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Interactive Effects of CO_2 and O_2 in Soil on Root and Top Growth of Barley and Peas

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Summary. Barley and pea plants were grown under several regimens of different compositions of soil atmosphere, the O_2 concentration varying from 0 to 21 % and the CO_2 concentration from 0 to 8 %. In absence of CO_2, the effect of O_2 on root length in barley was characterized by equal root lengths within the range of 21 to 7 % O_2 and a steep decline between 7 and 0 %. In peas, while showing the same general response, the decline occurred between 14 and 7 % O_2. Root numbers of the seminal roots of barley decreased already with reduction in O_2 concentration from 21 to 14 %. Dry matter production was affected somewhat differently by O_2 and CO_2 concentration. Dry matter production in barley was reduced at 14 % O_2 while root length decreased between 7 and 0 %. In peas, dry matter production was favored by low CO_2 concentrations except where there was no oxygen. At 21 % O_2, increasing CO_2 concentrations did not seem to affect root length up to concentrations of 2 % CO_2. At 8 % CO_2, root length was decreased. The interactive effects of CO_2 and O_2 are characterized by a reduced susceptibility to CO_2 at O_2 values below 7 %, and a very deleterious effect of 8 % CO_2 at 7 % O_2.

Root length is affected by CO_2 and O_2. Decreasing O_2 concentrations and increasing CO_2 concentrations cause a reduced root elongation (2, 3, 4, 5, 6, 7, 8, 9). The susceptibility and limits of tolerance to changes in the concentrations of these gases can be assumed plant specific (4, 5, 9). However, there is only limited information on the interactive effects of O_2 and CO_2 on root morphology and dry matter production of tops and roots. Furthermore, the results seem to be contradicting, especially concerning the limits of tolerance to CO_2 at falling O_2 concentrations. Some investigations show relatively high CO_2 concentrations tolerated by plants at low levels of O_2 with the inhibiting effect occurring when the CO_2 concentration exceeds that of the O_2 concentration (4, 5, 6, 7). These experiments, however, have been conducted in soils containing a relatively high moisture content thus apparently offering a strongly reduced O_2 supply to the roots. Experiments in water cultures, on the other hand, show much lower tolerance limits to CO_2 as demonstrated by Stolwijk & Thimann (9) and Geisler (2). The tolerance limits are between 1 and 5 % CO_2. Generally speaking, comparison of these experiments and their results may be difficult since the experimental conditions vary in many aspects. An important factor may be the O_2 concentration especially in comparison of the water cultures and the investigations in soils. Under field conditions, a negative correlation may be expected between O_2 and CO_2 concentration, diffusion being the controlling factor. When the reduction of O_2 is not caused by biological processes but by displacing the soil air as is the case after irrigation or heavy rains the composition of the soil atmosphere is probably characterized by low O_2 and equally low CO_2 concentrations (6). The investigation of these composition patterns should therefore be of interest.

Materials and Methods

Barley and pea plants were used in the experiments. The plants were grown in containers filled with a mixture of sand and compost. The containers were tubes with a diameter of 5 cm and a height of 50 cm; the tubes were perforated on their entire length so as to ensure equally good gas exchange at all depths. Five tubes were combined in 1 vessel through which the gas mixtures were forced. The vessels were sealed using a plastic cover with small slits so that the tops of the plants were in normal air. To mix the gases for the aeration treatments, air, nitrogen and CO_2 from gas cylinders were used. The concentrations of the gases were controlled using a Beckman Oxygen Analyser for O_2 and an Infrared Gas Analyser for CO_2. Needle valves and flow meters served to conduct the mixing of the gases. The concentrations were measured before entering the vessels and as a control occasionally at the outlet. The flow of the gas mixtures was kept at 10 liters per hour. There were only minor deviations amounting to 0.5 % CO_2 and correspondingly lower O_2 concentrations. The consequence of the increase in CO_2 and decrease in O_2 within the vessels, due to the respiratory activity of the soil, is neglectable for the O_2 treatments but should be considered with regard to the CO_2 treatments which are about 0.5 % higher than in the gas mixtures forced into the vessels. There was no water supply during the period of duration of the experiment. When the experiments were finished after 18 days there were no signs of wilting or any growth impairment and the sand compost mixture was still moist at the deeper parts of the tubes. The low water supply was intentionally kept in order to ensure good diffusion conditions and to reach an O_2 concentration on the root surface as close as possible to the controlled concentration in the treatment.

Table I. *Interactive Effects of CO_2 and O_2 in Soil on Root Length of Barley and Peas*

Plants were grown in the greenhouse, the day temperature was 28° and the night temperature was 18°. In barley, the mean value at the seminal roots were measured. The main root was measured in the pea plants.

Species	O_2%	(CO_2 + HCO_3^-)% 0	1	2	8	$\bar{x}$
		cm	cm	cm	cm	cm
Barley	0	7.2	10.5	16.4	7.4	10.4
	7	30.3	25.9	24.7	6.2	21.8
	14	29.9	25.9	26.6	19.8	25.6
	21	31.0	29.2	22.4	15.5	24.5
	$\bar{x}$	22.3	23.3	22.5	12.2	20.6
Peas	0	7.0	11.1	14.2	10.0	10.6
	7	33.0	39.8	41.4	3.3	29.4
	14	48.0	42.3	37.1	26.6	38.5
	21	49.9	49.0	48.5	38.2	46.4
	$\bar{x}$	34.5	35.6	35.3	19.5	31.2

Shortest significant ranges*

Barley:				Peas:			
p	: (2)	(3)	(4)	p	: (2)	(3)	(4)
R_p 5 %	: 4.07	4.29	4.44	R_p 5 %	: 6.05	6.38	6.59
R_p 1 %	: 5.41	5.64	5.80	R_p 1 %	: 8.05	8.39	8.62

* Duncan's multiple range test (1)

Results

Root length was not much affected between 21 to 7 % O_2 and 0 to 2 % CO_2 in barley (table I). Peas showed the same general response but root length decreased already at 14 % O_2. There was a promotive effect on root length at 1 and 2 % CO_2 and 7 % or 0 % O_2. 8 % CO_2 was inhibiting at all O_2 concentrations but especially at 7 %. Peas seemed more resistant to 8 % CO_2 at 21 % O_2 than barley.

The total length of the seminal root system of barley showed the same general trend in response to CO_2 and O_2 as the individual roots (table II).

Table II. *Interactive Effects of CO_2 and O_2 in Soil on the Total Length of the Seminal Root System of Barley*

Plants were grown in the greenhouse, the day temperature was 28° and the night temperature was 18°.

Species	O_2%	(CO_2 + HCO_3^-)% 0	1	2	8	$\bar{x}$
		cm	cm	cm	cm	cm
Barley	0	41.6	56.0	69.8	29 5	49.2
	7	129.9	138.6	130.5	28 2	106.8
	14	166.3	167.6	152.3	116.5	150.7
	21	174.1	164.2	139.0	100.2	144.4
	$\bar{x}$	128.0	131.6	122.9	68.6	112.8

Shortest significant ranges:

p	: (2)	(3)	(4)
R_p 5 %	: 12.9	13.6	14.0
R_p 1 %	: 17.2	17.9	18.4

Table III. *Interactive Effects of CO_2 and O_2 in Soil on Total Dry Matter Production of Barley and Peas*

Plants were grown in the greenhouse. The day temperature was 28° and the night temperature was 18°.

Species	O_2%	(CO_2 + HCO_3^-)% 0	1	2	8	$\bar{x}$
		mg	mg	mg	mg	
Barley	0	61.5	72.8	58.9	42.2	58.9
	7	70.2	72.0	78.3	34.1	63.7
	14	78.0	77.4	75.7	59.0	72.5
	21	92.1	91.4	72.0	61.1	79.2
	$\bar{x}$	75.5	78.4	71.2	49.1	68.6
Peas	0	160.0	115.8	72.8	40.2	97.2
	7	278.8	352.4	224.2	41.1	224.1
	14	245.4	375.5	212.9	255.4	272.3
	21	295.2	353.2	273.6	265.7	269.9
	$\bar{x}$	244.9	299.2	195.9	150.6	222.6

Shortest significant ranges

Barley:				Peas:			
p	: (2)	(3)	(4)	p	: (2)	(3)	(4)
R_p 5 %	: 7.24	7.63	7.88	R_p 5 %	: 41.4	43.6	45.1
R_p 1 %	: 9.63	10.04	10.32	R_p 1 %	: 55.0	57.4	59.0

However, the total length decreased at the 0% level of CO_2 from 21 to 14% O_2 while the mean values of the lengths of the seminal roots did not show any difference (table I versus table II). Clearly, the elongation of the individual roots was not affected by the drop in O_2 but the number of seminal roots decreased with reduction in the O_2 concentration this leading to a smaller total length of the root system.

There was a general agreement between the responses of root length and total dry matter production (table III). However, the correlations between the treatments and the responses were not so strong as in the case of root length. Noticable was the promotive effect in peas produced by 1% CO_2 at all levels of O_2 except 0% O_2.

Discussion

There is a promotive effect of low CO_2 concentrations up to 2% on root length in the absence of O_2 or at low O_2 concentrations. If this should be a general response to interactive effects of CO_2 and O_2 it could explain, at least partly, the contradicting results concerning the reaction curves of root length to CO_2. The higher tolerance limits normally determined in experiments in soils (4, 5, 6) in contrast to water culture results (2, 9) could then be caused by the low O_2 concentrations at the root surface which have to be assumed in soils especially under conditions of a water content close to the field capacity. The dominating effect of the water suction in soils on root length over the reaction to CO_2 concentration has been shown by Grable and Danielson (4). The changing diffusion conditions for O_2 and not the water content may be the controlling factor. This view is supported by the low tolerance limits to CO_2 found by Stolwijk and Thimann (9) in well aerated gravel cultures and the somewhat higher limits found by Geisler (2) in non-aerated water cultures.

Dry matter production in peas is favored by low CO_2 concentrations and is severely curtailed by low O_2 concentrations. In contrast, there is no increase in dry matter in barley due to low CO_2 concentrations but the plants are not very sensitive to lack of O_2. Similar results have been already reported (2, 4, 5, 9).

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