The Morphogenetic Effect of Oxygen on Roots[1]

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Aeration as a factor influencing root growth has been investigated repeatedly (8, 12, 16). Root elongation has been found to be especially sensitive to aeration, O_2 being the essential and morphogenetically effective part of the air (9, 15). The results of investigations on the effect of aeration on root branching are not in accordance. There are observations indicating increased number of laterals in nonaerated water cultures (7), whereas other reports describe decreasing root branching with decreasing O_2 level (6, 10, 16, 18).

Under natural conditions in soils, the O_2 supply to the roots is controlled by the O_2 diffusion through the soil (6, 23), the rate of diffusion depending largely on the soil water content (24). Frequent changes in the degree of aeration, caused mainly by increasing or decreasing water content of the soil, result in the roots being subjected to very low levels of O_2 in water-saturated soils and a relatively favorable supply under drier conditions. But there have been no investigations on the effect of changing aeration on root growth, although this effect is one of the main characteristics controlling the O_2 supply to roots under natural conditions. An attempt was therefore made to study root growth responses to changing aeration.

The adaptation of the root morphology to prevailing soil conditions has been emphasized as an important feature in the uptake of water and nutrients from the soil (14, 19). The results of the present investigations will therefore be expressed in values which describe the root habit in terms of root elongation, root length, number of laterals and density of the root system, rather than in terms of fresh weight or dry matter production.

Materials and Methods

Peas in water culture were used as test plants. The plants were grown in Hoagland's solution in the glass house. The nutrient solution was replaced twice weekly. The glass containers had a volume of 2 liters and were covered with aluminum foil to protect the roots from the light. The temperature in the glass house varied in a daily rhythm according to the outside temperature; however during the course of the experiments, the temperature curves of successive days were almost identical owing to the stable weather conditions.

The peas were allowed to germinate on wet filter paper and as soon as the root tips were visible the seeds were transferred to a tray covered with a glass plate. The atmosphere within the tray was saturated with water vapor. The seeds were placed on a wire net so that the roots could grow undisturbedly downwards. After 5 days, the roots had reached a length of 6 to 8 cm and uniform seedlings were selected as test plants and transferred to the experimental jars in the glass house. Air was bubbled through the water cultures according to the test conditions. The O_2 content was determined using the Winkler method. Aerated water cultures showed values of 7 to 8 mg O_2/liter and nonaerated ones 3 to 4 mg O_2/liter, thus indicating that a certain amount of O_2 was still available to the roots. After interrupting the aeration the O_2 dissolved in the water was depleted to this level within a few hours, the time varying with the amount of roots in the container. The CO_2 concentration did not rise above 30 to 60 mg/liter, a value which is not critically high for root development (11). In some experiments, the living roots were stained in order to measure their elongation after a change in the aeration treatment. The roots were dipped for less than a minute in a solution of tannic acid (0.3 %) and then for a few seconds in ferric sulfate solution (0.1 %), this treatment resulting in a slightly bluish color of the root epidermis which could thus be distinguished from the additional growth occurring after the staining procedure. This treatment may result in a slight damage to the meristematic tissue which, however, can be neglected since all plants were treated similarly and the root elongation was obviously not much affected.

With the exception of the stained roots, different samples were used for measuring the root characteristics before and after treatments or before and after growth periods.

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Table I. *Effect of Changes in Aeration on Root Elongation in Long Term Treatments*
Peas were grown in Hoagland solution. The temperature varied between night 12° and day 26°.

Pretreatment for a period of 16 days	Length of main root (cm)	Treatment during subsequent 10 days	Length of main root (cm)	Elongation during 10 days (cm)
Aerated	34.2	Aerated	54.9	20.7
Nonaerated	23.7	Nonaerated	28.5	4.8
Aerated	34.2	Nonaerated	36.8	2.6
Nonaerated	23.7	Aerated	45.6	21.9
$LSD_{5\%}$	1.9		5.5	
$LSD_{1\%}$	2.5		7.7	

Results

Table I shows the results of an experiment in which peas were grown under 2 distinctly different aeration conditions, namely continuously aerated and nonaerated. In the nonaerated cultures, the root length is far below that in the aerated ones. After a pretreatment of 16 days, some of the experimental plants were subjected to a change in aeration from aerated to nonaerated and vice versa. As can be seen from the additional growth after the change in aeration, the elongation seems to be determined by the air supply existing during the observation period and be independent of the foregoing treatment.

The response of roots to changes in the air supply was investigated for a short period of 28 hours to establish whether there exist transitory effects such as stimulations or retardations immediately after the change in aeration (table II). The recorded data do not seem to indicate such responses.

Results are shown (table III) from an experiment with regularly changing aeration within a 24-hour cycle. Taking the difference in length between the continuously aerated roots and the nonaerated ones, it is possible to calculate theoretical values for the root elongation as a function of daily hours of aeration. These figures are in good agreement with the measured ones. The elongation rates are specific for main roots and laterals (table IV), the rates declining with increasing order of the laterals. The elongation of the different orders of laterals generally follows the same response pattern to aeration as shown by the main root.

The absolute number of primary and secondary

Table II. *Effect of Changes in Aeration on Root Elongation in Short Term Treatments*
Details are given in table I.

Pretreatment for a period of 15 days	Subsequent treatment during test period of 28 hr	Elongation of primary root laterals during test period (cm)
Aerated	Aerated	2.05
Aerated	Nonaerated	1.03
Nonaerated	Aerated	1.87
Nonaerated	Nonaerated	0.94
$LSD_{5\%}$		0.36
$LSD_{1\%}$		0.56

Table III. *Effect of Regular Changes in Aeration on Root Elongation*
Details are given in table I. Age of plants was 5 days at the beginning of test period.

Treatment: hr of aeration for 24-hr cycle	Elongation during test period of 7 days (cm)	Elongation difference between continuously aerated and nonaerated (cm)	Elongation calculated* (cm)
24 (Continuous aeration)	27.5	17.9	...
22	28.2	18.4	16.4
18	21.5	12.3	13.4
16	17.3	11.9	11.9
8	12.5	2.9	6.0
4	11.8	2.2	3.0
0	9.6	...	...
$LSD_{5\%}$	1.5	1.3	
$LSD_{1\%}$	2.0	1.7	

* Calculated from the ratio of hours of aeration to total hours.

Table IV. *Elongation (cm) of Main Roots and Laterals in Aerated and Nonaerated Water Cultures*

Peas were grown in Hoagland solution. The temperature varied between night 17° and day 28°. Age of plants was 19 days. Test period was 24 hours.

	Aerated	Nonaerated
Main root	3.02 ± 0.03	0.6 ± 0.005
Primary laterals	2.64 ± 0.03	0.33 ± 0.001
Secondary laterals	0.92 ± 0.02	0.27 ± 0.001

laterals is much higher in the aerated plants than in the interrupted or nonaerated cultures (table V). However, the latter are characterized by a closer spacing of the laterals and by their earlier development, this being shown by the occurrence of tertiary laterals in cultures with low O_2 supply.

Discussion

Changes in the O_2 supply do not seem to affect the growth potential of roots in terms of root elongation. After short periods or long periods of O_2 shortage, the roots respond immediately to an increased O_2 supply with elongation rates which seem to be neither restricted nor stimulated by the foregoing aeration treatment. Such a response would suggest that the growth potential of the plant root is relatively independent of the external O_2 supply. The observations of others (3, 15) confirm that low O_2 concentrations or even O_2 free media, while stopping root growth, do not kill roots. Consequently, it should be assumed that the internal O_2 supply from the shoot to the roots (4, 7) is large enough for the maintenance of the full viability of the latter. The findings by Schramm (21) that the respiration rates of roots from aerated and nonaerated cultures did not differ markedly would support this assumption. It therefore seems possible that there exists a physiological distinction between the external O_2 supply, which is formatively effective, and the internal O_2 supply, which maintains the viability of the root tissues.

As investigations by Amoore (1, 2) and Kojima (13) have shown, lack of O_2 inhibits cell mitosis whereas its effect on cell elongation seems to be relatively small (13). Responses of mitotic processes to O_2 may occur within periods as short as 15 minutes as has been demonstrated in shoots (18). It seems therefore possible that the energy needed for cell division is normally supplied by processes using the external O_2 supply, whereas the internal O_2 supply is reserved for the maintenance of cell viability. It has been speculated that the respiratory mechanism may differ under different environmental conditions (22), and a distinction between a ground respiration and a respiration activated from outside has been suggested in connection with the uptake of nutrients (17).

The results of the experiments reported show that the development of lateral roots is positively correlated with the length of root from which the laterals originate, which results in a higher absolute number of laterals in aerated cultures. However, the density of the root system is greatly enhanced by reducing O_2 supply owing to a higher number of laterals per unit root length and to an accelerated development of laterals. In this way the root habit is greatly changed by aeration. It seems unlikely that the effect of O_2 on root branching is a direct one; rather this phenomenon should be considered in view of the interactions between the growth of the root tip and the development of laterals.

In applying the present findings to field conditions, it has to be taken into account that a continuously aerated water culture probably offers a better O_2 supply to roots than can ever be achieved in the field. On the other hand, nonaerated cultures can be compared with a soil environment offering a highly reduced O_2 supply, such as a water-saturated soil. However, waterlogged soils are detrimental to roots not only owing to O_2 deficiency but also because of

Table V. *Number of Laterals as Affected by Aeration*

Details are given in table IV.

Treatment	Order of laterals	Number of laterals	
		Absolute	Per cm of originating root
Continuously aerated	Primary laterals	123	2.29
	Secondary laterals*	68	1.63
	Tertiary laterals**	...	...
Aeration interrupted for 16 hr out of each 24 hr	Primary laterals	93	3.54
	Secondary laterals*	44	2.29
	Tertiary laterals**	1–2	0.5
No aeration	Primary laterals	77	3.93
	Secondary laterals*	35	2.39
	Tertiary laterals**	4–5	1.00
$LSD_{5\%}$ (for primary laterals)		12.1	0.16
$LSD_{1\%}$		16.7	0.21

* Secondary laterals on the first 10 laterals of the main root.
** Tertiary laterals on the first 10 laterals of the main root (estimated).

products of incomplete metabolism of microorganism which can be toxic to root tissues as well as high levels of CO_2 above the tolerance limits of roots. In water cultures, such secondary effects of O_2 deficiency can probably be disregarded and changes in the root morphology should be attributed solely to the lowered supply to the roots. It can therefore be assumed that the experimental conditions are relatively close to the variation in aeration normally occurring under field conditions, which is not characterized by extremes such as total dryness or waterlogging so much as by frequent changes between water-saturated soils, drained soils, and soils that are beginning to dry up.

Since the findings suggest that there is an almost linear correlation between aeration and root elongation, increasing root elongation should be connected with decreasing soil water content, the growth being checked only when the dryness of the soil begins to take effect immediately on the roots. Observations by Weaver and Clements (25) and Ronnike (20) confirm that as the soil water content begins to decrease, root elongation is stimulated.

Root branching seems to be equally closely correlated with the soil water content, branching activity and high root density being favored with decreasing aeration; this would resemble the situation in soils with high water contents. The development of a dense root system in moist soil zones is well known.

Summary

Pea roots in water cultures were subjected to different aeration conditions. Root elongation and root branching were strongly affected by the air supply, elongation being favored by increasing aeration and branching activity by decreasing aeration. By changing the aeration conditions from full aeration to no aeration and vice versa it was shown that the extent of root elongation depends on the availability of oxygen. However, it appears that the viability of the root tissues is independent of the external oxygen supply, thus allowing an undisturbed growth potential under extreme shortage of external O_2. The formative influence of oxygen on root branching is characterized by a greatly enhanced root density due to a higher number of laterals per unit root length producing them and accelerated development of laterals of a higher order.

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