		Kovacs (1971)
		Jenny and Grossenbacher (1963)
		Juniper and Roberts (1966)
		Vancura (1964)
		Vancura and Hanzlikova (1972)
	H. distichon L.	Vancura (1964)
Corn	*Zea mays* L.	Grineva (1961, 1963)
		Jones and Morré (1967)
		Juniper and Roberts (1966)
		Morré et al. (1967)
	Z. minima Hort.	Vancura (1967)
		Samtsevich (1965)
		Juo and Stotzky (1970)
	Z. indurata Sturtev	Juo and Stotzky (1970)
Oats	*Avena sativa* L.	Rovira (1956)
		Schroth and Hildebrand (1964)
		Shapovalov (1972)
Phalaris	*Phalaris tuberosa* L.	Rovira (1959)
Ragi	*Eleusine coracana* L.	Balasubramanian and Rangaswami (1969)
Sorghum	*Sorghum vulgare* Pers.	Balasubramanian and Rangaswami (1969, 1971, 1973)
Wheat	*Triticum aestivum* L.	Ayers and Thornton (1968)
	T. vulgare Vill.	McDougall (1968, 1970)
		Bowen and Rovira (1966, 1973)
		McDougall and Rovira (1965, 1970)
		Rovira (1973)
		Vancura (1964)
		Vancura and Hanzlikova (1972)
Gymnosperms		
Pine	*Pinus mugo* Turra	Mason et al. (1970)
	Pinus radiata D. Don	Bowen (1968, 1969)
		Bowen and Theodorou (1973)
	P. ponderosa Laws	Reid (1974)
	P. strobus L.	Slankis et al. (1964)

(Dawes and Bowler, 1959; Brams, 1969) and gymnosperms (Bowen, 1968, 1969; Reid, 1974). Some roots, such as those of water hyacinth and duckweed, do not have a mantle of secretory cells. Mantles in these aquatic plants are composed of degenerating and/or degenerated cells.

2.3.2. Age and stage of development

As plants age, exudation of the various classes of compounds often does not remain the same. Age and stage of development have both a quantitative

and qualitative influence upon the carbohydrate content of alfalfa root exudates (Hamlen, et al., 1972). Initially, significant increases in the pentoses, arabinose, ribose, and xylose were observed in exudates but were not detected in exudates from plants eight weeks old or older. Glucose, fructose, and mannose increased in concentration from the fourth to the sixth week, but fructose and mannose disappeared by the tenth week. An investigation of the amino acids exuded from alfalfa plants also demonstrated that age significantly affected exudation (Richter, et al., 1968). The amino nitrogen/plant/week in 3 to 10, 11 to 18, 21 to 28, 29 to 34, and 51 to 57 day old cultures was 0.46, 0.24, 0.33, 0.33, and 0.61 mg, respectively.

Smith (1970) demonstrated that there were appreciable differences in the amounts and kinds of amino acids, amides, organic acids, and carbohydrates exuded from sugar maple trees of different ages. Carbohydrates from 3 week old seedlings were more diverse and abundant than those from mature trees. Amino acids, amides, and organic acids were released in greater diversity and quantities from unsuberized root tips of mature trees than from seedling roots. These data suggest that extrapolation of root exudate information obtained with seedlings or young plants to situations involving roots of mature plants should be made only with caution.

An analysis of the amino acids of sorghum, sunnhemp, ragi, and tomato, at 15 day intervals after seeding, demonstrated that age and plant type affect the exudate composition (Balasubramanian and Rangaswami, 1969) (Table IV). In all, 17 amino acids were identified from exudates of the four plant species. Sorghum exuded 7, while sunnhemp and ragi exuded 9 amino acids each at 15 days. By the 30th day, 11 amino acids were detected from sorghum, sunnhemp, and ragi, while tomato exuded only 8. In general the number of amino acids increased, yet the relative amounts decreased over the 45 day period. The amounts and kinds of sugars exuded by the four plant species also varied with the age of the plant. Xylose was not detected until 30 or 45 days after seeding. Fructose was detected at 15, 30, and 45 days in sorghum root exudates, at 30 and 45 days in sunnhemp exudates, at 30 days in ragi exudates, and at 45 days in tomato exudates. Glucose was present in all exudates regardless of age or species. The total amount of sugars exuded decreased over the 45 day period with the lowest amounts of sugar exudation occurring at the 45th day.

The quantity of protein present in root exudates from dwarf corn, flint corn, pea, and sunflower fluctuated with development of the plants (Juo and Stotzky, 1970). This fluctuation was not uniform among the four species and there was no apparent pattern of release that could be associated with stage of development although soluble protein content of roots increased as maturation approached. Had Juo and Stotzky (1970) identified the various stages of development attained, more meaningful evaluations of the fluctuations might have been possible. The major proteins in root exudates appeared to be non-basic, soluble proteins. Some qualitative differences in the exudate protein were detected. Analyses of composite

samples taken over the 82 to 90 day period, however, indicated that 12 to 14 protein components were present compared with the 1 to 4 detected in exudates obtained weekly. Apparently many proteins were present in quantities too dilute to detect in the weekly samplings but were detectable in the composite samples.

Vancura and Hovadik (1965) compared root exudates of tomato at the initial growth stage and at the fruiting stage. At the initial growth stage, 15 amino acids were identified. Relatively high concentrations of glutamic acid, threonine, and α-alanine were present, while only trace amounts of citrulline,

TABLE IV

Effects of age of plant on micrograms of amino-N and sugars exuded per plant per week for four crop plants[a,b]

Crop plant	1st to 15th day		16th to 30th day		31st to 45th day	
	Amino-N	Sugars	Amino-N	Sugars	Amino-N	Sugars
Sorghum	0.22	38.3	0.19	44.8	0.14	27.1
Sunnhemp	0.28	31.7	0.38	22.4	0.18	19.6
Ragi	0.15	19.6	0.10	16.8	0.09	14.0

3rd to 10th day	11th to 18th day	21st to 28th day	29th to 34th day	51st to 57th day
Alfalfa (Amino-N only)				
0.46	0.29	0.33	0.33	0.61

[a] From Hale et al., 1971, Academic Press, New York, with permission.
[b] Recalculated from original data of Balasubramanian and Rangaswami (1969) for sorghum, sunnhemp, and ragi and from data of Richter et al. (1968) for alfalfa.

ornithine, and proline were found. Tyrosine and 3 other unidentified ninhydrin-positive substances were found at the fruiting stage. Much smaller quantities of fumaric, oxalic, malic, glycolic, and succinic acids were present in exudates of tomatoes in the fruiting stage than in exudates of tomatoes in the initial stage of growth.

Where age has an effect on exudation, there is also a corresponding effect on the microorganism population in the rhizosphere. The root tip region of wheat is almost devoid of microorganisms, but as roots age, the number of microorganisms present increases (Rovira, 1973). This is true also of *Pinus radiata* roots which at 4 days had only 1.2 to 1.5% of the surface colonized by microorganisms but after 90 days, had 37% of the surface colonized (Bowen and Theodorou, 1973).

2.3.3. Species

A comparative analysis of the root exudates of barley, bean, cucumber, and wheat illustrated that significant differences do occur between and within the monocotyledonous and dicotyledonous groups, as well as species (Vancura and Hanzlikova, 1972). The highest amounts of total nitrogen, amino nitrogen, peptides, and proteins were found in cucumber. About 20% of the total nitrogen in bean was in the protein and peptide form, while in barley, cucumber, and wheat 45% of the total nitrogen was protein or peptide nitrogen. Root exudates of bean and cucumber contained the highest concentration of amino acids, while root exudates of cucumber and wheat had the highest protein and peptide content. Bean and wheat root exudates contained much higher levels of reducing compounds than barley or cucumber. There was no correlation between the classification of the plants and the kind of oligosaccharides and monosaccharides exuded. For example, wheat roots exuded 66% more glucose than barley, while bean exuded 50% more glucose than cucumber. The relative concentrations (percent of total) of glucose were 1.0, 3.0, 2.0, and 5.0 in barley, wheat, cucumber, and bean root exudates, respectively. Only barley and bean roots exuded deoxyribose.

Qualitative differences in the protein content of root exudates of corn, pea, and sunflower assayed throughout the life of the plants were very pronounced (Juo and Stotzky, 1970). In eight of 11 assays, flint corn root exudates exhibited more protein bands than sunflower root exudates. In only two of the 11 assays did the protein patterns of flint and dwarf corn root exudates differ.

There are other studies showing differences in root exudates among species for amino acids, amino nitrogen, organic acids, aliphatic acids, and aromatic acids (Rovira, 1956, 1959; Ayers and Thornton, 1968; Kovacs, 1971).

Differences between varieties or cultivars have also been shown. Kraft (1974) tested exudates of six lines of pea for reducing sugars and phenols. Peas with pigmented seeds produced similar amounts of exudate phenols and reducing sugars from germinating seeds and seedling roots. In contrast, exudates from the line Dark Skin Perfection, a green seeded variety, contained only trace amounts of phenols but approximately the same levels of reducing sugars as the pigmented seed lines. In a comparison of the carbohydrates exuded from three cultivars of soybeans, Keeling (1974) found that there were significant quantitative differences. No qualitative differences were detected and he reported that there was a direct relationship between the amount of carbohydrate exuded by a germinating soybean seed and seed rot caused by *Pythium* spp.

3. ENVIRONMENTAL FACTORS AFFECTING ROOT EXUDATION

Investigations of the effects of environmental factors on exudation, where cause and effect relationships are clear, are relatively few. Many investigators

have used the microbial populations in the rhizosphere as an indication of effects of varying environment (see Section 4.6). Light and temperature are known to affect rates of photosynthesis and translocation of photosynthate to the roots. Both these environmental factors affect root exudation.

3.1. Effects of light intensity and temperature

Rovira found that shading subterranean clover reduced the amounts of serine, glutamic acid and β-alanine exuded from roots. Similarly, shading reduced the amounts of aspartic and glutamic acids, phenylalanine, and leucine exuded by tomato roots but increased the amounts of serine and asparagine (Rovira, 1959). The defoliation of sugar maple trees caused increased quantities of fructose, cystine, glutamine, lysine, phenylalanine and tyrosine to be exuded (Smith, 1972). Trees with foliage exuded greater amounts of sucrose, glycine, homoserine, methionine, threonine, and acetic acid as determined by quantitative thin-layer chromatography. Differences were statistically significant to indicate that the number of leaves affects the quantity of exudates occurring from roots of sugar maple.

The effect of temperature on exudation from roots of strawberry was investigated by Hussain and McKeen (1963) who found that greater amounts of amino acids were exuded at 5 to 10°C than at higher temperatures. Similarly, Schroth et al. (1966) showed that pea seeds exuded at a higher rate at 27°C than at 37°C. Nezgovarov et al. (1970) also found that cooling caused an increased exudation from cucumber plants. In contrast, Rovira (1969) observed that with rising temperatures, the quantity of root exudates increased but also there were changes in the relative proportions of the amino acids exuded. Tobacco roots release appreciably higher levels of electrolytes when the roots are incubated for one minute in a 50°C water bath (Wills and Moore, 1969).

When corn and cucumber seedlings were grown under favorable temperatures (19°C) and exposed for three days to 5°C, i.e., "cold shock", significant quantitative and qualitative changes occurred in the exudates (Vancura, 1967). Three different oligosaccharides and fructose were detected in exudates of treated plants, and there was a marked rise in the level of exudation from both the corn and cucumber seedlings. If "cold shock" causes an alteration of membrane permeability, then reabsorption of substances by affected plants should be substantially higher than by unaffected plants. Vancura's work supports this concept. On the other hand, Shapovalov (1972) found that the increase in exudation of scopoletin from soybean and oat roots with a drop in temperature from 44°C to 24°C was only temporary.

How temperature influences the physiology of the plant to bring about changes in exudation is not clear. Temperature affects membrane permeability and, at the lower temperatures, the reduced metabolic energy may

allow substances to leak out of the cells more rapidly. With regard to seedlings, lower temperatures might affect translocation. In the case of seeds, Vancura (1967) points out that they absorb much more water at the lower temperatures and it may have something to do with the greater amount of exudates after an initial 48 hours of germination.

Shapovalov (1972) explained the effect of temperature on the exudation of scopoletin from soybean and oat roots by setting apart three stages based on the Q_{10} of the exudation rate. In the range of 20 to 24°C, the process appeared to be one of diffusion from free space; from 23 to 30°C he claimed the process involved activated diffusion, probably across the plasmalemma; and in the range of 40 to 60°C, exudation probably increased sharply as a result of the denaturation of protein. At least a portion of the denatured protein may have been in the plasmalemma.

3.2. Effects of soil pH and CO_2 concentration

The effects of soil pH on exudation are difficult to measure because of the dynamic nature of the processes occurring at the root—soil interface. Lundegardh and Stenlid (1944) reported that hydrogen ion concentration had little or no effect on the loss of organic compounds from roots. Smiley and Cook (1973) attempted to measure the pH of the rhizosphere. They removed roots of wheat plants from the soil with gentle shaking. Soil adhering to the roots was designated rhizosphere soil and its pH measured under different treatments. Three weeks after planting, with ammonium phosphate and ammonium sulfate as fertilizer, rhizosphere soil pH was lower than surrounding soil. With ammonium nitrate as fertilizer, there was no difference in pH between rhizosphere and bulk soils. Riley and Barber (1969) attributed these kinds of changes to the ability of roots to take up a larger number of anions than cations under certain conditions, leaving behind acid forming ions.

The amount of $^{14}CO_2$ exuded from roots of wheat seedlings following pulse labelling with $^{14}CO_2$ was found by McDougall (1970) to be 20, 306 counts per minute at pH 5.9 and 7,057 counts per minute at pH 6.41. The effect of the pH level was not associated with cellular breakdown because it was unlikely that the internal pH of the wheat roots would undergo a change in pH level corresponding to that of the external pH. It was postulated that the external pH altered the ionic states of compounds released from the root cells, and this in turn affected their rate of reabsorption. Treatment of plants with compounds such as napthalene acetic acid and trichloroacetic acid causes changes in the permeability of membranes in addition to any pH effect.

The effect of salts on exudation may be correlated with pH. For example, Bonish (1973) found that below pH 5.5, salts caused a decrease in the exudation of cellulase from red clover roots compared to the amounts

exuded into distilled water. Above pH 5.5 salts caused an increase in exudation, but this was less if calcium chloride was present in the nutrient solution.

3.3. Soil solution salt and ionic concentration

The availability and concentration of mineral nutrients can affect exudation. Qualitative and quantitative differences in the exudation of amides and amino acids from axenic pine seedlings grown under conditions of nitrogen deficiency, phosphate deficiency, and nutrient sufficiency were reported by Bowen (1969). Considerably more amino nitrogen was exuded from phosphorus deficient plants than from those grown in nutrient sufficient medium while nitrogen deficient plants exuded much less amino nitrogen compounds.

Shay and Hale (1973) grew axenic peanut plants in nutrient solutions containing 10, 20, 35, and 50 mgl^{-1} calcium and found that exudation of sugars was four times greater at 10 mgl^{-1} than at 50 mgl^{-1}. There were also differences in the amounts of the several sugars exuded at the various calcium concentrations. The authors concluded that low calcium concentrations increased the permeability of root cell membranes causing an increase in sugar exudation. Rovira (1959) failed to show an effect of calcium concentration on exudation of amino acids from tomato, subterranean clover, and phalaris grass, but the lowest concentration of calcium used was in the calcium sufficient range for these plants.

Membranes have specific ion requirements. The role of Ca^{2+} in maintaining the functional and structural integrity of the plasmalemma is well documented (Nieman and Willis, 1971). Adequate levels of Ca^{2+} and other divalent ions decrease permeability while high levels of monovalent cations induce injury to all membranes, causing increases in permeability. A sodic medium composed of relatively high concentration of Na^{+} along with low concentrations of Ca^{2+} is required, not only to prevent Na^{+} injury, but also to maintain differential permeability. Shay and Hale (1973) have demonstrated that the lack of Ca^{2+} in the bathing medium of peanut roots has an effect on exudation of sugars. The data suggest that at low levels of calcium there is an increase in membrane permeability which allows a quantitative increase in the exudation of sugars. Siegel and Daly (1966) and Siegal (1970) have demonstrated that treatment with poly-L-lysine increases the exudation of betacyanine while Ca^{2+} prevents that process. Whatever way the role of ions in membrane permeability is viewed, the role of calcium remains unique and suggests further study.

3.4. Soil moisture and moisture stress

Moisture stress has been demonstrated to affect the amounts of root exudates. If the rooting medium is allowed to become dry and then watered,

the amounts of exudate are increased. Vancura (1964) was able to recover 0.4 to 0.5 mg of organic compounds exuded from the roots of wheat and barley seedlings 10 days after water stress was relieved. This amounted to 7 to 10% of the total dry weight of the aerial parts of the plant. No attempt was made to differentiate between seed exudate and root exudate. Katznelson et al. (1954) carried out experiments under non-sterile conditions, but were able to show that greater amounts of ninhydrin reacting compounds occurred in leachates from plants if the supporting rooting medium had been allowed to dry and then rewetted, than from plants not subjected to such moisture stress. Similarly, Ivanov et al. (1964) demonstrated that there was a greater movement of foliage applied ^{14}C from one plant to another through the rooting medium if the soil was first allowed to dry to 35% and then brought to 70% of full moisture capacity, than if the soil was maintained at 70% throughout. What effect the two treatments might have had on the growth rates of the plants and thus on the proximity of the two root systems is not clear.

Indirect evidence indicates that soil moisture stress affects root exudation (Couch and Bloom, 1960). Several species were grown with varying irrigation conditions and cycles representing degrees of moisture stress. Egg hatch of nematode *Meloidogyne incognita* was used to assay root exudates obtained from the non-axenic rooting media. Non-amino acid fractions of extracts from a cyclic SC (saturation capacity) → PWP (permanent wilting percentage) → SC, reduced egg hatch, but greatest inhibition resulted from exudates of plants under cyclic FC (field capacity) → PWP → SC patterns.

Osmotic shock accompanied by thermal shock such as the root cells would experience under some experimental conditions results in the release of up to 3.5% of the protein in the cells (Amar and Reinhold, 1973). In this study plant tissues were removed from 0.5 *M* sucrose solution at 25°C and placed in distilled water at 2°C. The source of the protein was postulated to be the one involved in active transport in the cell wall or plasmalemma. Immersion in calcium sulfate solution restored the plant tissue to its original state after the shock treatment.

3.5. Oxygen concentration

The balance between aerobic and anaerobic conditions affects root exudation. Grineva (1961) subjected roots of young corn and sunflower plants to periods of anaerobiosis by immersing them in water. There was an increase in the dry weight of exudates and in the proportions of oxidizing compounds. Grineva concluded that cessation of aerobic respiration induced a shift in metabolism resulting in active secretion of non-metabolized compounds. However, the treatment also provided a means of leaching the roots, resulting in the increased yield of exudates. Root anaerobiosis also was found to induce the formation and excretion of ethanol at the expense of

the sugar content (Grineva, 1963). It is interesting that Allen and Newhook (1973), several years later, showed that zoospores of *Phytophthora cinnamomi* migrate towards an ethanol gradient in capillaries the size of soil pores. Not only do the motile spores migrate but germ tubes are oriented towards the gradient. Without the ethanol gradient, there was a disorientation of movement.

Woodcock (1962) incubated bean seeds for 3 days and found that under increased anaerobiosis germination decreased slightly and exudation increased. However, placing seeds in pure oxygen had a similar effect.

The root exudation of foliage applied herbicides is also affected by the balance between aerobic and anaerobic conditions. Hurtt and Foy (1965) applied dicamba (2-methoxy-3,6-dichlorobenzoic acid) and picloram (4-amino-3,6-trichloropicolinic acid) to Black Valentine bean, and found that both compounds were exuded by roots into the nutrient solution. When anaerobic conditions were imposed by bubbling N_2 into the nutrient solution, an increase in exudation of picloram but not of dicamba occurred.

Ayers and Thornton (1968) grew wheat and pea seedlings aseptically in both sand and solution cultures. The total amino-N and the proportions of several amino acids exuded were influenced by O_2 and CO_2 concentrations in the rooting medium. More ninhydrin-active compounds were exuded from pea roots under conditions of soil—air (i.e., air enriched to 0.5% CO_2), than with other gas mixtures.

Rittenhouse and Hale (1971) reported that, although there were no effects on growth, peanut root exudation of sugars increased with a decrease in aerobiosis. The effect was different for young plants (2 weeks old) because they exuded more galactose and dihydroxyacetone under the more aerobic conditions created by bubbling oxygen into the nutrient solution bathing the roots.

Although specific information on the effects on exudation is lacking, the effects of reduced oxygen tension on respiration are well known. One would expect that a reduction in aerobic respiration of roots would reduce energy available for retention of the active transport system. The permeability of the cellular membrane would change as a result and some substances could possibly leak out of the cells and be considered exudates. For a broad discussion of the effects of oxygen concentrations on root activities, the reader is referred to Stolzy (1974).

Evidence which might indicate an effect of anaerobiosis on exudation comes from the work of Hiatt and Lowe (1967) with excised barley roots. Six day old barley roots were incubated anaerobically for 15 minutes to 4 hours. Organic acid content of the roots decreased rapidly during the first 30 minutes and then changed little for 30 minutes. After an hour the organic acid loss from the roots increased and these acids appeared in the circumambient solutions. This was attributed to injury of the cell membrane after an hour under anaerobiosis. Amino acids were lost less rapidly but over the 4 hour duration of the experiment.

4. EVALUATION OF METHODS OF INVESTIGATION

Precise studies of root exudation have been conducted under well defined or controlled conditions to avoid alteration by microorganisms or contributions from leaf leachates and decomposing organic matter. Many of these investigations, therefore, place the plant under conditions much removed from natural conditions. Extrapolation from one set of conditions to another should be done with extreme caution. However, the establishment of cause and effect relationships in the rhizosphere requires some simplification and control of the system employed. A number of techniques have been developed, some of which are described in a general way.

4.1. The use of isotopes

The use of isotopes has not been exploited sufficiently in studying the interactions between roots and their environment and especially in tracing root exudates. One of the earliest reports of work done under controlled conditions showing that exudates do, in fact, come from intact, attached roots, was by Slankis et al. (1964). As early as 1957, Akhromeiko and Shestokova reported that soil of potted oak and ash seedlings became radioactive in a period of 4 days if labelled P was applied to the leaves as sodium phosphate. Slankis et al. (1964) dispelled any doubts about the source of the radioactivity by showing that 0.825% of the applied radioactive material could be recovered in the axenic rooting medium of 9 month old pine seedlings. Autoradiograms showed radioactivity throughout the roots after 8 days exposure of the needles to $^{14}CO_2$.

McDougall (1968) used a pulse labelling method of incorporating $^{14}CO_2$ into the metabolic pathways of 8 day old wheat seedlings growing axenically in test tubes. Fifty to sixty μCi of $^{14}CO_2$ were introduced into the stoppered test tubes and the plants allowed to continue photosynthesis. After 2 hours, almost all of the ^{14}C appeared in root exudates. This represented the time for $^{14}CO_2$ to be absorbed, incorporated into sucrose, translocated to the roots, and exuded. Sites of exudation along roots were detected by placing the roots, still attached to the rest of the plant, between strips of chromatographic paper, allowing two hours for exudation to occur and then using a strip scanner to measure the radioactivity. Deliberate damage to the roots increased loss of radioactive compound through the wound.

Balasubramanian and Rangaswami (1971) applied ^{14}C glucose to 3 day old sorghum plants (*Sorghum vulgare* Pers.) which grew with their roots under axenic conditions. Root exudates were collected every 24 hours for 3 days. About 0.065% of the total radioactivity applied to the foliage was detected in the root exudates within a 72 hour period. Greater radioactivity appeared in sugars than in amino acids exuded. Radioactivity was detected in glucose, fructose, an unidentified sugar, glutamic and aspartic acids and an

unknown substance. Within 72 hours, 18% of the radioactivity exuded from non-axenic roots was incorporated into microorganisms in the rhizosphere.

4.2. Foliar application of chemicals

Foliar application of chemicals exerts a direct influence on the quantity and quality of root exudation (Mitchell and Linder, 1950; Balasubramanian and Rangaswami, 1969; Rovira, 1969; Sethunathan, 1970a,b) as well as on the rhizosphere microflora (Bloom and Walker, 1955; Ramchandra-Reddy, 1968a,b; Sethunathan, 1970a,b). Katznelson (1965) observed that foliar application of chemicals is a more direct means of influencing rhizosphere populations, including potential pathogens, than soil treatments. For these reasons, foliar applications of chemicals to control rhizosphere microflora and plant health may be gaining importance in modern agriculture.

Measurement of exudation of foliage applied compounds has been used to study the effects of various factors on the absorption and translocation processes. α-Methoxyphenylacetic acid (MOPA) was the first reported excreted exogenous compound (Preston et al., 1954). Several other compounds have been reported as exuded from roots (Linder et al., 1958; Mitchell et al., 1959). Foy et al. (1971) showed that out of thirty-one compounds, picloram, dicamba, and 2,3,6-trichlorobenzoic acid were definitely exuded from roots and caused injury to untreated adjacent plants regardless of whether the rooting medium was sand, soil, or solution or whether the chemical was applied by leaf dipping, spraying, drop application or application through a severed petiole. When the root system was excised, only a small amount of picloram leaked out of the stems of treated plants. Neither picloram nor dicamba was exuded from roots which had been steamed or from roots of plants with steam girdled stems. The influence of aeration on exudation depended upon the chemical applied. The total amount of herbicide exuded into the rooting medium during a 4 day period was 10 to 15% of the amount applied to the foliage.

Although not quantified, changes in microbial populations in the rhizosphere have sometimes been used to show that foliar applications of antibiotics, mineral elements, and metal chelates are either exuded as such and affect populations of microorganisms or else they alter the normal exudation pattern to such an extent that microbial populations are altered (Ramchandra-Reddy, 1968a,b; Rao et al., 1972). Sullia (1968) used this technique to study effects of foliar application of gibberellic acid and indole-3-acetic acid. There was an increase in the total number of fungi but no change in species of fungi in the rhizosphere population.

Balasubramanian and Rangaswami (1969) observed that generally foliar applications of 0.1% of N as sodium nitrate increased the concentration of amino acids but reduced total sugar exuded by sorghum, sunnhemp, ragi, and tomato. Applications of P as sodium phosphate reduced the concentrations of amino acids and increased the exudation of sugars.

In a more recent investigation, Balasubramanian and Rangaswami (1973) applied 0.1% sodium nitrate, 0.1% sodium phosphate, 25 ppm 2,4-dichlorophenoxyacetic acid and 200 ppm Dithane Z-78 and measured the effects on the quantity and quality of sugars and amino acids exuded from the roots of sorghum and sunnhemp. Sodium nitrate decreased amino acid exudation in sorghum but increased it in sunnhemp whereas sodium phosphate decreased amino acid exudation. 2,4-D enhanced exudation of amino acids. Correlations of these effects with changes in populations of fungi, bacteria and actinomycetes were attempted (see Section 4.6).

Foliar application of chemicals can be a useful tool in root exudation investigations. Selection of chemicals and adjuvants for foliar application might lead to control of rhizosphere microorganisms or increased availability of nutrients either through exudation of the applied chemicals or through changes in the natural exudates. More work needs to be done in this area. In addition, factors affecting exudation, sources of exudates, and mechanisms of desorption from attached root systems can be quantitatively investigated if measured amounts of known compounds are applied.

4.3. Gnotobiotics

The gnotobiotic cultivation of plants, including axenic culture, has been reviewed by Hale et al. (1973). Cultivation of plant cells, tissues or organs in the absence of microorganisms has been practiced for several years. Gnotobiotic culture of higher plants beyond the seedling stage is of recent development, but is useful in the quantitative measure of root exudation from intact plants throughout the life cycle of the plant in question.

The axenic plant in comparison with the non-axenic plant shows differences in growth to varying degrees of magnitude depending upon the conditions under which the control plants and the axenic plants are grown. The general appearance of the axenic plant is reported to resemble very closely the appearance of the non-axenic plant. However, some reports show lesser growth rates of axenic plants, some show no difference, and some show an increased growth rate (Hale et al., 1973).

However great the problems involved in making comparisons between axenic and non-axenic plants, or between axenic and natural systems, the gnotobiotic technology holds forth promise of being one of the most productive ways of studying root exudates and root exudations from plants at predetermined stages of development. Probably, the greatest advantage of gnotobiotic techniques is in establishing model systems of plant—microbe interactions.

4.4. Quantification of exudation

Exudation of measurable quantities of water soluble organic compounds occurs from roots grown in test tubes, flasks or other containers, but little or

no information is available on quantities of organic compounds exuded from roots under natural conditions in soil because satisfactory methods of measuring exudation into soil have not been developed. Leaching of the soil—root complex has been used in experiments involving interactions but does not lend itself to quantitative measure of individual exudates on two counts: (1) leaching may or may not extract all the compounds to be measured and (2) compounds still in the root may be leached out. Removal of roots before extracting the soil has also been attempted. The removal process results in injury of the roots and a quantitative increase in exudates. This was one of the criticisms of the work of Miller and Schmidt (1965) who quantified several amino acids in autoclaved soil and in soil in which Black Valentine beans had been grown for 24 days. Considerably greater quantities (2 to 4 times) of amino acids were extracted with ammonium acetate from the soil in which the beans had been grown than from autoclaved soil. Results were expressed as μg amino acids/250 g dry soil. Such quantitative

TABLE V

Amounts of amino-nitrogen and sugars lost from seedling roots of various crop species[a,b]

Species	Amount recalculated to μg/plant/week	Reference
Amino-N		
Wheat	0.81	Ayers and Thornton (1968)
Peas	3.30	Ayers and Thornton (1968)
Alfalfa	0.37	Richter et al. (1968)
Sorghum	0.22	Balasubramanian and Rangaswami (1969)
Sunnhemp	0.28	Balasubramanian and Rangaswami (1969)
Ragi	0.15	Balasubramanian and Rangaswami (1969)
Tomato	0.05	Balasubramanian and Rangaswami (1969)
Pinus radiata	0.73	Bowen (1968)
Phaseolus vulgaris	60 to 104[c]	Miller and Schmidt (1965)
Sugars		
Sorghum	38.3	Balasubramanian and Rangaswami (1969)
Sunnhemp	31.7	Balasubramanian and Rangaswami (1969)
Ragi	19.6	Balasubramanian and Rangaswami (1969)
Tomato	7.46	Balasubramanian and Rangaswami (1969)
Peanut	3.80	Hale (1968)

[a] Hale et al., 1971, Academic Press, New York, with permission.
[b] Grown in nutrient solution except as noted.
[c] Plant grown in sterile soil and soil extracted for analysis; fertilized with KNO_3. Some root injury on removal from soil.

TABLE VI

Micrograms of amino-nitrogen in root exudates of peas and corn[a]

Variants	Per plant	Per gram of roots		Above ground part, fresh	Per surface decimeter of absorbing surface of roots
		Fresh	Dry		
Peas	6.81	9.90	71.84	5.76	21.07
Corn	3.86	3.40	24.78	2.48	2.24
Peas: corn ratio	1.76	2.91	2.89	2.32	9.40

[a]Data from Manorik and Belima, 1969, Plenum, New York, with permission.

expression does not indicate the concentration in the rhizosphere environment where the influences on soil microorganisms are most intense.

Quantitative expressions of exudation into nutrient solutions are more common, but no uniform convention has been adopted for expressing quantities exuded. Hale et al. (1971) recalculated data from a variety of sources and restated them in μg/plant/week (Table V). In this way, varying amounts of amino acids and sugars were shown for several species and experimental conditions. Since all the data thus compared were for seedling plants grown in nutrient solution, the comparisons appeared valid. Amounts of amino nitrogen ranged from 0.3 to 3 μg per plant per week and amounts of sugar ranged from 4 to 41 μg per plant per week. Manorik and Belima (1969) believed that the best way to express the amount of exudate for the sake of comparison is, as the amount of exudate per unit area of absorbing root surface (Table VI). Such an expression would eliminate errors caused by differences in growth rate and nutritional status of the plants, but measurement for the estimation of the absorbing root surface is difficult and for the amount of exuding root surface, even more difficult.

Expressions based on the dry weight of roots are also misleading because only a small fraction of the root system may be involved in exudation of particular compounds, and concentrations given are much less than those the microorganisms would be exposed to in the rhizosphere along those segments of the root where exudation occurs.

The problem of expressing the amount and concentration of exudates, particularly those released under natural conditions, remains one that has not been dealt with satisfactorily.

4.5. In situ vs. model systems

Whether exudation from roots or other underground plant parts is studied in natural systems (*in situ*) or in model systems, there are advantages and

TABLE VII

Studies of exudation *in situ*

Advantages	Disadvantages
1. May reveal the net result or fate of exudates in the rhizosphere ecosystem. (Bioassay is especially valuable for net ecological effect of exudation.)	1. Compounds exuded in small amounts may be lost. Ephemeral or rapidly used compounds are not detectable, or if so, not in quantities actually exuded.
2. May be able to determine changes in the plant exudates made by microorganisms either externally or by absorption and release of the altered exudate.	2. Cannot determine what compounds are being released specifically by the root, which by microorganisms, and how they interact allelochemically.
3. No extrapolation needed since measurement is made in a "natural" system. May reveal a more accurate picture than model systems for certain exudates.	3. Extraction of the rhizosphere to obtain exudates may remove compounds from within microbial cells as well as from within roots, if present. Extraction procedures may not remove some exudates from adsorption sites on soil particles (Paul and Schmidt, 1960).
4. A variety of sites and ecosystems can be selected.	4. It is unclear what constitutes the "rhizosphere soil" sample. The rhizosphere sample needed for assay is variable depending upon the nature of the exudate, the concentration at which it is effective, and the specific role of the exudate in the rhizosphere ecosystem.
5. Some compounds may persist long enough in the rhizosphere to be detected in which case exudates may be sampled throughout the life cycle of the plant or throughout the growing season. (But this can also be done in some model systems.)	5. Rhizosphere bioassays used may not be representative of natural conditions (e.g. artificially high spore densities that are conventionally used may yield false results — Griffin and Ford, 1974).

disadvantages which favor a combined approach. Some of the advantages and disadvantages for each approach are listed in Tables VII and VIII. Interpretation of data using either approach must include a consideration of the factors listed.

4.6. Bioassay methods

In early investigations, higher bacterial, actinomycete, and fungal populations occurred (by dilution plating) in soil adjacent to roots than in soil distant from roots or adjacent to glass rods (Starkey, 1931). This constituted

TABLE VIII

Studies of exudation in model systems

Advantages	Disadvantages
1. Components of the complex rhizosphere ecosystem can be selected and used as models.	1. Some knowledge of the rhizosphere ecosystem may be incomplete for model construction.
2. Exudates from each organism in the system and from the interactions of organisms in the model can be measured qualitatively and quantitatively.	2. Artifacts in the model are difficult to avoid.
3. Conditions affecting the component or model are, for the most part, under the control of the investigator or can be monitored.	3. Some difficulty may be experienced in extrapolating from the model to the natural system. Results may be misleading or suspect leading to faulty interpretation.
4. An axenic model can be established as a control for comparison.	4. Techniques for re-infestation of sterilized rooting media to re-establish pre-sterilization microbial populations have not been perfected (Danielson and Davey, 1969; Lindsey, 1967). Re-infestation of sterilized media may result in different equilibria among organisms than occur in natural equilibria and climax populations are not the same.
	5. No sterile soil is available that is not subject to interferences in chemical assays of exudates.
	6. Some models are expensive to maintain because of environmental controls required and because size of plant may be a limiting factor.

presumptive evidence that roots were releasing energy-yielding carbon and nitrogen substrates that supported growth of these microorganisms. Direct microscopic observation of bacterial and fungal development on root surfaces (Linford, 1942; Starkey, 1938), and more recently of fungal mycelial lengths in the rhizosphere (Parkinson and Thomas, 1969) support similar conclusions. Within limits, such determinations are useful today as assays for exudation. For example, Bowen and Rovira (1973) have recently attempted to construct a model in which the number of bacteria per mg dry root of wheat was correlated with the quantity of exudate released by wheat roots. Other bioassays for exudation include fungus spore germination assays in rhizosphere or spermosphere soil, spore germination in water droplets on

root surfaces, and in crude exudates or exudate fractions of the growth solution of axenic plants. Similar assays may be performed, with modifications, for nematode hatching factors, zoospore chemotactic responses, growth of bacteria, or allelopathic responses of higher plants. Separation of plant parts from the test organism by an air gap can be used to bioassay volatile exudates.

Different types of information such as the sites of exudation, the quality and quantity of energy yielding exudates produced, whether inhibitors or stimulators are exuded, the timing of exudation changes, and extent of exudate diffusion and persistence in soil, may be gained from these assays. Many assays are subject to artifacts, however, and responses observed in axenic crude exudates, for example, may not be observed in rhizosphere bioassays in the presence of microbial antagonism from other rhizosphere inhabitants. Thus it is better to use two or more types of bioassays, with at least one in non-sterile rhizosphere soil, if the ecological importance or the net effect of exudation by a given plant is to be ascertained. Here also, bioassay with the propagule naturally occurring in soil is critical. Conversely, the extent of propagule germination in rhizosphere soil is not necessarily a direct indicator of the quantity of stimulatory exudate produced, as is sometimes inferred by researchers, since inhibitors and antagonists in the rhizosphere may also be important. A direct assay on the surface of roots, in the absence of soil, would give to some degree, accurate information on the actual compounds exuded by plants, depending on the specificity of the nutritional requirements of the microorganism used.

4.6.1. Quantitative bioassays for exudates

Estimation of the relative magnitudes of populations of bacteria, actinomycetes, and fungi in the rhizoplane or rhizosphere versus non-rhizosphere soil has been used extensively in bioassays for total soluble and insoluble exudates and sloughed cells. However, this type of assay is subject to many variables, due to the different ways rhizoplane and rhizosphere soil samples are obtained, and to problems associated with the limitations of soil dilution plating. Direct comparisons of data on microbial populations obtained on these bases, to the quantities of soluble exudates produced in axenic or semiaxenic cultures, present many pitfalls. Also, sloughed cells and insoluble exudates may contribute significant organic carbon sources to the growth of these populations.

Positive correlations have been obtained in some cases. Recently Balasubramanian and Rangaswami (1973) reported that the application of 2,4-D to leaves of sunnhemp and sorghum resulted in increased rhizosphere populations of bacteria, actinomycetes, and fungi and these population increases were correlated with increased exudation of sugars and amino acids in both plant species. Foliar application of sodium nitrate, sodium phosphate, and Dithane Z-78 resulted in microbial population changes of less predictive

value relative to the amounts and types of sugars and amino acids exuded. In the Bowen and Rovira (1973) model mentioned previously, it was indicated that 1.3×10^6 and 1.5×10^6 bacteria/mg dry root were supported by 2 and 8 week old wheat roots. Parallel studies demonstrated that 1 to 2% of the carbon reaching the roots was released as water soluble exudate, insoluble mucilaginous material, and sloughed root cap cells. Assuming this material was 40% carbon and was released as sucrose, calculations indicated that up to 6.8×10^6 bacterial cells/mg root would be produced. There was good agreement between these values considering the gross assumptions made. In the quantitative bioassays for exudates, exudate utilization by fungi and actinomycetes, the time relationships of exudation, and other complicating factors mentioned by Bowen and Rovira (1973) need to be considered.

Magyarosy and Hancock (1974) examined microbial populations in surrounding soil and the exudation of squash hypocotyls, for squash mosaic virus infected plants and healthy plants. The former exuded more ^{14}C assimilates and supported higher microbial populations. Surprisingly, however, chlamydospore germination of *Fusarium solani* f. sp. *cucurbitae* in water droplets on bare hypocotyls (no soil present) was not greater for plants producing more exudates. Reduced chlamydospore germination occurred in soil adjacent to the hypocotyls on virus-infected plants (Diaz-polanco et al., 1969). Griffin (1972) reported that mechanical injury of peanut pods greatly increased conidial germination by *Aspergillus flavus* in soil adjacent to pods. Parallel studies by Hale and Griffin (1974) indicated a corresponding increase in exudation of certain sugars and amino-N compounds following mechanical injury of pods.

Bioassays of microbial populations and spore germination in the rhizosphere and spermosphere at various distances from the plant surface are a function of how far exudates diffuse in soil, and also are related in some degree to the quantity of exudate produced. Unfortunately, studies of this type usually do not include parallel studies on the quantities of organic energy-yielding substrates exuded under axenic conditions. When volatile stimulants are involved, bioassays may show stimulation at greater distances from the root surface than when soluble exudates alone are produced (Coley-Smith, 1960).

4.6.2. Qualitative bioassays for exudates

Most bioassay procedures are for soluble exudates. Presently there are no effective bioassays that identify insoluble exudates and sloughed cells. Information and confirmation on the sites of exudation has been gained from bioassays, however. Griffin (1969) observed that chlamydospore germination by *F. oxysporum* in the rhizosphere of peanuts began at a mean distance of 9.5 mm from the root tip and increased greatly over the following 5 mm. Depending upon the latent period for spore germination, the rate of root tip growth, and the distance of the observed spores from the

root surface, bioassays of sites of exudation from growing root tips are subject to the error that the actual site of exudation may be somewhat nearer to the root tip than indicated by the bioassay. Bowen and Rovira (1973) demonstrated exudation by mature parts of roots by transplanting axenic *Pinus radiata* roots to non-sterile soil, and determining the bacterial population following incubation. Direct microscopic observation of bacteria on root surfaces yielded information on cell junctures as possible microsites of exudation (ref. Rovira, 1965). More recently, scanning electron microscopy of bacteria on root surfaces has provided information on the areas of root exudation (Rovira and Campbell, 1974). Similar information was gained by observing spore germination at wound sites versus non-wounded areas of peanut fruits in soil (Griffin, 1972).

Presumptive or definitive information on the types and amounts of compounds exuded by roots or other plant parts can be gained from bioassays if the exogenous nutritional requirements (e.g. amino acids, sugars, organic acids, etc.) for spore germination (Griffin, 1972) or growth (Katznelson, 1965) are defined. The more specific the nutritional requirement (Frenzel, 1960), the more precise the information gained. Chemical analysis procedures are generally more suitable for obtaining information of this type. However, knowledge of unusual nutritional requirements for organisms stimulated in the rhizosphere of a plant may often give clues as to the type of compounds to be chemically assayed in exudates (Papavizas and Kovacs, 1972). In addition, bioassays may reveal differential exudation of inhibitors and stimulators over time, as suggested by the data (Chaturvedi and Muralia, 1974) obtained for fungal spore germination in crude exudates of cumin seeds. Bioassays of propagule germination in soil adjacent to plant parts have yielded information that suggests roots of plants exude substances that may directly (Kraft, 1974) or indirectly (Diaz-polanco et al., 1969; Magyarosy and Hancock, 1974) account for differences in resistance to infection by soil-borne plant pathogens.

5. SUMMARY AND CONCLUSIONS

Exudation of organic substances from roots can be viewed as a physiological process governed by a variety of factors which lead to the establishment of diffusion gradients and active transport from within the root to its surface. Factors which affect photosynthesis, translocation, and contents of soluble pools also affect root exudation. The sites of exudation along the root surface vary with the nature of the exudate, the plant species, and the experimental procedures, many of which affect cell membrane permeability.

Bioassays of exudates should not only measure their ecological impact but also need to be coupled with other measurements of the quantity and kind of exudates involved. A relatively large contribution to the carbon and

nitrogen sources in the rhizosphere occurs in the form of sloughed material, a result of growth of the root.

Some standardization of procedures and methods of quantitatively expressing exudation would help those working in this area of research to compare results. The losses of carbon and nitrogen from the plant can only be surmised until more quantitative information becomes available. Some loss by the plant may be compensated by the beneficial effects of exudates in the rhizosphere ecology. The possibility of altering exudate patterns by application of chemicals to the foliage may offer some advantage in controlling colonization of roots by microorganisms or in controlling the growth of adjacent unwanted plant species.

6. REFERENCES

Akhromeiko, A. I. and Shestokova, V. A., 1957. A study of the role of microorganisms in the uptake and release of phosphorus and sulfur by seedlings of maple, oak, and ash. Mikrobiologia, 27 [in English translation 'Microbiology']: 66—73.

Allen, R. N. and Newhook, F. J., 1973. Chemotaxis of zoospores of *Phytophthora cinnamomi* to ethanol in capillaries of soil pore dimensions. Trans. Br. Mycol. Soc., 61: 287—302.

Amar, L. and Reinhold, L., 1973. Loss of membrane transportability in leaf cells and release of protein as a result of osmotic shock. Plant Physiol., 51: 620—625.

Arisz, W. H., 1956. Significance of the symplasm theory for transport across the root. Protoplasma, 44: 1—62.

Ayers, W. A. and Thornton, R. H., 1968. Exudation of amino acids by intact and damaged roots of wheat and peas. Plant Soil, 28: 193—207.

Baker, K. F. and Snyder, W. C., (Editors), 1965. Ecology of Soil-borne Plant Pathogens, Prelude to Biological Control. Univ. Calif. Press, Berkeley, 571 pp.

Balasubramanian, A. and Rangaswami, G., 1969. Studies on the influence of foliar nutrient sprays on the root exudation pattern in four crop plants. Plant Soil, 30: 210—220.

Balasubramanian, A. and Rangaswami, G., 1971. A technique to study the exudation of foliar applied chemicals through plant roots and their uptake by rhizosphere microorganisms. Int. Symp. on use of Isotopes and Rad. in Agric. and Anim. Hus. Res., New Delhi, pp. 530—535.

Balasubramanian, A. and Rangaswami, G., 1973. Influence of foliar application of chemicals on the root exudations and rhizosphere microflora of *Sorghum vulgare* and *Crotalaria juncea*. Folia Microbiol., 18: 492—498.

Beevers, H., 1969. Metabolic sinks. In: J. D. Eastin, F. A. Haskins, C. Y. Sullivan and C. H. M. Van Bauel (Editors), Physiological Aspects of Crop Yield. Amer. Soc. Agron., Crop Sci. Soc., Madison, Wis., pp. 169—181.

Bidwell, R. G. S., 1974. Plant Physiology. Macmillan, New York, 643 pp.

Blomquist, R. V. and Kust, C. A., 1971. Translocation pattern of soybeans as affected by growth substances and maturity. Crop Sci., 11: 290—293.

Bloom, J. K. and Walker, J. C., 1955. Effect of nutrient sprays on fusarium wilt of tomato. Phytopathology, 45: 443—444.

Bonish, P. M., 1973. Cellulase and red clover exudates. Plant Soil, 38: 307—314.

Bonner, J., 1950. The role of toxic substances in the interactions of higher plants. Bot. Rev., 16: 52—65.

Borner, H., 1960. Liberation of organic substances from higher plants and their role in the soil sickness problem. Bot. Rev., 26: 393—424.
Bowen, G. D., 1968. Chloride efflux along *Pinus radiata* roots. Nature (London), 218: 686—687.
Bowen, G. D., 1969. Nutrient status effects on loss of amides and amino acids from pine roots. Plant Soil, 30: 139—142.
Bowen, G. D. and Rovira, A. D., 1966. Microbial factor in short-term phosphate uptake studies with plant roots. Nature (London), 211: 665—666.
Bowen, G. D. and Rovira, A. D., 1973. Are modelling approaches useful in rhizosphere biology? In: T. Rosswall (Editor), Modern Methods in the Study of Microbial Ecology. Bull. Ecol. Res. Comm. (Stockholm), 17: 443—450.
Bowen, G. D. and Theodorou, C., 1973. Growth of ectomycorrhizal fungi around seeds and roots. In: G. C. Marks and T. T. Kozlowski (Editors), Ectomycorrhizae — Their Ecology and Physiology. Academic Press, New York, pp. 107—150.
Brams, E., 1969. The mucilaginous layer of citrus roots — its delineation in the rhizosphere and removal from roots. Plant Soil, 30: 105—108.
Carson, E. W., (Editor), 1974. The Plant Root and its Environment. Univ. Press of Va., Charlottesville, 691 pp.
Chaturvedi, S. N., Suadhana, B. S. and Muralia, R. N., 1974. The influence of cumin seed exudates on fungal spore germination. Plant Soil, 40: 49—56.
Clark, R. E., 1949. Soil microorganisms and plant roots. Advan. Agron., 1: 242—288.
Coley-Smith, J. R., 1960. Studies of the biology of *Sclerotium Cepivorum* Berk. IV: Germination of sclerotia. Ann. Appl. Biol., 48: 8—18.
Couch, H. B. and Bloom, J. R., 1960. Influence of soil moisture stresses on the development of the root-knot nematode. Phytopathology, 50: 319—321.
Danielson, R. M. and Davey, C. B., 1969. Microbial recolonization of a fumigated nursery soil. For. Sci., 15: 368—380.
Dawes, C. J. and Bowler, E., 1959. Light and electron microscope studies of the cell wall structure of the root hairs of *Raphanus sativus*. Am. J. Bot., 46: 561—565.
De Candolle, A. P., 1832. Physiologie Vegetale. Paris.
Diaz-polanco, D., Smith, S. H. and Hancock, J. G., 1969. Effect of virus infection on stem rot of squash caused by *Fusarium solani* f. sp. *cucurbitae*. Phytopathology, 59: 18—22.
Esau, K., 1953. Plant Anatomy. John Wiley and Sons, Inc., New York, 735 pp.
Evanari, M., 1961. Chemical influences of other plants (allelopathy). In: W. Ruhland (Editor), Encyclopedia of Plant Physiology. Springer-Verlag, Berlin, 16: 691—736.
Floyd, R. A. and Ohlrogge, A. J., 1970. Gel formation on nodal root surfaces of *Zea mays* I: Investigation of the gel's composition. Plant Soil, 33: 331—343.
Foy, C. L., Hurt, W. and Hale, M. G., 1971. Root exudation of plant growth regulators. In: Biochemical Interactions Among Plants. Conf. Proc. Envir. Subcomm., Natl. Comm. Int. Biological Program, Natl. Acad. Sci., Washington, D.C., pp. 75—85.
Frenzel, B., 1960. Zur Atiologie der Anreicherung von Aminosauren und Amiden im Wurzelraum von *Helianthus annuus* L.: Ein Beitrag zur Klarung der Probleme der Rhizosphere. Planta, 55: 169—207.
Garb, S., 1961. Differential growth inhibitors produced by plants. Bot. Rev., 27: 422—443.
Greaves, M. P. and Darbyshire, J. F., 1972. The ultra-structure of the mucilaginous layer of plant roots. Soil Biol. Biochem., 4: 443—449.
Griffin, G. J., 1969. *Fusarium oxysporum* and *Aspergillus flavus* spore germination in the rhizosphere of peanut. Phytopathology, 59: 1214—1218.
Griffin, G. J., 1972. Conidial germination and population of *Aspergillus flavus* in the geocarposphere of peanut. Phytopathology, 62: 1387—1391.
Griffin, G. J. and Ford, R. H., 1974. Soil fungistasis: fungus spore germination in soil at

spore densities corresponding to natural population levels. Can. J. Microbiol., 20: 751—754.
Griffin, G. J., Hale, M. G. and Shay, F. J., 1976. Nature and quantity of sloughed organic matter produced by roots of axenic peanut plants. Soil Biol. Biochem., 8: 29—32.
Grineva, G. M., 1961. Excretion by plant roots during brief periods of anaerobiosis. Soviet Pl. Physiol., 8: 549—552.
Grineva, G. M., 1963. Alcohol formation and excretion by plant roots under anaerobic conditions. Soviet Pl. Physiol., 10: 361—369.
Grodzinsky, A. M., 1965. Allelopathy in the life of plants and their associations. Acad. Sci. Ukrain, Kiev., 200 pp. [in Russian].
Hale, M. G., 1968. Losses of organic compounds from *Arachis hypogaea* L. growing in gnotobiotic conditions. Bull. Assoc. Southeastern Biologists 15: 39 (abstr.).
Hale, M. G., 1969. Loss of organic compounds from roots I: Cultural conditions for axenic growth of peanut, *Arachis hypogaea* L. Plant Soil, 31: 463—472.
Hale, M. G. and Griffin, G. J., 1974. Effect of injury on exudation from immature and mature peanut fruits under axenic conditions. Plant Physiol. Ann. Suppl. 53: 13 (Abstr.).
Hale, M. G., Foy, C. L. and Shay, F. J., 1971. Factors affecting root exudation. Adv. Agron., 24: 89—109.
Hale, M. G., Lindsey, D. L. and Hameed, K. M., 1973. Gnotobiotic culture of plants and related research. Bot. Rev., 39: 261—273.
Hamlen, R. A., Lukezic, F. L. and Bloom, J. R., 1972. Influence of age and stage of development on the neutral carbohydrate components in root exudates from alfalfa plants grown in a gnotobiotic environment. Can. J. Plant Sci., 52: 633—642.
Head, G. C., 1964. A study of exudation from root hairs of apple roots by time-lapse cinephotomicrography. Ann. Bot., 28: 495—498.
Helder, R. J. and Boerma, J., 1969. An electron-microscopical study of the plasmodesmata in the roots of young barley seedlings. Acta Bot. Neerl., 18: 99—107.
Hiatt, A. J. and Lowe, R. H., 1967. Loss of organic acids, amino acids, K and Cl from barley roots treated anaerobically and with metabolic inhibitors. Plant Physiol., 42: 1731—1736.
Hiltner, L., 1904. Über neuere Erfahrungen und Probleme auf dem Gebiet der Bodenbakteriologie und unter besonderer Berücksichtigung der Gründüngung und Brache. Arb. Deut. Landw. Ges., 98: 59—78.
Holm, L., 1971. Chemical interactions between plants on agricultural lands. In: Biochemical Interactions Among Plants. Conf. Proc. Envir. Subcomm., Natl. Comm. Int. Biological Program, Natl. Acad. Sci., Washington, D.C., pp. 95—101.
Hurtt, W. and Foy, C. L., 1965. Some factors influencing the excretion of foliarly applied dicamba and picloram from roots of Black Valentine beans. Plant Physiol. (Suppl.), 40: xlviii. (Abstr.).
Hussain, S. S. and McKeen, W. E., 1963. Interactions between strawberry roots and *Rhizoctonia fragariae*. Phytopathology, 53: 541—545.
Ivanov, V. P., Yacobsen, G. A. and Fomenko, B. S., 1964. Effect of soil moisture on metabolism of root excretions. Soviet Pl. Physiol., 11: 538—545.
Jenny, H. and Grossenbacher, K., 1963. Root-soil boundary zones as seen by the electron microscope. Proc. Amer. Soil Sci. Soc., 27: 273—277.
Jones, D. D. and Morré, D. J., 1967. Golgi apparatus mediated polysaccharide secretion by outer root cap cells of *Zea mays* II: Isolation and characterization of the secretory products. Z. Pflanzenphysiol., 56: 166—169.
Juniper, B. E. and Roberts, R. M., 1966. Polysaccharide synthesis and fine structure of root cells. J. R. Microsc. Soc., 85: 63—71.
Juo, P. and Stotzky, G., 1970. Electrophoretic separation of proteins from roots and root exudates. Can. J. Bot., 48: 713—718.

Katznelson, H., 1965. Nature and importance of the rhizosphere. In: K. F. Baker and W. C. Snyder, (Editors), Ecology of Soil-borne Plant Pathogens. Univ. Calif. Press., Berkeley, pp. 187—209.

Katznelson, H., Rouatt, J. W. and Payne, T. M. B., 1954. Liberation of amino acids by plant roots in relation to desiccation. Nature (London), 174: 1110—1111.

Keeling, B. L., 1974. Soybean seed rot and the relation of seed exudate to host susceptibility. Phytopathology, 64: 1445—1447.

Kovacs, M. F., Jr., 1971. Identification of aliphatic and aromatic acids in root and seed exudates of pea, cotton and barley. Plant Soil, 34: 441—451.

Kraft, J. M., 1974. The influence of seedling exudates on the resistance of beans to *Fusarium* and *Pythium* root rot. Phytopathology, 64: 190—193.

Krichbaum, R., Lutige, U. and Weigl, J., 1967. Mikroautoradiographische Untersuchung der Auswaschung des "anscheinend freien Raumes" von Maiswurzeln. Ber. D. Bot. Ges., 80: 167—176.

Lawn, R. J. and Brun, W. A., 1974. Symbiotic nitrogen fixation in soybeans I: Effect of photosynthetic source-sink manipulation. Crop Sci., 14: 11—16.

Leppard, G. G., 1974. Rhizoplane fibrils in wheat; demonstration and derivation. Science, N.Y., 185: 1066—1067.

Linder, P. J., Craig, J. C., Jr. and Walton, T. R., 1957. Movement of C^{14} tagged alpha-methoxyphenylacetic acid out of roots. Plant Physiol., 32: 572—575.

Linder, P. J., Craig, J. C., Jr., Cooper, F. E. and Mitchell, J. W., 1958. Movement of 2,3,6-trichlorobenzoic acid from one plant to another through their root systems. J. Agric. Fd. Chem., 6: 356—357.

Lindsey, D. L., 1967. Growth of beans, tomatoes, and corn under gnotobiotic conditions. Phytopathology, 57: 960—964.

Linford, M. B., 1942. Methods of observing soil flora and fauna associated with roots. Soil Sci., 53: 93—103.

Lundegardh, H. and Stenlid, G., 1944. On the exudation of nucleotides and flavonones from living roots. Archs. Botan., 31: 1—27.

Lyon, T. L. and Wilson, J. K., 1921. Liberation of organic matter by roots of growing plants. New York Agr. Exp. Sta. Mem., 40: 7—44.

Magyarosy, A. C. and Hancock, J. G., 1974. Association of virus-induced changes in laimosphere microflora and hypocotyl exudation with protection to *Fusarium* stem rot. Phytopathology, 64: 994—1000.

Manorik, A. V. and Belima, N. I., 1969. Method of studying root exudates and of calculating their amounts. Soviet Pl. Physiol., 16: 297—302.

Mason, G. F., Bhar, D. S., and Hilton, R. J., 1970. Root growth studies on mugho pine. Can. J. Bot., 48: 43—47.

McDougall, B. M., 1968. The exudation of ^{14}C-labeled substances from roots of wheat seedlings. Trans. Ninth Inter. Congr. Soil Sci., Adelaide, pp. 647—685.

McDougall, B. M., 1970. Movement of ^{14}C-photosynthate into roots of wheat seedlings and exudation of ^{14}C from intact roots. New Phytol., 69: 37—46.

McDougall, B. M. and Rovira, A. D., 1965. Carbon-14 labelled photosynthate in wheat root exudates. Nature (London), 207: 1104.

McDougall, B. M. and Rovira, A. D., 1970. Sites of exudation of ^{14}C labelled compounds from wheat roots. New Phytol., 69: 999—1003.

Miller, R. H. and Schmidt, E. L., 1965. Uptake and assimilation of amino acids supplied to sterile soil: root environment of the bean plant (*Phaseolus vulgaris*). Soil Sci., 100: 323—330.

Mitchell, J. W. and Linder, P. J., 1950. Absorption and translocation of radioactive 2,4-D by bean plants as affected by cosolvent and surface agents. Science, N.Y., 112: 54—55.

Mitchell, J. W., Smale, B. C. and Preston, W. J., Jr., 1959. New plant regulators that exude from roots. J. Agric. Fd. Chem., 7: 841—843.

Mitchell, J. S., Linder, P. J. and Robinson, M. B., 1961. Mechanism of root exudation of alpha methoxyphenylacetic acid in the bean plant. Bot. Gaz., 123: 134—137.

Mollenhauer, H. H. and Morré, D. J., 1966. Tubular connections between dictyosomes and forming secretory vesicles in plant golgi apparatus. J. Cell. Biol., 29: 373—376.

Morré, D. J. and Mollenhauer, H. H., 1973. The endomembrane concept: a functional integration of endoplasmic reticulum and golgi apparatus. In: A. W. Robards (Editor), Dynamics of Plant Ultrastructure. McGraw-Hill, London, pp. 84—137.

Morré, D. J., Jones, D. D. and Mollenhauer, H. H., 1967. Golgi apparatus mediated polysaccharide secretion by outer root cap cells of *Zea mays* I: Kinetics and secretory pathway. Planta, 74: 286—301.

Muller, C. H., 1966. The role of chemical inhibition (allelopathy) in vegetational composition. Bull. Torrey. Bot. Club, 93: 332—351.

Nezgovarov, L. A., Solv'ev, A. K. and Rodina, L. N., 1970. Effect of separate cooling of roots and above ground organs on the damage of heat-loving plants by soil microflora and on the level of root exudation. Soviet Pl. Physiol., 17: 765—772.

Nieman, R. H. and Willis, C., 1971. Correlation between the suppression of glucose and phosphate uptake and the release of protein from viable carrot root cells treated with monovalent cations. Plant Physiol., 48: 287—293.

Northcote, D. H. and Pickett-Heaps, J. D., 1966. A function of the golgi apparatus in polysaccharide synthesis and transport in the root-cap cells of wheat. Biochem. J., 98: 159—167.

Oaks, A., 1965. The soluble leucine pool in maize root tips. Plant Physiol., 40: 142—148.

Papavizas, G. C. and Kovacs, M. F., 1972. Stimulation of spore germination of *Thielaviopsis basicola* by fatty acids from rhizosphere soil. Phytopathology, 62: 688—694.

Parkinson, D. and Thomas, A., 1969. Quantitative study of fungi in the rhizosphere. Can. J. Microbiol., 15: 875—878.

Paul, E. A. and Schmidt, E. L., 1960. Extraction of free amino acids from soil. Proc. Soil Sci. Soc. Am., 24: 195—198.

Pearson, R. and Parkinson, D., 1961. The sites of excretion of ninhydrin positive substances by broad bean seedlings. Plant Soil, 13: 391—396.

Preston, W. H., Mitchell, J. W. and Reeve, W., 1954. Movement of alpha-methoxyphenylacetic acid from one plant to another through their root systems. Science, N.Y., 119: 437—438.

Ramchandra-Reddy, T. K., 1968a. Plant treatment in relation to the rhizosphere effect II: Foliar application of certain chemicals and antibiotics in relation to the rhizosphere microflora of rice (*Oryza sativa* L.). Plant Soil, 24: 102—113.

Ramchandra-Reddy, T. K., 1968b. Plant treatment in relation to the rhizosphere effect III: Foliar application of certain trace elements and metabolic chelates in relation to rhizosphere microflora of rice (*Oryza sativa* L.). Plant Soil, 24: 114—118.

Rao, V. R., Jayakur, M., Sharma, K. R. and Mukerj, K. G., 1972. Effect of foliar spray of morphactin on fungi in the root zone of *Capsicum annuum*. Plant Soil, 37: 179—182.

Reid, C. P. P., 1974. Assimilation, distribution and root exudation of ^{14}C by ponderosa pine seedlings under induced water stress. Plant Physiol., 54: 44—49.

Richter, M., Wilms, W. and Scheffer, F., 1968. Determination of root exudates in a sterile continuous flow culture II: Short-term and long-term variations of exudation intensity. Plant Physiol., 43: 1747—1754.

Riley, D. and Barber, S. A., 1969. Bicarbonate accumulation and pH changes at the soybean (*Glycine max* (L.) Merr.) root-soil interface. Proc. Soil Sci. Soc. Am., 33: 905—908.

Rittenhouse, R. L. and Hale, M. G., 1971. Loss of organic compounds from roots II: Effect of O_2 and CO_2 tension on release of sugars from peanut roots under axenic conditions. Plant Soil, 35: 311—321.

Rovira, A. D., 1956. Plant root excretions in relation to the rhizosphere effect I: The nature of root exudates from oats and peas. Plant Soil, 7: 178—194.

Rovira, A. D., 1959. Root excretions in relation to the rhizosphere effect IV: Influence of plant species, age of plant, light, temperature and calcium nutrition on exudation. Plant Soil, 11: 53—64.

Rovira, A. D., 1965. Plant root exudates and their influence upon soil microorganisms. In: K. F. Baker and W. C. Snyder (Editors), Ecology of Soil-borne Plant Pathogens. Univ. Calif. Press, Berkeley, pp. 170—186.

Rovira, A. D., 1969. Plant root exudates. Bot. Rev., 35: 35—57.

Rovira, A. D., 1973. Zones of exudation along plant roots and spatial distribution of microorganisms in the rhizosphere. Pestic. Sci., 4: 361—366.

Rovira, A. D. and Campbell, R., 1974. Scanning electron microscopy of microorganisms on the roots of wheat. Microb. Ecol., 1: 15—23.

Samtsevich, S. A., 1965. Active excretion of plant roots and their significance. Soviet Pl. Physiol., 12: 731—740.

Schroth, M. N. and Hildebrand, D. C., 1964. Influence of plant exudates on root-infecting fungi. Ann. Rev. Phytopath., 2: 101—132.

Schroth, M. N. and Snyder, W. C., 1961. Effect of host exudates on chlamydospore germination of the bean root rot fungus, *Fusarium solani* f. *phaseoli*. Phytopathology, 51: 389—393.

Schroth, M. N., Weinhold, A. R. and Hayman, D. S., 1966. The effect of temperature on quantitative differences in exudates from germinating seeds of bean, pea and cotton. Can. J. Bot., 44: 1429—1432.

Sethunathan, N., 1970a. Foliar sprays of growth regulators and rhizosphere effect in *Cajanus Cajan* Millsp. I: Quantitative changes. Plant Soil, 33: 62—70.

Sethunathan, N., 1970b. Foliar sprays of growth regulators and the rhizosphere effect in *Cajanus Cajan* Millsp. II: Qualitative changes in the rhizosphere and certain metabolic changes in the plant. Plant Soil, 33: 71—80.

Shapovalov, A. A., 1972. Effect of increased temperature in kinetics of fluorescent component exudation from soybeans and oat roots. Soviet Pl. Physiol., 18: 135—138.

Shay, F. J. and Hale, M. G., 1973. Effect of low levels of calcium on exudation of sugars and sugar derivatives from intact peanut roots under axenic conditions. Plant Physiol., 51: 1061—1063.

Siegel, S. M., 1970. Further studies on regulation of betacyanin efflux from beet root tissue: Ca-ion-reversible effects on hydrochloric acid and ammonia water. Physiol. Plant., 23: 251—257.

Siegel, S. M. and Daly, O., 1966. Regulation of betacyanin efflux from beet root by poly-L-lysine, Ca-ion and other substances. Plant Physiol., 41: 1429—1434.

Slankis, V., Rueneckles, V. C. and Krotkov, G., 1964. Metabolites liberated by roots of white pine. Physiol. Plant., 17: 301—313.

Smiley, R. W. and Cook, R. J., 1973. Relationship between take-all of wheat and rhizosphere pH in soils fertilized with ammonium vs. nitrate-nitrogen. Phytopathology, 63: 882—890.

Smith, W. H., 1970. Root exudates of seedling and mature sugar maple. Phytopathology, 60: 701—703.

Smith W. H., 1972. Influence of artificial defoliation on exudates of sugar maple. Soil Biol. Biochem., 4: 111—113.

Starkey, R. L., 1931. Some influences of higher plants upon the microorganisms in soil IV: Influence of proximity to roots on abundance and activity of microorganisms. Soil Sci., 32: 367—393.

Starkey, R. L., 1938. Some influences of the development of higher plants upon the microorganisms in the soil VI: Microscopic examination of the rhizosphere. Soil Sci., 45: 207—209.

Stolzy, L. H., 1974. Soil atmosphere. In: E. W. Carson (Editor), The Plant Root and Its Environment. Univ. Press of Va., Charlottesville, pp. 335—355.

Subba-Rao, N. S., Bidwell, R. G. S. and Bailey, D. L., 1961. The effect of rhizoplane fungi on the uptake and metabolism of nutrients by tomato plants. Can. J. Bot., 39: 1759—1764.

Sullia, S. B., 1968. Effect of foliar sprays of hormones on the rhizosphere mycoflora of leguminous weeds. Plant Soil, 24: 292—298.

Vancura, V., 1964. Root exudates of plants I: Analysis of root exudates of barley and wheat in their initial phases of growth. Plant Soil, 21: 231—248.

Vancura, V., 1967. Root exudates of plants III: Effect of temperature and "cold shock" on the exudation of various compounds from seeds and seedlings of maize and cucumber. Plant Soil, 27: 319—328.

Vancura, V. and Hanzlikova, A., 1972. Root exudates of plants IV: Differences in chemical composition of seed and seedlings exudates. Plant Soil, 36: 271—282.

Vancura, V. and Hovadik, A., 1965. Root exudates of plants II: Composition of root exudates of some vegetables. Plant Soil, 22: 21—32.

Wardlaw, I. F., 1974. Phloem transport: physical, chemical or impossible? Ann. Rev. Pl. Physiol., 25: 515—539.

West, P. M., 1939. Exudation of thiamin and biotin by the roots of higher plants. Nature (London), 144: 1050—1051.

Whittaker, R. H. and Feeny, P. P. 1971. Allelochemics: chemical interactions between species. Science, N.Y., 171: 757—770.

Wills, W. H. and Moore, L. D., 1969. Heat-induced susceptibility of black shank resistant tobacco to *Phytophthora parasitica* var. *nicotianae*. Phytopathology, 59: 1974—1975.

Woodcock, W. P., 1962. Influence of aeration on exudation from seeds and on growth of root-rot fungi. Phytopathology, 52: 927 (Abstr.).

Woods, R. W., 1960. Biological antagonisms due to phytotoxic root exudates. Bot. Rev., 26: 546—569.

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