ROOT AERATION AND CROP GROWTH

"The assumption is not unwarranted that frequently soil aeration constitutes a limiting factor for the growth of some type of crops and that it may be an ecological factor of significance."

Hoagland

I. INTRODUCTION

Crops, as far as they belong to the higher plants, have developed a structure adapted to utilizing two distinct environments. The aerial surroundings mainly provide light, carbon dioxide and oxygen, while the soil usually is the source of water, minerals and minute quantities of a varied array of soluble organic substances. Contact with and utilization of the soil environment is performed by the root system, besides its function of providing anchorage for the plant.

If we are to understand the relation between crop growth and root aeration the functions the root system has to perform must be clearly described. The impairment of these functions under conditions of inadequate oxygen supply is the cause of restricted growth of the crop.

The substance, which is extracted from the soil in the largest quantities, is water. For an effective extraction the root system has to develop a large surface permeable to water and an efficient conducting system. Besides being large, this root-soil interface should be well distributed throughout the soil volume occupied by the root system. These same requirements have to be met in order to function effectively in the absorption of mineral nutrients (Kullmann, 1957; Geisler, 1963/1964; Newman and Andrews, 1973).

Besides water and mineral nutrients the soil contains an enormous array of soluble organic substances as the result of enzymatic and microbial activities. Essentially a very large number of these substances can enter the root and are indeed absorbed in minute quantities (Kloke, 1963).

But next to supplying the above-ground parts of the plant with basic substances for its synthetic processes the root also converts part of its absorbed minerals into organic material. Thus its metabolism is an integral part in the overall process of growth, development and production of the total plant. Besides taking into account this conversion of part of the mineral ions into organic derivatives, it must be realized that the root is also the seat of production of many other substances, including those with growth regulating capacity. In considering the importance of the contribution of root performance to the well-being and productivity of the plant these latter aspects should not be forgotten.

Last of all the root system - usually only a part of it - can function as a storage organ. This also implies periods of high metabolic activity, which results in certain demands on its environment.

For an optimum development and functioning of the root system the soil surroundings have to be favourable. Quite a number of factors are involved: i.e. reasonable values of water content, chemical fertility and pH, no mechanical impediment to root penetration and not toxic substances. But our discussion will mainly be restricted to effects of supply with oxygen and removal of carbon dioxide.

A general cutline concerning the requirements of the root system and the basic factors involved in its supply will be presented. Attention will then be given to the response in root growth and resulting effects of poor development on soil utilization. A review of the effects of inadequate aeration conditions on root metabolism will then lead to an attempt at integration and depiction of integral crop response.

For more detailed information the reader is referred to the list of more recent reviews, mentioned in the references.

II. OXYGEN REQUIREMENT OF THE ROOT SYSTEM

In considering the root-soil interrelationships in aeration the first thing that is needed is some information on the oxygen requirements of the root system. Although root oxygen consumption has been measured in numerous experiments, we are still confronted with a lack of really adequate data in many cases.

In table 1 some of the available data on root oxygen consumption are summarized.

Table 1. Some data on oxygen consumption by root tissues

Species	Type of root tissue	Consumption in µg/g dry weight/hour approximate values	Author
wheat	seedling roots	4200	Coster 1932/33
rice	seedling roots	3000	
onion	young root tips	10000-30000	Berry and Norris 1949
	differentiated tissue	4000-9000	
potato	mature roots	9400-17000	Bushnell 1956
wheat	young root tissue	1710	Eliasson 1959
barley	young seedling root	4480-5600	Pitman 1969
maize	young root zones	3600-7200	Luxmoore et al. 1970
rice	young root zones	2520-12600	
melon	mature roots	15000	Vartapetian et al. 1970

From a physiological point of view one must take into account the type of root material that has been used. Most often the investigation has been performed using young, vigorously growing roots. Even quite often the zones near the tip have been utilized. These are the zones with a high proportion of live parenchymatic cells, with only little lignified tissue and without suberized outer layers. Oxygen consumption of these young roots as expressed on unit dry weight is apt to be high in comparison to older and thickened roots (Schmucki, 1949). Also the temperature under which the determinations were performed in the laboratory are often rather high in comparison to those pertaining

in the soil during long periods. Thus it makes little sense to utilize these figures without some transformation in calculating oxygen consumption of a whole root system.

Oxygen consumption of total, intact root systems in the soil has also been measured in different investigations. A few data are compiled in table 2.

Table 2. Approximate data on oxygen consumption by soil and root systems

Crop	Soil type	Soil only 1 $O_2/m^2/day$	Plant in situ 1 $O_2/m^2/day$	Source
potato	sand		3.4	
	sandy clay loam	5.4	4.1	
	sandy clay loam	10.2	2.8	Hawkins 1962
kale	sand		4.4	Hawkins 1962
tobacco	fen soil	10.6	3.6	
potato			2.8	
kale			5.6	
tobacco			3.0	
	sandy clay loam	2.2	-	Brown et al. 1965
	peat top soil	10.8	-	

It seems worthwhile to compare these two sets of data. This can be done by utilizing data on root mass in the soil for potatoes (Goedewaagen and Schuurman, 1950) and for maize (Barber, 1971). If this is done there is a reasonable agreement, taking into account the uncertainties in conversion factors involved.

From an ecological point of view the question arises, whether account should be taken of respiration of the aseptic root proper or the oxygen consumption of the root and its attached rhizosphere. As the rhizosphere sensu stricto is an integrated part of any root in the soil it seems appropriate to use the latter data. Most consumption data on excised roots have been obtained on non-aseptic roots, so that the respiration of some kind of rhizosphere population is included.

The variation in values can be related to a number of different factors. First of all the respiration of the roots will differ from species to species (Coster, 1932/33; Hawkins, 1962; Brown et al., 1965; Fiscus and Kramer, 1970) or even between cultivars of one

species. But as a metabolic process respiration is sensitive to temperature, and as the values were obtained under variable circumstances this explains part of the variation as well.

Quite often a hundred percent increase in respiration has been encountered over 10°C rise in temperature (Berry and Norris, 1949; Eliasson, 1959). Within a range of about 0 - 35°C, in which many roots are viable, oxygen consumption may thus vary by a factor of about 8. Poor aeration is thus less deleterious at low temperature because root demand is less (Cannon, 1924). This is often clearly demonstrated by the resistance of many vegetations against flooding in winter.

As oxygen moves into the soil it mainly diffuses along a gradient of decreasing partial pressure. Roots in the soil will thus encounter quite different oxygen pressure conditions at their surface in relation to their location in the soil and the conditions immediately surrounding them (Wiegand and Lemon, 1958). We must therefore consider the problem to what extent root respiration is affected by oxygen pressure in the medium.

Differing according to temperature one usually finds that root respiration goes on unimpaired over the first range of decrease in pressure (Cannon, 1924; Geisler, 1967). So quite often oxygen content can be lowered to 10% in the gas phase without an effect on root metabolism. But below a certain oxygen content root respiration gradually declines as oxygen pressure is lowered.

As long as all internal cells are still adequately supplied root respiration will remain constant. But at a certain moment the decline in oxygen pressure through the respiring tissue inwards will become limiting for the innermost cells. According to Greenwood (1969) the affinity of cytochrome for oxygen is so high that the actual rate of respiration would only be impaired at values lower than 0.004 atm. O_2. A calculation - assuming a root of 0.74 mm thickness - shows that 1/100 atm. pressure of oxygen at the root surface would allow all internal tissues to be adequately supplied. The decline in oxygen consumption with still lower external pressures may thus partly be accounted for by the fact that an increasing volume of internal tissue is inadequately supplied.

In figure 1 an example of the response curve is given (Greenwood, 1969). Identical results have been obtained by others (Wiersum, unpubl.),

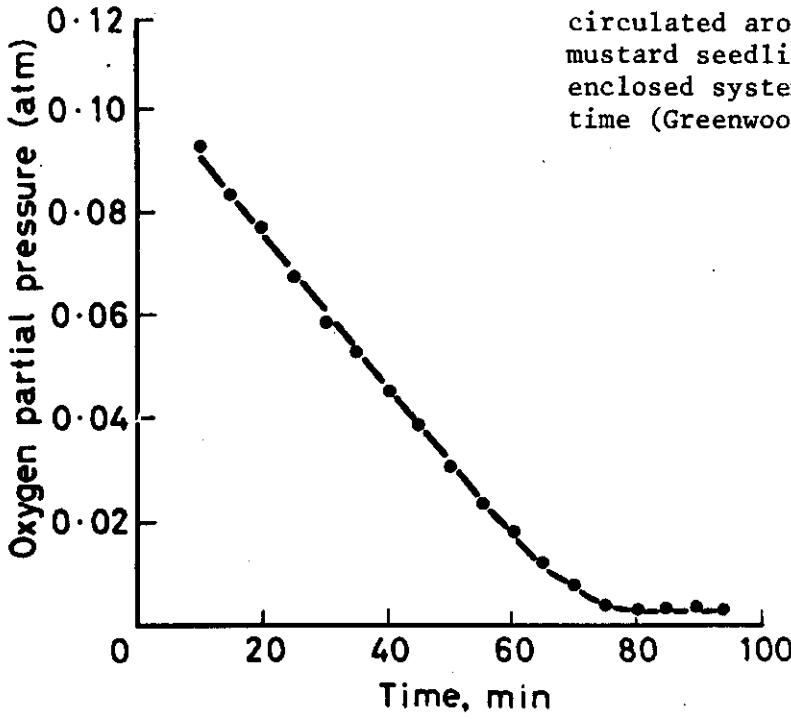


Fig. 1. Oxygen partial pressure in nutrient solution that had been rapidly circulated around excised roots of mustard seedlings in a gas-free enclosed system for the indicated time (Greenwood, 1969).

the decline usually starting at higher oxygen values because longer diffusion paths are involved (Schmucki, 1949). This longer diffusion path must partly be attributed to the stagnant film of water surrounding the root (Wiegand and Lemon, 1958).

From the forementioned facts we must conclude that by falling oxygen pressure from a certain state onward an increasing volume of root tissue is impaired in its function. At what stage and after what time such conditions become lethal to the root is difficult to say. There is evidence that root growth activity stops within a few minutes after withdrawal of oxygen, but if poor aeration does not last too long, growth will be continued as soon as conditions again improve (Rosene and Bartlett, 1950; Huck, 1970; Willey, 1970; Williamson, 1970). In a number of cases death of the roots has already occurred within 24 hours, but this may largely depend on the ambient temperature (Williamson and Splinter, 1968). It seems safe to put the limiting value of oxygen pressure required at the root surface at the value where total root function is still unimpaired. But it may be quite difficult to obtain the exact unequivocal value under all circumstances.

From an ecological point of view these limiting values in oxygen supply are an important soil parameter. The measured values encountered

in literature are within a rather wide range. Table 3 summarizes the data derived from a number of investigations.

Table 3. Some data on the oxygen and carbon dioxide concentration in the (soil) atmosphere at which reduction in growth has been observed

Crop plant	O_2 in percent of atmosphere	CO_2 in percent of atmosphere	Source
arable crops		5-20	Chapin 1902
grass	6-10		
wheat, oats	10-15		Kopecky 1914
barley	15-20		
sugar beets	15-20		
tomato		9.1	Erickson 1946
maize	1-10		Gill and Miller 1956
maize	5.25		Danielson and Russell 1957
	10		Tackett and Pearson 1964
barley	7		Geisler 1967a
peas	14		
tomato	3.5		Aubertin et al. 1968
tobacco	2.5	18.5	Williamson and Splinter 1968

This variation in limiting values may partly be related to the fact that not always the same response factor has been compared with the oxygen supply. One can conceive that it does make some difference whether death of the root, root growth or activity in uptake is used as criterion. There is some evidence, that indicates that the oxygen requirements both for growth and nutrient uptake are at the same level (Wiersum, 1967), while for a quiescent root it may be lower.

Although we have a fair picture of the relationship between root respiration and oxygen supply in some of their essential links, a

number of important data are still mostly lacking. In relation to defining limiting conditions for crop response one should be able to depict the oxygen consumption of the root system as it develops in time, taking into account the changes in age and activity of the tissues and aslo change in root thickness. Besides the scarcity of data in this field the situation is even worse if one considers the problem of defining the variation of oxygen consumption over different layers of the soil profile. As roots differ in age and activity the weight of root mass in a certain layer is no direct measure of its requirements for oxygen supply. It is still extremely difficult in linking tillage and drainage effects via parameters on soil physics with the root oxygen demand at different depths.

III. OXYGEN SUPPLY TO THE ROOTS

Roots can be supplied by oxygen along two distinct pathways. For most crop plants external supply from the soil atmosphere is the dominating aspect. But there is a gradual shift via a number of species to those plants adapted to swamp conditions, where internal oxygen supply through the intercellular spaces is normal.

The plant, depending on external oxygen supply to its roots, ultimately derives its oxygen from the air. This transport process from air to root can be strongly influenced by practical measures, relating to achieved alterations in soil structure and water content.

In well structured soils at a reasonable moisture content - a local pF of 2-3 - oxygen content in the soil air is mostly still higher than 15-18% at 1-2 meters depth. Carbon dioxide often does not rise above 2-4% under the same conditions. But much lower O_2-values have also been observed, especially as soil moisture content increases (Wiegand and Lemon, 1958; Lipps and Fox, 1964; Patrick et al., 1969; Enoch and Dasberg, 1971).

But as soil structure deteriorates and water content rises the relation between rate of diffusion and air-filled pore space becomes more intricate. Evidence points to the fact that in these circumstances a part of the air filled pore space lacks continuity. Ultimately this process of gaseous diffusion into the soil may be so strongly impeded that no oxygen can be detected at shallow depths (Currie, 1962; Grable, 1966).

Inversely with a decrease in oxygen the carbon dioxide content will rise. But a certain decrease in oxygen content does not necessarily imply the same percentage increase in carbon dioxide content, as its concentration is more highly buffered by the varying solubility in the water phase (Enoch and Dasberg, 1971).

Growth and performance of the roots is also restricted by high concentrations of carbon dioxide (Chapin, 1902; Cannon, 1924; Willey, 1970). But the effective concentrations have been demonstrated to be rather high. Also there is evidence that deleterious effects of carbon dioxide increase at lower oxygen concentration (Geisler, 1969). But as influx of oxygen and efflux of carbon dioxide are so intimately related, the discussion is mainly restricted to oxygen supply. The

more so as an inadequate oxygen supply is apt to occur before toxic carbon dioxide concentrations are encountered.

That this first step in oxygen supply can already influence crop performance has already clearly been illustrated in numerous publications. For various soils, differing in their structural characteristics, quite a range of limiting pore space has been found necessary to assure adequate aeration (table 4).

Table 4. Some data indicating the amount of air-filled pore space necessary on different soils to give adequate aeration (O_2-diffusion in gas phase)

Crop plant	Soil type	Air-filled pore volume in %	Source
tomato	clay	28	Flocker et al. 1959
	clay loam	36	
arable crops	sandy, low org. matter	ca. 25	Boekel 1963
	sandy, high org. matter	ca. 20	
arable crops	heavy clay	10-15	Boekel 1965/66
	sandy clay	15-20	
	sandy soil	20-25	

In the soil the root will always be covered by a thin film of water, the thickness of which is influenced by the moisture tension (pF) of the soil. As diffusion in water is slower by a factor 10^4 than diffusion in air, the thickness of this film becomes highly important in determining oxygen supply (Wiegand and Lemon, 1958). It is fortunate that we now have a method for measuring the potential rate of oxygen supply to the root surface by inserting a micro-electrode into the soil on which the conditions at the root surface are more or less simulated (Letey and Stolzy, 1964). By means of these Oxygen Diffusion Rate measurements it has become quite clear that in many soils at reasonable aeration conditions variations in moisture tension may be the dominating factor in regulating oxygen supply to the root. That a certain interaction has to be expected between

moisture content and soil structure is illustrated in figure 2.

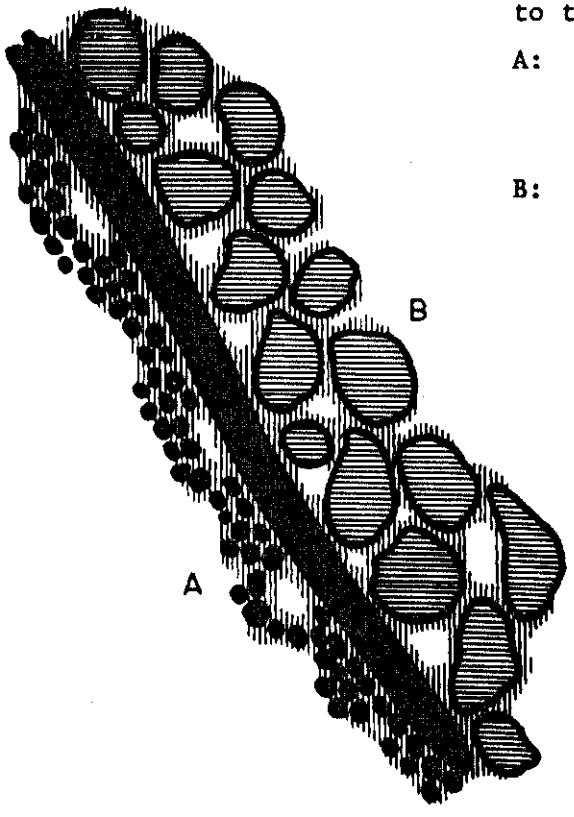


Fig. 2. Factors influencing oxygen supply to the root surface.

A: only a few air-filled pores near the root surface; long average diffusion distance in water.

B: frequent occurrence of air near the root surface.

The drawback of this O.D.R. measurement is, however, that unless additional measurements are made the obtained values only have relative significance and are only valid within one type of soil (McIntyre, 1966, 1971). But they may be of high importance in demonstrating the fluctuations that occur at a chosen site (Wiersum, unpublished results).

The method also allows the establishment of limiting O.D.R. values for root growth (table 5). That crops can differ in their requirements has now been confirmed by exact measurements.

In considering root aeration it must be taken into account that the living soil also consumes oxygen. Depending on type of soil, moisture content and temperature the requirements will vary. But the most important factor influencing soil oxygen demand will be its

Table 5. A summary of data on critical O.D.R.-values

Crop plant	O.D.R. in g $cm^{-2}min^{-1}$	Source
tomato	80×10^{-8}	Doyle, MacLean 1958
peas	$70\text{-}100 \times 10^{-8}$	Cline Erickson 1959
tomato	$18\text{-}23 \times 10^{-8}$	Stolzy et al. 1961
citrus	$24\text{-}33 \times 10^{-8}$	Stolzy et al. 1963
tomato	38×10^{-8}	Fulton, Erickson 1964
Newport bluegrass	$20\text{-}40 \times 10^{-8}$	Letey, Stolzy 1964
barley	40×10^{-8}	
corn	19×10^{-8}	
snap dragon	65×10^{-8}	Stolzy and Letey 1964
sunflower	40×10^{-8}	
tomato	40×10^{-8}	
tomato	15×10^{-8}	Aubertin et al. 1968

organic matter content, unless this happens to be mainly completely converted organic material (stable humus). Soil oxygen consumption can rise to values as high as 10 l O_2 $m^{-2}day^{-1}$. So the soil may consume as much oxygen as the crop root system and quite often even more (table 2).

Although research has now provided us with numerous data to link soil aeration with yield, it is still very difficult to handle this knowledge for practical purposes. What is ultimately required would be the procedure to translate the total oxygen requirement of soil + roots into a set of soil physical conditions so that diffusion could meet the demand. The further step then required would be the knowledge how to achieve these physical conditions by soil management practices. Bridging these gaps in our knowledge is still an important task.

Nevertheless our existing knowledge on limiting values can be very profitably utilized to detect shortcomings in the field and indicate the necessity for taking measures.

Besides the external supply all roots possess a certain capacity for internal longitudinal oxygen transport (Van Raalte, 1941; Greenwood, 1969). Plants genetically adapted to anaerobic soil

environment completely rely on this transport and possess the large intercellular spaces needed to facilitate the diffusion. Oxygen may even pass into the root surrounding soil layer (Van Raalte, 1941; Armstrong, 1967, 1970). But modern experiments have now clearly demonstrated that the conditions for internal lengthwise oxygen transport occur in all plants, albeit in varying degree.

For most crop plants the question arises whether this internal supply through the leaves downward has a worthwhile contribution (Greenwood, 1967). Evidence available points to the fact that this transport can only cope with the demand of a restricted length of young root tissue, e.g. 2-3 cm. As the young root tips are mostly at larger distances from the aerial parts of the plant and the relative volume of intercellular space declines as the older cortex sloughs off, its contribution to total consumption seems negligible for most cases (Eavis et al., 1971; Luxmoore and Stolzy, 1972). But the possibility does exist that some oxygen from better aerated layers in the soil moves downward through the intercellular spaces of the root tissue towards the young root parts occurring in poorly aerated layers.

A certain adaptation of root structure to poor aeration conditions has been observed, resulting in larger internal air space in the root. But this adaptation is only of value if it has developed from the beginning and would hardly have an effect if arising at the tip of a long, normally structured root. Another adaptation is the development of an internally better aerated and more superficial root system when parts of the deeper lying root system have suffered damage as the result of inadequate aeration.

Although swamp plants, such as rice, must obtain all their oxygen by means of internal transport, there may be situations during development of the plant when anatomical structures are not entirely adequate. This condition can effect performance of the crop (Alberda, 1953).

IV. EFFECTS OF RESTRICTED OXYGEN SUPPLY ON THE PHYSIOLOGY OF THE ROOTS

The complaint of Grable (1966) that few areas of scientific research are as unintelligible as the relationship between soil aeration and plant growth does not surprise us anymore after the demonstration of the complexity of the problem in the former chapters. A number of factors vary in relation to differring soil aeration: e.g. soil water content, porosity and density, nutrient availability, each of which can affect root performance on its own. Some of these factors are directly related to soil aeration as they are controlling oxygen transport in the soil. Poor aeration acts on restriction of water and nutrient supply indirectly by means of reduced root growth and by affecting root metabolism. Plant roots have to deal with all of them and frequently it is rather difficult to find the actually limiting factor in any prevailing situation. The variable results and even discrepancies found in literature already indicate that effects of soil aeration on root growth, root performance and root activities are mediated by a scala of physiological processes that will remain insufficiently understood as long as our experimental information is incomplete. We realize, therefore, that we can not present a final solution of the problem, but we will try to discuss a number of aspects that will facilitate an evaluation of experimental data.

One of the main aspects we have to face first is whether deficient gas exchange is restricted to short time periods or persistent for a longer time. This makes such a difference that a separate discussion is justified, if not essential.

Prolonged lack of aeration

In the life cycle germination of the seeds is the first step to be affected. During normal germination respiration rate increases with the water content. This would suggest that lack of aeration could easily become the limiting factor for germination. In vitro experiments with water soaked seeds, however, showed that aeration of the soaked seeds did not improve germination to any extent. Sometimes it even resulted in increased inhibition whereas bubbling carbondioxide through the soaking water appeared to be favourable. This whole phenomenon seems to be due to supraoptimal water contents

which tend to be increased by oxygen and decreased by carbondioxide. Hence for most of our crop plants very wet soils may be assumed to limit germination via the induction of supraoptimal water contents in the seeds (Barton and McNab, 1956; Allarup, 1959; Roberts, 1962) to which seeds with a high oil content are less susceptible (Vegis, 1964). The high water contents of soaked seeds are believed to perform a distinct barrier to oxygen diffusion to the germ since in some cases harmful effects can be depressed by aerating with high O_2 levels. Since the seeds are placed normally in the very top layer of the soil and seeding is postponed to the time a good seed bed is available reduction of germination is of minor importance in practical agriculture unless soil slaking occurs. Most of the effects of lack of aeration are appearing in the later phases and in particular during the vegetative phase.

After germination roots protruding in wet soils are encountering gradually decreasing oxygen and increasing carbondioxide levels. The rate of elongation then depends on the sensitivity of the species involved, on the actual levels of O_2 in the soil and on the supply of oxygen through the interconnected air channels in the shoot and the root tissues. When the aeration of the soil is insufficient but rather constant, the plants are forced to get adapted to this situation. Two main types of adaptation have been reported: adaptation via root anatomy and adaptation of root morphology, which are eventually supplementary. Tentatively a third type, metabolic adaptation, may be mentioned.

Anatomical adaptation

Many species naturally growing on poorly aerated media show large air channels in the cortex of their roots (Oryza, Phragmites). The meaning of these pores for the oxygen supply of the roots has been studied extensively. It has been demonstrated that these channels are able to conduct large amounts of oxygen from the atmosphere to the oxygen requiring sites of the roots, so that even the environment of the roots may obtain some oxygen via these channels when in a reduced state (Van Raalte, 1940; Greenwood, 1970). Armstrong (1964) measured in bog plants oxygen diffusion rates as large as 2×10^{-7} g

O_2 per minute and per cm^2 of root diameter. In genetically adapted species this transport seems to guarantee optimal growth rates of the roots. In species which are able to form secondary air channels in the cortex at low oxygen levels, the stimulus for the onset of cell destruction to form these voids is unsufficiently known but they are common in waterculture and moist soil. In any case maize roots which show this anatomical adaptation start growing in well aerated media. The lysigenous cavaties in the former may occupy from 30 to 45% of the root diameter but they are restricted to basal parts not closer than 2 or 2.5 cm to the root apex. Nevertheless they are providing the growing zone with sufficient oxygen. Obviously normal intercellular spaces up to 1 or 1.5% of the root diameter are sufficient to bridge a 2 to 2.5 cm distance (see also Greenwood, 1969). It is, however, equally clear that this adaptation has its limitations. Even with these lysigenous channels growth rates get reduced after reaching a length of about 20 cm. This length is not a fixed value since it depends on the oxygen requirement. In our case 20 cm holds when the roots are well supplied with nitrogen and when they are kept at 20-25°C. Without nitrogen nutrition growth inhibition starts at 40-50 cm. The same holds for well-supplied roots when the temperature is lowered to 15°C, indicating that the potential oxygen consumption rate determined by the metabolic activity, is involved in the response. Several authors have shown that the oxygen originates from the shoot environment (Teal and Kanwisher, 1961; Armstrong, 1967) and Van der Heide and coworkers (1969) demonstrated that the effect of insufficient root aeration was much more severe when the shoot environment was O_2-free, especially in darkness. In the light roots profited from oxygen produced in photosynthesis. In principle air entering the basal parts of a root system would also be able to provide deeper roots with oxygen. Whether this is important under normal conditions is unknown, but favourable effects of leaving part of a root system above the nutrient solution as reported by Went (1947) may indicate a possible role.

Summarizing we may state that how important this type of adaptation may be, in practice it only prevents an early check of root elongation and in addition it is only effective as long as the cortex stays intact.

An additional problem arises with regard to the air supply to branch roots.

Morphological adaptation

Not all species are developing secondary air spaces and even with these spaces ultimately elongation rates of the root axes are reduced without proper external oxygen supply. The reduced elongation rate may be assumed to lead to a diminished apical dominance which in turn means that secondary axes get more chances. Whether this is the only reason or not, it is a well established fact that insufficient oxygen supply leads to an increased growth of early primary branches, to an increased number of branches per cm of axis and often to an increased number of adventitious axes on the stem base (Williams and Barber, 1961; Vose, 1962; Geisler, 1965). Some authors believe that the development of the latter is promoted as a consequence of the reduced cytokinin production by the poorly aerated roots (vide Reid, 1973). Stienstra and Brouwer ( ) observed increasing numbers of nodal axes per tiller in perennial ryegrass with higher soil water tables (figure 3). Plants profit from their tendency to raise adventitious roots since this adaptation leads to an escape from a situation of very poor aeration and a compensatory development of

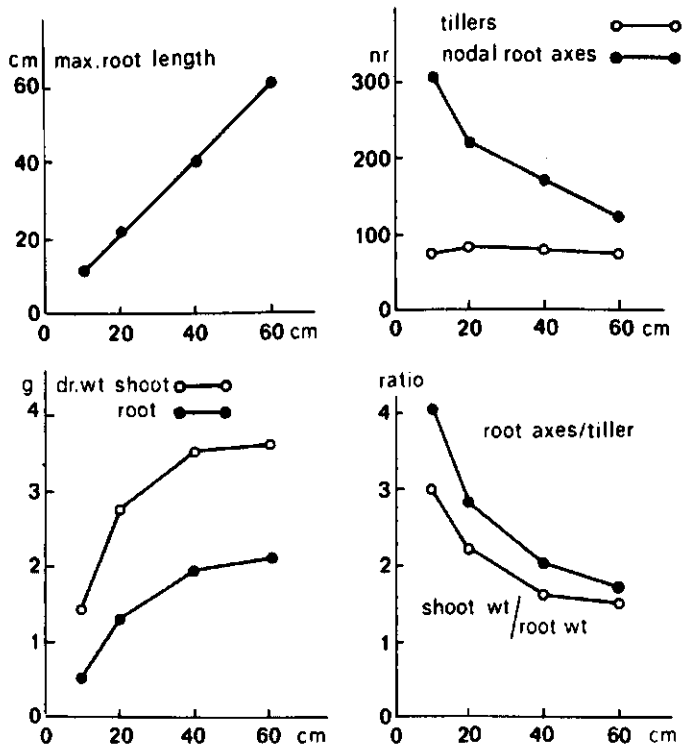


Fig. 3. Effect of soil water table (0-60 cm below surface) on various aspects of growth of perennial ryegrass plants.

roots where the stress is less severe (Alberda, 1956). Although the situation is still suboptimal for absorption the greater number of active root tips per gram of root weight compensates, sometimes more than compensates, for this (Vose, 1962).

Metabolic adaptation

Hence both types of adaptation, whether or not appearing together, are quite effective in maintaining a high level of absorption capacity under unfavourable conditions (table 6).

Table 6. Root exudation at the cut surface in mg per gram fresh weight per hour of excised root systems as affected by aeration at 25°C.

	Treatment	
Pretreatment: plus aeration	+	- aeration
maize	112	8
cucumber	159	11
tomato	104	35
barley	101	22
Pretreatment: minus aeration		
maize	108	106
cucumber	167	171
tomato	154	158
barley	93	89

It is, however, quite questionable whether these anatomical and morphological features alone are sufficient explanation. Van der Heide a.o. (1963) showed that barley roots grown in poorly aerated nutrient solutions contained a higher concentration of soluble carbohydrates which in turn, they believed, should explain the high chloride absorption rates found in their experiments. Furthermore, it is quite clear that this is only one of the biochemical changes that are evoked by anoxia. Reid (1973) lists a number of them but the meaning of these factors for root activity remains obscure for the time being. In addition the large number of papers devoted to abnormal metabolic pathways induced by lack of aeration seems to indicate that these play a more important role when conditions of poor aeration follow periods of favourable gas exchange and will be

considered in the next section.

Adapted root systems - either due to the presence of large air filled lacunae, or to an abundant branching in the marginally aerated top soil, or to adaptation of metabolic pathways - are functioning very well.

Reduced oxygen supply after periods of normal aeration

All data from the literature indicate most harmful effects when formerly well-aerated roots are suddenly deprived of oxygen. In waterculture elongation of maize roots stops directly after aeration is stopped (figure 4). Most likely lack of oxygen is the primary

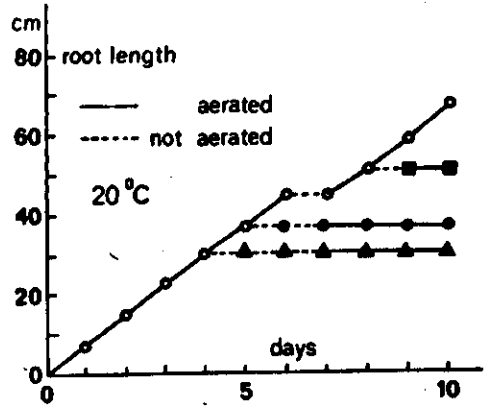


Fig. 4. Stopping aeration of formerly well-aerated roots inhibits root growth. Reversibility depends on the duration of the period without aeration.

reason of this growth reduction, the first signs of which can be already induced by changing the oxygen content of the aerating gas from 20% to 10%. When normal aeration is restored, it depends on various circumstances whether elongation growth will again continue or not. Most of them can be reduced to the same denominator: oxygen requirement. At lower temperatures roots can stand longer periods of anoxia than at higher temperatures, dormant roots longer than actively living roots, woody roots longer than N-rich roots and roots deprived of carbohydrates (ringed plants, defoliated plants) longer than roots with a high content of carbohydrates.

High levels of carbondioxide are only harmful when at the same time the oxygen concentration is reduced. Since in the soil CO_2-levels always rise together with a reduction of the O_2-availability it is difficult to discern which of these two acts as the causal factor.

In addition a number of other factors may be involved which are induced at the same time.

Since the importance of O_2 rests on its role as the final electron acceptor in respiration, oxygen limitation induces fermentation to go on in the root tissue (Pasteur effect). According to Goddard and Bonner (1960) the critical O_2-range for a gradual change from oxidative respiration to fermentation may be as high as 5% O_2. When fermentation occurs the endproducts may reach harmful concentrations. Kenefick (1962) found high ethanol concentrations in leaves of flooded sugar beets whereas Fulton and Erickson (1964) observed the same phenomenon to occur in the xylemsap of flooded tomato plants.

In addition to changes in the metabolism of plant roots at various levels of aeration soil micro-organisms may contribute to the accumulation of special constituents (Dubinina, 1962). The well-known anaerobic methane production is only one of a series, methane, ethane, propane and butane, but also unsaturated hydrocarbons as ethylene, propylene and butene have been demonstrated. From all these compounds only ethylene is affecting root growth at concentrations measured in poorly aerated soils (Smith a.o., 1969; Crossett a.o., 1971; Dowdell a.o., 1972). These papers experimentally confirm earlier suggestions made by Kramer (1951) and Jackson (1956) that visible effects of waterlogging on tomato plants (epinasty) very much resemble effects of exposure to ethylene. Also the roots themselves show an enhanced production of ethylene when under aeration stress. Hence ethylene appears as a third factor besides oxygen deficiency and high carbondioxide concentrations, that could act as a primary factor in root response to anoxia. Species differences in susceptibility are of the same order as those found for the other items. Most likely all three are involved.

Whereas the adapted root system even under very deficient gas exchange shows absorption rates for water and minerals which are mostly comparable and sometimes exceeding those of normally aerated roots when calculated on a weight basis, reduced aeration affects both processes quite considerably when occurring after a period of normal supply. The most harmful effects of flooding have been described frequently (reviews by Kramer, 1969; Grable, 1964). When

the aeration of maize roots is stopped at once both elongation growth (figure 4) and absorption of potassium, nitrate and phosphorus are reduced to about zero values (figure 5) whereas water absorption may continue at about the same rate. Using bean plants water absorption rates are reduced too. The check of elongation and mineral absorption

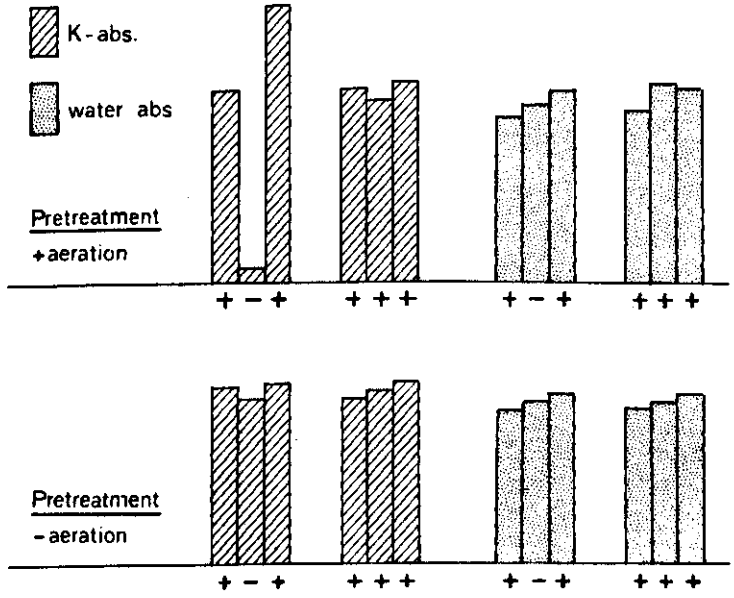


Fig. 5. Effect of alternating 24 hrs periods of plus and minus aeration on potassium and water absorption by maize roots formerly grown plus or minus aeration.

is conceivable with our knowledge that both processes are directly dependent on the energy production involving ATP formation (Brouwer, 1965; Grable, 1964). Since the energy liberated from 1 mole of glucose is more than 10 times higher in aerobic respiration than in fermentation (686 vs 54 k cal. per mole) some authors suggest (vide Grable, 1964) that plants may suffer from lack of energy when not aerated. However, this can not be the primary reason since it has been shown that under these conditions reserve carbohydrates are accumulated to levels well above those of the control plants (Brouwer, 1963; Van der Heide a.o., 1965) even in the unaerated roots themselves. The almost instantaneous response (figure 4) demonstrates either the failure to make use of the fermentation process or a very high sensitivity to the end

products of fermentation. However, the transport of carbohydrates to the root system does not respond immediately, although the distribution does. Instead of flowing directly to the growing apices as occurs with sufficient aeration, after a reduction of the O_2-supply carbohydrates are deposited more equally spread over the whole root system which results in locally higher levels (figure 6). Nevertheless mineral absorption was checked.

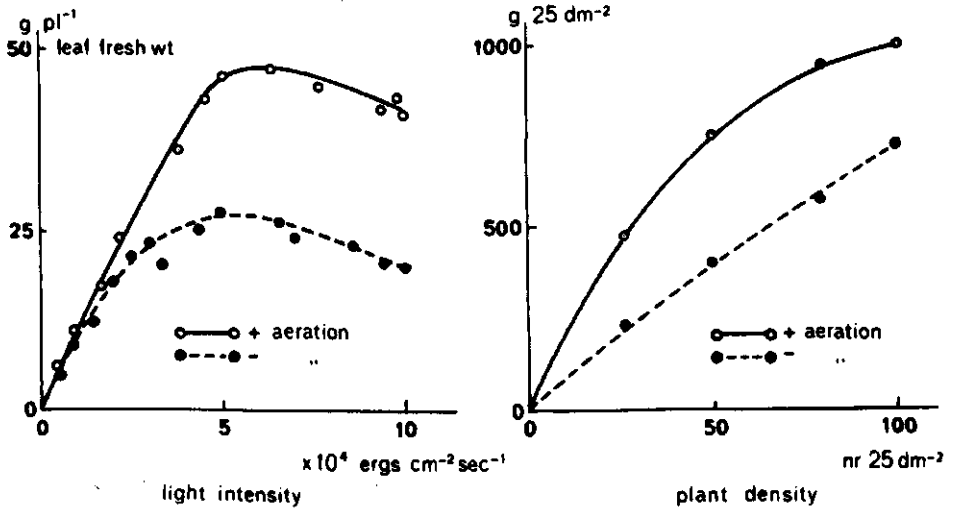


Fig. 6. Effect of light intensity (left) and planting density (right) on the response of *Phaseolus* beans to aeration.

Unlike mineral absorption water absorption - apart from root pressure phenomena which contribute only a few percent in total water uptake - does not directly depend on the energy supply. The forces involved in water transport originate from the transpiration process. The root system acts simply as a conductor (Kramer, 1949) for water. Lack of oxygen does not affect conductivity instantaneously. From the similarity with the response to metabolic inhibitors like KCN, which reduces mineral absorption immediately at concentrations of about 10^{-5} M (Brouwer, 1953) but water absorption only after about 3 hours and then at much higher concentrations (10^{-3} M) one may assume that membrane structures are not much affected by oxygen deficiency during short periods. Contrary CO_2 accumulation affects water conductivity of the living tissue more directly. The response is rather complicated.

At first water conductivity decreases resulting in a reduced transpiration. Then the root tissue is gradually damaged untill death occurs which increases water conductivity and transpiration to values well above those of the control plants. Finally decay products and bacteria will block the xylem vessels and drastically reduce water absorption in flooded soil regions. Kramer (1951) and Jackson (1955) showed that pressing nitrogen gas through the soil prevented these effects on water conductivity which indicates that the main reason is an accumulation of toxic substances presumably carbondioxide.

In addition to mineral and water absorption the production of phytohormones like cytokinins represents another major function of the root system (Livne and Vaadia, 1972). These authors suggest that poor aeration like other stress conditions might also affect cytokinin production. In most cases this production is correlated with root growth and especially with cell multiplication rates. Reduced cytokinin production will lead to symptoms of early senescence as has been found frequently. On the other hand IAA oxidase activity may be restricted just by lack of oxygen or due to the accumulation of a phenolic inhibitor of IAA oxidase (Kefford, 1962). In addition ethylene originating from the root tissue itself or from activities of soil micro-organisms may interfere with various auxin controlled processes. A more detailed review of the effects of anoxic conditions on the metabolism of hormones can be found elsewhere in this series (Reid, 1973).

In addition to hormone synthesis roots are involved in the synthesis of various other organic substances among which amino acids are well-known. The energy consuming nitrate reduction is for a minor part (grasses) or completely (apples) with numerous transitions in between boudn to the root system (Kursanow, 1963). There is, however, rather scarce information on the effects of aeration on this activity.

V. ROOT AERATION AND CROP GROWTH

After we have seen the consequences of insufficient gas exchange on root activities we will consider in what respect roots may fail to supply the shoots optimally with essentials for their growth, performance and maintenance. One possible reason for the discrepancies found in the literature may be that shoot requirement is not constant, but depends on the other prevailing conditions and on growth stage. Hence the effect of suboptimal root activity will depend on various factors, a number of which will be discussed below. To find out what effect of soil aeration might be expected we need a clear picture of the limiting factor of growth in that particular situation. Therefore we have to consider first of all shortly some main principles of crop growth.

Arable crops are sown rather densely so that during vegetative development land surface is gradually covered and some time before flowering or tuberization practically all light is intercepted. Further leaf growth does not contribute to more light interception. It only serves a gradual replacement of ageing leaves so far as light interception is concerned. Dry matter production starts more or less exponential as long as new leaves contribute to more light absorption, but becomes more or less linear after reaching the closed crop stage. The slope of the linear part of the curve depends on the prevailing light climate and on the photosynthetic capacity of the species which shows only minor differences (Sibma, 1968). During seed, tuber, or bulb, development leaf growth is mostly checked or strongly reduced and soon, especially in determinate crops, leaves start senescing and leaf area decreases gradually. Crop growth rate diminishes concomitantly. Root growth gets reduced soon after reaching a closed crop surface and is often checked completely during the generative phase (Brouwer, 1962). This check of root growth accompanied by a check of synthetic capacity (Hofstra, 1964; Kende, 1965) may be the direct reason for accelerated senescence after flowering.

The general picture of crop growth presented above is subject to changes in any period, and rather sensitive during the exponential phase, where leaf growth contributes most strongly to an increase in light interception. Any growth reduction postpones the time of

reaching complete light interception and maximum crop growth rate. In the linear phase (closed crop surface) only those factors are harmful which are reducing photosynthetic capacity. Watson (1952) showed that most factors are much more effective in reducing leaf area growth than in reducing photosynthesis per unit leaf area. Finally during ripening, factors which hasten senescence will lead to an earlier check of crop growth.

In conclusion we are now aware that during development of a crop from planting to ripening we are facing quite different situations even when the environment would be constant, which is by no means the case in most of our situations in practice. The support given to the above ground parts by the roots may be roughly distinguished in the supply of water and nutrients and in the supply of essential synthetic products, among which hormones play an important role. In the complex relationship between roots and shoots the relative importance of the synthesis and absorption function of the roots depends on the requirements of the shoots. Since these requirements are changing all the time during the development of a crop, it is comprehensible that a uniform response to O_2-deficiency is not likely to exist and this is one of the most obvious conclusions in reviews in the literature on soil aeration.

Germination

In germination oxygen consuming biochemical processes are limiting the rate of supply to the developing seedling with essentials for its growth. Low oxygen tensions are harmful especially when the other conditions as temperature and water supply are favourable. The anaerobic breakdown of substrate easily gives rise to accumulation of toxic endproducts of fermentation, which in turn damages the vigour of the seedling irreversibly. Here again low temperature tends to reduce the damage. Oxygen deficiency is most likely the primary cause since excess of carbondioxide has been shown in many cases to stimulate germination by increasing the permeability of the seed coat.

For further development of the seedling soil aeration primarily affects root growth and root activity, but via these also shoot

development. Since in the former chapter principal differences between a fluctuating situation and constant oxygen deficiency are discussed, we will use the same subdivision in describing the effects on shoot growth.

Vegetative development

Steady situation

Vegetative development is characterized by a rapid increase in absorbing surface of both leaves and roots. Leaf area and root surface are kept in pace with one another by a kind of functional equilibrium (Brouwer, 1967). Leaf growth rate cannot exceed the possibilities created by the absorption of nutrients and the synthetic activity of the roots, whereas root growth rate depends on the availability of carbohydrates and possibly also on hormones produced in the above ground parts. Serious competition between leaves and roots, with the consequence of a shift in the equilibrium, may be expected when the supply of one of the essentials for growth becomes limiting. So water shortage tends to reduce the growth of the whole seedling, but leaf growth is more affected than root growth. The same holds for nitrogen deficiency. On the contrary low light intensities tend to reduce the growth of the whole seedling, but root growth more than leaf growth. This means that with shortage of essentials to be absorbed by the roots the relative growth rates of the roots, being closer to the source, are less affected than the relative growth rates of the shoots, as they depend on what the roots do not use. When a deficiency of essentials which are produced in the shoots, occurs the relative growth rate of the shoot is less affected than that of the more distant roots. Since these ratios are based on weights, instead of on more sophisticated activity ratios, the picture gets more complicated when at the same time morphological changes are induced. All those factors that are increasing the absorption rate of the roots, e.g. finer branching, tend to increase shoot : root - ratios. Factors that reduce the water loss per gram of leaves e.g. by induction of thicker leaves, will also tend to increase the shoot : root - ratio on a weight basis, under conditions of other factors remaining the same.

We have seen that soil aeration primarily affects the extension growth of the roots. This effect may be rather considerable and might reduce the absorption rate considerably. Hence top growth will be reduced too. The effect is counteracted, however, by intensified branching leading to a greater number of absorption zones per gram. Whether these changes will affect top growth depends on the ultimately resulting absorption capacity which may be smaller, the same or even greater than that of the controls. Brouwer (1960) with bean seedlings on water culture and Troughton (1972) with perennial ryegrass found reduced relative growth rates of the tops when not aerated. In both cases the shoot : root - ratios were not affected. Obviously the root activity per gram of roots was the same so that shoot growth simply followed the reduced root growth. With maize we obtained a reduction of root growth under the same circumstances. As shoot growth was comparable with that of the aerated controls, a higher absorption per gram of roots under constant low oxygen supply must have occurred. Finally Vose (1962) found that lack of aeration resulted in a reduced root weight and an increased shoot weight with cocksfoot on water culture. Obviously the finer branching of the not aerated roots resulted in a greater absorption capacity even in the oxygen deficient medium. Since in addition the reduced rate of increase in weight of the unaerated roots made them less competitive for the carbohydrates produced in the shoots, shoot growth favoured from that situation but could only do so because light intensity was obviously limiting.

Using a series of light intensities we found (Brouwer, 1960) that the effect of oxygen deficiency of the root medium was more severe the higher the light intensity (figure 6). It is conceivable that this fits with the assumption that the water balance is involved in this reaction. Evidence for this is strengthened by the observation of a distinct diurnal pattern in leaf elongation rate being strongly reduced during the light period and showing only minor or no reduction during the nights.

In agreement with this picture the effect of no aeration on bean growth appeared to depend on plant density (figure 6). At low light intensity and/or dense planting the demand for water per root system

decreases and instead of aeration light absorption becomes the limiting factor. The higher the light intensity the larger the water stress developed in unaerated plants. Mineral content of these bean plants was not affected at all. In terms of dynamics of growth this means that in freely growing plants relative growth rates of the root weight are reduced due to lack of aeration, that relative growth rate of root number and root surface is much less reduced and that notwithstanding the relatively greater surface of the latter per gramme of weight the absorption capacity of the whole root system is still inhibited so that a reduced relative growth rate of the shoot results (Troughton, 1972).

At low light intensities and higher planting densities dry matter distribution in the control plants shows a reduced percentage deposited in the roots (Brouwer, 1962). This reduction may be so large that the availability of carbohydrates becomes more limiting for root growth than the oxygen supply. As a consequence root growth of unaerated plants will be similar to that of the aerated plants. The absorptive capacity may still be lower but its effect on leaf growth may be negligible since ultimately carbohydrate supply is limiting and the only difference between the two sets remains the growth pattern during a 24 hour cycle where the leaves of the unaerated plants grow predominantly during the dark period and those of the aerated plants during the light, growth being retarded during the night due to lack of carbohydrates in the latter.

Transferred to field conditions this means that in cases where the finer branching will not completely substitute for the lower weights the effect of poor aeration will be most harmful in the early stages. When crop growth rate of the control plants gradually reaches its maximum level (closed crop surface) the unaerated plants still stay behind but from the time the latter reach the stage of a closed crop both are growing at the same rate unless differences in photosynthetic capacity are occurring. We will return to that aspect later on.

The response to lack of aeration in nutrient solutions appeared to be caused primarily via the water balance of the plants. In water culture minerals are liberately supplied. Under field conditions

such a situation can hardly be expected. The restricted soil volume available for root growth excludes a lot of ions available under well-aerated conditions from being reached by the extending roots. This holds especially for the soil-bound nutrients like potassium and phosphate. The performance of plants on compacted transportation tracks in crop fields learns that we are dealing with mineral deficiencies in these cases. Hammond a.o. (1956) observed a very reduced root growth accompanied by a reduced shoot development in badly aerated parts of a cornfield. In their case the effect on shoot growth could be prevented completely by an extra potassium fertilization. The root system remained restricted to a rather superficial soil layer but appeared to be able to absorb sufficient potassium for normal crop growth if supplied at proper concentrations. Using various depths of the water table Sieben (1963) demonstrated with a number of crops that a reduction of the available soil volume resulted in a reduced growth of both roots and shoots. In his case additional nitrogen fertilization (figure 7) resulted in a normal crop performance with equal seed yields although root weight was still reduced. Without the extra fertilization a normal closed crop surface was not obtained and we found a very close correlation between light interception by the crop just before heading and final yield indicating that the effect on leaf area development governed the response to poor aeration and that net assimilation rate was not affected.

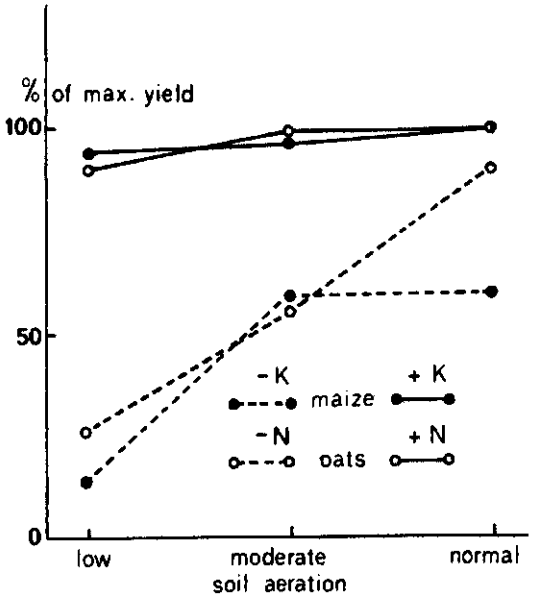


Fig. 7. Effect of various levels of soil aeration on yield. Extra potassium prevents this effect in maize (from Hammond a.o., 1956) whereas extra N did the same in an experiment with oats (Sieben, 1963).

(dotted lines = without extra fertilization; full drawn lines = with extra fertilization)

The results mentioned above demonstrate that soil aeration may restrict root growth but that it does not affect too much the absorptive capacity for minerals per unit weight. If the mineral supply appears to be the limiting factor a supply in higher concentrations will prevent effects on yield.

Finally we will mention results of Goedewaagen (1955) who got top yields of various crops on a very shallowly aerated mud of a virgin Dutch polder soil.

Fluctuating situations

We have already indicated that roots grown under conditions of sufficient aeration are very susceptible for oxygen deficiency. Growth and absorption are checked completely as well as synthetic activities. It is conceivable that the effect on shoot performance will be serious too. Kramer (1951) demonstrated a strong reduction of the water absorbing capacity of tobacco roots after flooding resulting in wilting of the plants. Prolonged lack of aeration caused the roots to die, made them more permeable for water and plants got turgid again. Later on secondary products were assumed to block the xylem vessels and plants wilted irreversibly. In such serious cases the only possibility for plants to survive appears initiation of adventitious roots at the stem base. Since this process takes some time crop growth reductions will be serious. In most cases, however, periods of bad aeration will be shorter. The harm done will depend on the time and the temperature. At higher temperatures shorter periods of lack of aeration are permissible before irreversible effects are obtained than at lower temperatures. The direct response at low temperatures is less severe too.

In most cases fluctuations of the ground water table are affecting only part of the root system, which part in principle reacts as described above. Whether the growth rate of the above ground parts will be affected depends on the percentage of roots damaged. When during the phase of rapid vegetative development a rather sharp shoot - root equilibrium exists any root damage will affect shoot growth too, directly by influencing the water status of the plants. Prolonged treatments interfere with the mineral status.

Fortunately plants are quite able to shift growth activity from one part of the root system to another. The distribution of root growth over various regions of the soil is mainly determined by local differences in external conditions since as a whole carbohydrate supply to the roots will be the main limiting factor. The most successful in attracting carbohydrates are those parts of the root system, which meet the most favourable complex of external conditions. Root accumulation around fertilizer bands demonstrates this very clearly. With varying depth of water table there will be a certain depth for each case, where an optimal condition of both air and water content in combination will exist. Under conditions of equal fertility throughout root growth will be favoured at this depth as in higher levels water supply will become sub-optimal and downwards the aeration. El Nadi, Locher and Brouwer (1969) showed that by varying the water supply including the reverse effect on the air supply, root growth could be shifted at will from one layer to another. Disturbing growth in one part of the soil by reducing the gas exchange immediately results in compensatory growth somewhere else. This means that moderate shifts in the water table will not affect shoot growth too much during periods when roots are able to grow. In this respect the typical differences between shoots and roots may be emphasized. Possibly as a consequence of the greater number of dormant or inhibited primordia roots are responding more readily than shoots do. Even adventitious roots at the stem base develop in a few days and the ability to do so is considered by various authors as an important contribution to survive flooding.

So far most attention has been payed to the effects on water and mineral absorption. In addition the other aspects, reduced hormone supply and production of toxic substances have to be mentioned. The effects of water and mineral absorption on development of leaf area and on growth during the vegetative stage are sufficiently described in monographs on these topics (Kramer, 1969; Slatyer, 1969; Mengel, 1968; Epstein, 1970), so that that part of the influence of lack of aeration is selfevident. Although everyone is aware of the essential role of hormones in plant life they do not seem to be limiting growth very often in agricultural practice. An enhanced auxin level may be responsible for the induction of adventitious roots at the stem base of flooded plants and Burrows and Carr (1969)

and Railton and Reid (1973) have demonstrated that flooded roots are delivering less cytokinin-like substances to the shoots. However, application of hormones individually or in combination fails to reduce the differences in growth resulting from flooding (Brouwer and Kleinendorst, 1967). The only effect that is reproducible is preventing the leaves of flooded plants from accelerated senescence. Flooded plants behave like nitrogen deficient and water stressed plants (Mothes a.o. 1956).

Generative stage

From the above it may be concluded that by morphological and physiological adaptations to constant lack of aeration and by adaptations of the growth pattern of the root system in fluctuating situations plants are able to alleviate the dramatic effects of poor aeration expected from physiological experiments. This only holds, however, for growth stages during which plants are able to shift to other patterns of root initiation and root growth. During the life cycle this ability is reduced in determinate plants the closer the plants approach the flowering, tuber- or bulb-forming stage with particularly sensitive periods during blooming and fruit setting. In perennials the same holds for periods of diminished tendency of root growth. At these stages plants are also very susceptible to drought injury for the same reason (Salter and Goode, 1967; Robelin, 1967).

It is likely (Livne and Vaadia, 1972) that even under favourable soil conditions senescence incident after flowering (Leopold, 1964) is mainly due to a reduced production of cytokinins by the root system the growth of which is checked or strongly reduced at that time. Since yield depends on the duration of green leaf area after fruit setting and this duration depends on cytokinin transport from the roots to the shoots any measure that favours cytokinin production like nitrogen supply will tend to increase yield whereas any measure that suppresses cytokinin supply like oxygen deficiency will reduce yield.

In this corollary we assume that aeration does not affect the photosynthetic activity of the leaves. From literature (Watson, 1952)

it may be concluded that most factors varied in agricultural practice are effective in determining yields predominantly by their effects on leaf area development and to a much smaller degree through their effects on net assimilation rate. This holds also for aeration although at treatments where the water balance is involved stomatal closure will reduce photosynthesis too (Troughton, 1972).

Severe nitrogen deficiency caused by lack of aeration reduces photosynthesis due to increased mesophyllresistance but the reduction in dry matter production as a consequence of a reduction in leaf area duration is more important.

VI. ADDENDUM

Soil aeration measurement

Soil aeration is the condition in the soil which is the result of its local content of oxygen, carbon dioxide and of compounds whose existence depends on the redox potential. As oxygen activity in the soil is highly correlated with redox potential, we will not pay much attention to the many toxic products that may arise in reducing conditions. A well-aerated soil has conditions which allow oxygen to enter the soil and spread through it at a rate high enough to cope with oxygen demands of roots and micro-organisms throughout the volume under consideration. If this is the case the efflux of the arising carbon dioxide will also be guaranteed.

To measure soil aeration status a choice must be made as to which parameter is to be used.

The soil consists of a mixture of three phases, two of them containing free oxygen. Thus the option exists to choose between measuring the composition of the gas phase or the conditions in the water phase.

In most older research and in much recent work attention is focussed on measuring the composition of the gas phase (Gieseke, 1930; Grable, 1966). For most of the relevant components, i.e. oxygen, carbon dioxide, hydrogen sulphide, ammonium, methane and ethylene, adequate methods were available. Measurements in the water phase have had to cope with the difficulty of obtaining unaltered samples of soil solution, till devices to measure conditions in situ became available. The situation in the soil

solution can now be characterised by a measurement of the potential supply rate of oxygen to a consuming centre (Lemon and Erickson, 1952), the redox potential (Grable and Siemer, 1968) or by analysing for products arising under reducing conditions or as a result of anaerobiosis.

In measuring the composition of the soil atmosphere one has to obtain a sample or to possess a measuring device which can be inserted. Obtaining a sample can be achieved by inserting wells or diffusion chambers into the soil in which the gaseous contents will equilibrate with those in the soil around. Samples can then be withdrawn and analysed by chemical means or by utilizing gas chromatography (Vilain, 1963) or an oxygen sensor (electrode). Another way is to carefully withdraw a small sample of soil air by suction through a narrow tube and analyse it (Patrick et al., 1969). Since recently small and very stable oxygen electrodes have become available, it has also become feasible to insert a probe containing an electrode directly into the soil and so measure oxygen content of the soil air in situ. Instead of analysing for oxygen, the amount of other components has been determined in the samples, most often carbondioxide.

The conditions in the soil solution with respect to aeration can be measured by two methods. By means of a redox potential measurement with a platinum electrode, information is obtained which is related to aeration status, but is not always directly and closely correlated with it. More recently a far more convenient and fast method has been developed (Lemon and Erickson, 1952; Poel, 1960; Danfors, 1962; Oden, 1962) in which the oxygen diffusion rate (O.D.R.) is measured. In this method the conditions around the inserted small platinum or gold electrode resemble those of the root. Thus this method gives an indication of the potential oxygen supply rate. This supply rate is dependent both on the local oxygen concentration in the gas phase and on its diffusion through the mixed solid particles-measure electrodes are used and care is taken to regulate the effective applied voltage, the method can only give relative values (McIntyre, 1966). But with certain restrictions these relative values can yield important information and correspond with other phenomena (Greenwood and Goodman, 1967; Wiersum, 1971).

The essential drawback of redox measurements or the determination of special constituents, especially toxic ones, of the soil solution is often the delay in formation and accumulation or removal following worsened or improved aeration conditions.

Parameters affecting soil aeration

In selecting the type of measurement to employ in the determination of the soil aeration status, the parameters affecting the measurement have to be considered. If information is wanted on the influence of altering a certain condition in the soil, one could expect that the measurement directly affected by this parameter is the most adequate.

Composition of the soil air is the result of a balance between replenishment and consumption or removal (efflux) of its constituents. To some extent the transport of the gases may occur by mass-flow related to pressure changes, but generally diffusion is more important (Grable, 1966; Currie, 1962). Both phenomena are sensitive to the pathway available, i.e. to the amount of continuous air-filled pore space (Franken, 1969). Total pore space, certainly within one type of soil, is inversely related to bulk density. But the distribution of pore space over pores of different diameter is more strongly correlated with soil texture and aggregation. To some extent visual assessment of soil structure has also shown to be correlated with aeration and crop performance (Peerlkamp, 1959).

Part of the total pore space is filled with a variable amount of water. As a consequence water content or soil moisture tension is a highly important factor. High water contents invariably restrict diffusion, partly by diminishing the pathway for gaseous diffusion and mainly by increasing the distance to be traversed in the water phase.

Another important parameter influencing the composition of the soil atmosphere is its temperature. First of all temperature has a direct effect on the diffusion constant, but it may be much more important in affecting consumption. Biological activity in the soil is highly sensitive to temperature - a Q_{10} of 2 or more is no exception - and thus consumption of oxygen or production of carbon dioxide can show large variations. Restricted diffusive capacity will

be more deleterious as temperature rises.

The situation in the soil water phase at the root surface will be governed by the conditions prevailing in the local soil air and the resistance involved in diffusion through the water film. As diffusion in solution is slower than that in air by a factor of ca. 10.000, the length of the pathway through the water film assumes an enormous importance. O.D.R.-values are highly sensitive to soil moisture tension, but on account of the intricate and variable structure of the boundary layer of solid soil particles, capillaries and water films no direct relationship with water tension and theoretically calculated water film thickness exists (see figure 2) (Kristensen and Lemon, 1964).

Although a measurement of O.D.R. constitutes an integration over all influences involved in oxygen supply to the electrode surface, which to quite an extent resembles root surface, it is far more sensitive to the situation in this boundary layer than to effects occurring during transport in the gas phase.

LITERATURE

Alberda, Th.: Plant and Soil 5, 1-28 (1953)

----------: In: De Plantenwortel in de landbouw (The Hague), pp. 98-106 (1955)

Allarup, S.: Phys. Plant. 12, 118-123 (1959)

Armstrong, W.: Nature 204, 801-802 (1964)

----------: Phys. Plant. 20, 540-553 (1967)

----------: Phys. Plant. 23, 623-630 (1970)

Aubertin, G.M., Richman, R.W. and Letey, J.: Agron. J. 60, 345-349 (1968)

Barber, S.A.: Agron. J. 63, 724-726 (1971)

Barton, L.V. and McNab, J.: Contr. Boyce Thompson Inst. 18, 339-356 (1956)

Berry, L.J. and Norris, W.E.: Biochim. Biophys. Acta 3, 593-606 (1949)

Boekel, P.: Neth. J. Agric. Sci. 11, 120-127 (1963)

----------: Bodem no. '65/'66, 2-9

Brouwer, R.: Verh. Kon. Ned. Ak. Wet. Amsterdam C-56, 129-138 (1953)

----------: Jaarboek I.B.S. Wageningen 1960, 11-21

----------: Neth. J. Agric. Sci. 10, 399-408 (1962)

----------: Jaarboek I.B.S. Wageningen 1963, 11-30

----------: Proc. 12th Easter School Agric. Scie. Univ. Nottingham, 153-166 (1965)

----------: Angewandte Botanik 41, 244-254 (1967)

Brown, N.J., Fountaine, E.R. and Holden, M.R.: J. Agric. Sci. 64, 195-203 (1965)

Burrows, W.J. and Carr, D.J.: Physiol. Plant. 22, 1105-1112 (1969)

Bushnell, J.: Amer. Potato J. 33, 203-210 (1956)

Cannon, W.A.: Ecology 5, 319-321 (1924)

Chapin, P.: Flora 91, 348-380 (1902)

Cline, R.A. and Erickson, A.E.: Proc. Soil Sci. Soc. Amer. 23, 333-335 (1959)

Coster, Ch.: Landbouw (Buitenzorg, Java) 8, 41-88 (1932/1933)

Crossett, R.N., Campbell, D.J. and John, A.: Ann. Rep. Letcombe Laboratory, 14-15 (1971)

Currie, J.A.: J. Sci. Food Agric. 13, 380-385

Danfors, E.: Grundförbättering 3, 137-150 (1962)

Danielson, D.E. and Russell, M.B.: Soil Sci. Soc. Amer. Proc. 21, 3-7 (1957)

Dowdell, R.J., Smith, K.A., Crees, R. and Restall, S.W.F.: Soil Biol. and Biochem. 4, 172-176 (1972)

Doyle, J.J. and Mac Lean, : Canad. J. Soil Sci. 38, 143-146 (1958)

Dubinina, I.M.: Fiziologya Rastenii (Engl.) 8, 314-322 (1962)

Eavis, B.W., Taylor, H.M. and Huck, M.G.: Agron. J. 63, 770-772 (1971)

Eliasson, L.: Physiol. Plant. 12, 551-558 (1959)

El Nadi, A.H., Brouwer, R. and Locher, J.Th.: Neth. J. Agric. Sci. 17, 133-142 (1969)

Enoch, H. and Dasberg, S.: Geoderma 6, 17-21 (1971)

Epstein, E.: Mineral nutrition of plants, John Wiley & Sons (1972)

Erickson, L.C.: Amer. J. Bot. 33, 551-561 (1946)

Fiscus, E.L. and Kramer, P.J.: Plant Physiol. 45, 667-669 (1970)

Franken, H.: Z. Acker- und Pfl. bua 130, 110-121 (1969)

Fulton, J.M. and Erickson, A.E.: Soil Sci. Soc. Amer. Proc. 28, 610-614 (1964)

Geisler, G.: Ztschr. Acker- und Pfl.bau 118, 399-410 (1963/1964)

----------: Plant Physiol. 40, 85-88 (1965)

----------: Arb. Landwirtsch. Hochschule Hohenheim Bd 40 (1967)

----------: Plant Physiol. 42, 305-307 (1967a)

----------: Ztschr. Acker- und Pfl.bau 130, 1-16 (1969)

Gieseke, F.: "Handbuch der Bodenlehre", Ed. Blanck, E., Bd. 6, 253-341 (1930)

Gill, W.R. and Miller, R.D.: Soil Sci. Soc. Amer. Proc. 20, 154-157 (1956)

Goddard, D.R. and Bonner, W.D.: Plant Physiol. 1A, 209-312 (1960)

Goedewaagen, M.A.J.: In: De plantenwortel in de landbouw (The Hague), pp. 98-106 (1955)

---------- and Schuurman, J.J.: Landbouwk. Tijdschr. 62, 469-482 (1950)

Grable, A.R.: Adv. of Agronomy 18, 57-106 (1966)

---------- and Siemer, E.G.: Soil Sci. Soc. Amer. Proc. 32, 180-186 (1968)

Greenwood, D.J.: New Phytol. 66, 597-606 (1967)

Greenwood, D.J. and Goodman, D.: J. Soil Sci. 18, 182-196 (1967)
----------: "Root growth", Ed. Whittington, W.J., Butterworths, London, 202-223 (1969)
----------: Rep. Progress Appl. Chemistry 55, 423-431 (1970)
Hammond, L.C., Allaway, W.H. and Loomis, W.E.: Plant Physiol. 30, 155-161 (1955)
Hawkins, J.C.: J. Sci. Food Agric. 7, 386-391 (1962)
Heide, H. van der, Boer-Bolt, M. de and Raalte, M.H. van: Acta Bot. Neerl. 12, 231-247 (1963)
Hofstra, J.: Acta Bot. Neerl. 13, 148-158 (1964)
Huck, M.G.: Agron. J. 62, 815-818 (1970)
Itai, C. and Vaadia, Y.: Phys. Plant. 18, 941-944 (1965)
Jackson, W.T.: Amer. J. Bot. 42, 816-819 (1955)
----------: Amer. J. Bot. 43, 637-639 (1956)
Kefford, N.P.: Plant Physiol. 37, 380-386 (1962)
Kende, H.: Proc. Nat. Acad. Sci. U.S. 53, 1302 (1965)
Kenefick, D.C.: Plant Physiol. 37, 434-439 (1962)
Kleinendorst, A. and Brouwer, R.: Jaarb. I.B.S. Wageningen, 29-38 (1967)
Kloke, A.: "Die Humusstoffe des Bodens als Wachstumfaktoren", Paul Parey, Berlin (1963)
Kopecky, J.: "Die physikalischen Eigenschaften des Bodens", Internat. Mitt. Bodenkunde 4, 173-175 (1914)
Kramer, P.J.: Plant Physiol. 26, 722-736 (1951)
----------: "Plant and Soil Water Relationships", Mc Graw Hill Book Company, New York, London, 104-149 (1969)
Kristensen, K.J. and Lemon, E.R.: Agron. J. 56, 295-301 (1964)
Kullmann, A.: Ztschr. Acker- und Pfl.bau 103, 189-197 (1957)
Kurssanov, A.L.: Adv. Bot. Res. 1, 209-278 (1963)
Lemon, E.R. and Erickson, A.E.: Soil Sci. Soc. Amer. Proc. 16, 160-163 (1952)
Letey, J. and Stolzy, L.H.: Hilgardia 35, 545-554 (1964)
Letey, J., Stolzy, L.H., Lunt, O.R. and Youngner, V.B.: Plant and Soil 20, 143-148 (1964)
Lipps, R.C. and Fox, R.L.: Soil Sci. 97, 4-12 (1964)
Livne, A. and Vaadia, Y.: In: Kozlowski III, Academic Press (1972)
Luxmoore, R.J., Stolzy, L.H. and Letey, J.: Agron. J. 62, 322-324 (1970)
Luxmoore, R.J. and Stolzy, L.H.: Agron. J. 64, 720-725 (1972)
McIntyre, D.S.: Austr. J. Soil Res. 4, 103-113 (1966)
----------: Advances Agron. 23, 235-283 (1971)

Mengel, K.: "Ernährung und Stoffwechsel der Pflanze", Fischer Verlag Stuttgart (1968)

Moss, D.N.: Crop Sci. 5, 280-281 (1965)

Mothes, K. and Engelbrecht, L.: Flora 143, 428-472 (1956)

Newman, E.I. and Andrews, R.E.: Plant and Soil 38, 49-70 (1973)

Odén, S.: Grundförbättring 3, 150-179 (1962)

Patrick Jr., W.H., Turner, F.T. and Delaune, R.D.: Dept. Agron. Louisiana State Univ., Bull. 641, 1-20 (1969)

Peerlkamp, P.K.: Meded. Landbouwhogeschool en Opzoekingsstat. Gent 24, 216-221 (1959)

Pitman, M.G.: Plant Physiol. 44, 1233-1240 (1969)

Poel, L.W.: J. Ecol. 48, 165-173 (1960)

Raalte, M.H. van: Ann. Jard. Bot. Buitenzorg 50, 99-113 (1940)

----------: Ann. Bot. Gardens Buitenzorg, Hors Série, 15-34 (1944)

Railton, J.D. and Reid, D.M.: Planta 111, 261-266 (1973)

Reid, D.M. and Crozier, A.: J. Exp. Bot. 22, 39-48 (1971)

Robelin, M.: Ann. Agron. 18, 579-599 (1967)

Roberts, E.H.: J. exp. Bot. 13, 75-94 (1962)

Rosene, H.F. and Bartlett, L.E.: J. Cell. Compar. Physiol. 36, 83-96 (1950)

Salter, P.J. and Goode, J.E.: Commonw. Agr. Bur. Res. Review 2 (1967)

Schmucki, S.: Diss. Univ. Zürich, 1-67 (1949)

Sibma, L.: Neth. J. Agric. Sci. 16, 211-216 (1968)

Sieben, W.H.: Landbouwk. Tijdschr. 76-20, 784-802 (1964)

Slatyer, R.O.: Plant-water relationships, Academic Press (1967)

Smith, K.A. and Robertson, P.D.: Nature 234, 148-149 (1971)

Stolzy, L.H., Letey, J., Szuszkiewicz, T.E. and Lunt, O.R.: Soil Sci. Soc. Amer. Proc. 25, 463-467 (1961)

----------, Gundy, S.D. van, Labanauskas, C.K. and Szuszkiewicz, T.E.: Soil Sci. 96, 292-298 (1963)

---------- and Letey, J.: Hilgardia 35, 567-576 (1964)

Teal, J.M. and Kanwisher, J.W.: J. exp. Bot. 17, 355-359 (1966)

Troughton, A.: Plant and Soil 36, 93-108 (1972)

Vartapetian, B.B., Andreeva, I.N., Maslova, I.P. and Davtian, N.G.: Agrochimica 15, 1-20 (1970)

Vegis, A.: Ann. Rev. Plant Physiol. 15, 185-224 (1964)

Vilain, M.: Ann. Agron. 14, 967-998 (1963)

Vose, P.B.: Ann. Bot. N.S. 26, 425-437 (1962)

Watson, D.J.: Advances Agron. 4, 101-145 (1952)

Went, F.W.: Plant Physiol. 18, 51-65 (1943)

Wiegand, C.L. and Lemon, E.R.: Soil Sci. Soc. Amer. Proc. 22, 216-221 (1958)

Wiersum, L.K.: Plant and Soil 27, 383-400 (1967)

----------: Acta Horticult. 23, vol. I, 318-326 (1971)

----------: Unpublished results (1973)

Willey, C.R.: Agron. J. 62, 224-229 (1970)

Williams, W.T. and Barber, D.A.: In: Mechanism in biological competition, pp. 132-144, Cambridge University Press, London (1961)

Williamson, R.E. and Splinter, W.E.: Agron. J. 60, 365-368 (1968)

----------: Agron. J. 62, 80-83 (1970)

o-o-o-o-o-o-o-o-o-o-o