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Morphological responses of barley roots to soil compaction and modified supply of oxygen

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The morphological changes in barley roots in response to soil compaction and hypoxia were quantified by image analysis. Based on the assumption that these soil stresses increase endogenous ethylene production in plants, changes indicating higher construction costs for roots, such as decreased specific root length, were expected. The hypothesis was found to be only partly correct. Most morphological changes of barley roots were probably a reaction to increased soil mechanical impedance. Examples of this are root width, which was increased by compaction apart from in wet soil, as well as increased width and specific volume, and a decreased specific length of roots in the deepest layer of well-aerated loose soil. However, in loose moist soil hypoxia prevented root growth, but did not change root morphology. The results suggest that severe hypoxia lessens the possibilities of roots to adapt to the hypoxic soil by reducing root growth and by preventing the formation of aerenchyma.

Key words: barley, compaction, scanning, hypoxia, image analysis, morphology

Introduction

In biology, stress can be defined as any environmental factor capable of inducing chemical and physical changes potentially injurious to the physiology of living organisms, as discussed in more detail by Levitt (1980) and Hale and Orcutt (1987). These changes, if sufficiently severe, bring about abnormal metabolism leading to reduction in growth, yield, or value, or death of the plant or plant part. The stress resistance of plants varies depending on their innate ability to avoid or tolerate detrimental factors, and on any adaption through changes in metabolism.

In soil, physical and chemical stresses may alter root growth and morphology and, thus, influence water and nutrient acquisition by plants as well as the supply of oxygen to the roots. Specific root surface area and specific root length are common indicators of gross morphology of the roots (see Boot 1989). Small values of these parameters represent inefficient use of photosynthates to construct a given length or surface area

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of roots, respectively. The significance of root width is obvious: assuming the roots (of volume V) are cylindrical and the density ($\rho = m/V$) of root biomass (m) is constant, the specific surface area (A/m) and the specific length (L/m) are inversely proportional to the radius (r) and the square of radius, respectively, of the root.

$$A = 2\,\pi\, r\, L = 2\,\pi\, r\,\frac{V}{\pi\, r^2} = \frac{2\,m}{\rho\, r} \Rightarrow \frac{A}{m} = \frac{2}{\rho\, r}$$

$$V = \pi\, r^2 L \Rightarrow \frac{L}{m} = \frac{1}{\rho \pi r^2}$$

Low values of specific root length may also imply a diminished efficiency of roots to obtain water and ions from the soil, since these root functions correlate more with the length than with the biomass of roots. The efficiency however depends also on additional factors such as branching patterns of roots as well as the diffusion and adsorption properties of water and ions in soil (Fitter 1996, de Willigen et al. 2000).

Several external stresses are known to change root morphology. The background of this study is in compaction problems of Finnish agricultural soils. Excessive soil compaction is common in soils wet at planting and harvest (see van Ouwerkerk and Soane 1994 for a more comprehensive discussion). In heavily compacted soil, increased mechanical impedance and retarded aeration (Simojoki et al. 1991) may restrict the growth of roots and change their morphology (Pietola 1991). Increased mechanical impedance induced e.g. by compaction or soil drying generally increases root width (Eavis 1972, Wilson et al. 1977). Both hypoxia and high mechanical impedance induce the formation of aerenchyma in roots (see Morgan and Drew 1997). Although much is known about the mechanisms by which plants respond to these stresses (see Bennie 1996, Drew and Stolzy 1996), empirical data relating the actual concentration of oxygen in soil air to the plant performance at various soil bulk densities and moisture contents are scarce. The stresses usually increase the production of ethylene, a plant hormone that is thought to have a central role in mediating root morphological responses to several stresses (Morgan and Drew 1997, Lynch and Brown 1997).

In this study, the aim was to apply image analysis (see Simojoki 2000a) to quantify the effects of compaction and hypoxia stresses on the widths, specific lengths, specific surface areas and specific volumes of barley roots. Quantitative data are needed to better interpret the effects of soil air oxygen concentration on plant growth with the aid of a mathematical model (Simojoki 2000b). The stresses were thought to induce root morphological changes similar to those generally induced by large concentrations of ethylene, such as increased root width and decreased specific root length. Thus, it was postulated that the stresses, besides reducing root growth, also would make use of photosynthates to construct the roots more inefficiently. The results are discussed in terms of plant adaptation to the soil stresses.

Material and methods

Description of the pot experiments

Root samples were taken from a series of three factorial pot experiments into the effects of soil compaction and hypoxia on barley (*Hordeum vulgare* L. cv. Kymppi) in phytotrons (Simojoki 2000b). Sieved fine sand soil was packed in the pots to a final volume of 2.72 dm^3 (depth 15 cm) at dry bulk densities (ρ_b) of 1.39 or 1.59 Mg m^{-3}. The soil was kept either wet (matric suction ψ_m < 10 kPa) or moist (ψ_m > 10 kPa) by watering the pots daily. The composition of soil air was regulated by flushing the soil with a gas of known O_2 concentration (0%, 2%, 10% or 20% in N_2). In each experiment four pots (ρ_b 1.39 Mg m^{-3}) had no lids (open pots) and received no gas flow.

Sampling and image analysis of roots

From a few pots root samples were taken at a harvest 11–12 days after sowing, just before the gas flow and soil moisture treatments were started. From the other pots the root samples were taken at a harvest about two months after sowing. The roots were sampled from half of the total soil volumes in each pot at 5 cm increments. The techniques of the pre-treatment, the digitisation with a desktop scanner and the image analysis of the root samples are detailed by Simojoki (2000a). After separating the mineral soil from the roots by hydropneumatic elutriation, and removing the remaining organic debris, the roots were stored in 15% ethanol solution for later image analysis.

Based on tests with dark metal wires a high brightness adjustment was first chosen to be used routinely for scanning the roots, but after noticing that some roots were not present in the images, the samples were additionally scanned at a lower brightness to improve the digitisation (Simojoki 2000a). As a consequence, however, some of the root samples were scanned only at high brightness. In order to avoid any systematic error the results were examined separately at each brightness level. The dry mass of scanned roots was determined by drying the roots in an oven at 70°C for 48 h.

Assuming the roots were cylindrical, with a radius equal to half of the measured width of the object, the surface area (A) and volume (V) were calculated for each length of root (object) on the tray(s) using the formulas given in the Introduction. The specific lengths, specific surface areas and specific volumes of roots were calculated by summing the lengths, areas and volumes, respectively, of all objects of the sample and dividing by the dry mass of the scanned roots. The average root width was calculated by dividing the total projection area of the roots by their total length. Anatomic features, such as aerenchyma or gas-filled porosity, were not measured directly, but any formation of aerenchyma was assumed to increase the specific volume of the roots.

Statistical analysis

For the statistical analyses of the root data the results of separate experiments were combined and analyzed as if the pots were completely randomized in one experiment. Multiple comparison of means was done using Tukey's test at the 5% significance level. The residual error term was used as an error term in calculating the significant differences between soil depths. For comparison of gas treatments an error term was calculated from the residual error term and the interaction of gas treatment and soil depth, using the Satterthwaite approximation.

Results and discussion

The roots in the compacted soil (1.59 Mg m^{-3}) were thicker than those in the loose soil (1.39 Mg m^{-3}), but only if the soil was not wet (Table 1). The thickening of roots due to soil compaction was more pronounced at 10% than at 20% O_2 in soil air. The morphological response of barley roots to soil compaction and aeration treatments was examined in the uppermost soil layer only, because root growth in the compacted soil was restricted to the uppermost 5 cm (Simojoki 2000b). Most root samples from the wet soil and all samples from the compacted soil were scanned only with the high scanner brightness adjustment (see the Material and methods). Although the analysis of these images underestimated the real width and specific length of roots, the effects of experimental treatments on root width can be safely compared.

In the loose moist soil the root morphology was, on average, not much affected by the various gas treatments (Table 2 and 3), although root growth was severely inhibited at 0–2% O_2. However, in the well-aerated soil (10–20% O_2 and open pots) roots in the surface layer were thinner, greater in their specific length or less in their specific volume than those in the deepest soil layer. Such differences were not observed in the

Table 1. The width of barley roots[A] at the depth of 0–5 cm in soil subjected to various compaction and aeration treatments[B].

Air-filled porosity %	O_2 concentration %	n	Width µm
Loose soil (1.39 Mg m^{-3})			
2–4	10	4	178^{a}
2–4	20	2	173^{a}
13–19	10	6	190^{ab}
13–19	20	8	190^{ab}
Compact soil (1.59 Mg m^{-3})			
1–2	10	2	162^{a}
1–2	20	2	191^{ab}
7–8	10	2	267^{c}
7–8	20	2	230^{bc}

[A] Measured with a high scanner brightness adjustment. Barley 58–61 d old. Means denoted with a different letter on the same column differ significantly ($P < 0.05$); n = number of replicate pots.

[B] The aeration treatments were started 11–12 d after sowing: soil was flushed continuously with a gas stream of known O_2 concentration, and soil air-filled porosity was regulated by daily watering.

pots at 0–2% O_2 nor in the pots harvested before applying the gas treatments.

The results agree with the findings that the width of well-aerated roots increases in response to increased soil mechanical impedance induced by compaction and drying (decreasing matric potential) of soils (e.g. Eavis 1972, Wilson et al. 1977). On the other hand, in deficiently aerated wet soils the width of roots may increase even if the mechanical impedance is small (Eavis 1972). In both instances the thickening of roots can be attributed to the increased production in roots of endogenous ethylene (Crossett and Campbell 1975, see Bennie 1996): the production is promoted both by mechanical impedance and hypoxic stresses (see Morgan and Drew 1997). The absence of any thickening of roots due to soil wetness (Table 1) supports the reasonable assumption that the roots grown at shallow depths were well-aerated. Indeed, independent of whether the soil was compacted or not, some roots in the wet soil were growing at the soil surface exposed to air containing 10–20% O_2, as visually observed at the end of the experiment.

Plants can adapt to soil hypoxia by changing the morphology and growing pattern of roots (Armstrong et al. 1991, Justin and Armstrong 1987). Shallow rooting improves the supply of oxygen to roots by shortening the diffusion routes of O_2 from the atmosphere through both the soil and plant. In theory, thin roots can take up O_2 from soil air more efficiently than thick roots in the sense that the critical O_2 concentrations at the root surface that keep the roots fully aerated is smaller for thin than for thick roots, assuming similar gaseous diffusivities in the roots (Lemon 1962). Accordingly, in response to hypoxia deeper in the soil, plants species may grow thin roots in well-aerated soil at shallow depths (Justin and Armstrong 1987, Armstrong et al. 1991), as observed in the surface layer of the wet soil (Table 1).

On the other hand, plants may adapt to the hypoxic soil by forming aerenchymatous root tissue, which increases the rate of internal aeration between the root and the aerial parts of the plant (Justin and Armstrong 1987, Armstrong et al. 1991). The formation of aerenchyma occurs in young roots (Thomson et al. 1990), induced by e.g. large mechanical impedance and hypoxia in soil. It is mediated by ethylene (Drew et al. 1979, see Morgan and Drew 1997) that also increases the width and decreases the specific length of roots (Crossett and Campbell 1975, see

Table 2. Total dry mass and width of barley roots[A] at three depths in loose moist soil subjected to various aeration treatments[B].

Treatment	n	Dry mass[C] g			Width µm		
		0–5 cm	5–10 cm	10–15 cm	0–5 cm	5–10 cm	10–15 cm
Barley 11–12 d old							
–	5	0.03^{a}	0.03^{a}	0.02^{a}	230^{ab}	242^{a}	245^{ac}
Barley 58–61 d old							
0% O_2	2, 3*	0.03^{a}	0.03^{a*}	0.03^{a}	244^{ab}	255^{a*}	228^{ac}
2% O_2	4	0.05^{ab}	0.05^{ab}	0.04^{a}	258^{ab}	299^{a}	266^{ac}
10% O_2	3	0.16^{b}	0.21^{bc}	0.51^{d}	226^{ab}	246^{a}	323^{c}
20% O_2	6	0.16^{bc}	0.27^{c}	0.43^{d}	216^{a}	247^{ab}	283^{bc}
Open pot	8	1.44^{e}	0.45^{c}	0.75^{d}	280^{b}	268^{ab}	284^{abc}

[A] Means denoted with a different letter on the same row or column differ significantly ($P < 0.05$); n = number of replicate pots.

[B] Dry bulk density 1.39 Mg m^{-3}, air-filled porosity in open pots 18–25%, in all others 13–19%. Soil was continuously flushed with a gas stream of known O_2 concentration beginning from 11–12 d after sowing. Open pots received no gas flow.

[C] Statistical analysis with logarithm transformed data

Bennie 1996, Jackson 1991). Consequently, this adaptation mechanism is important deeper in the hypoxic soil, where the conditions favour accumulation of ethylene. As the width and specific volume of roots in the loose soil were largest, and the specific lengths least, in the deepest soil layer of the most well-aerated treatments in the present study (Tables 2 and 3), the responses were probably induced by large mechanical impedance rather than by hypoxia. The impedance deeper in the soil must have been considerably higher than that in the surface layer, especially after watering.

The fact that the morphology of barley roots

Table 3. Specific length, surface area and volume of barley roots[A] at three depths in loose moist soil subjected to various aeration treatments[B].

Treatment	n	Specific length m g^{-1}			Specific surface area cm^{2} g^{-1}			Specific volume cm^{3} g^{-1}		
		0–5 cm	5–10 cm	10–15 cm	0–5 cm	5–10 cm	10–15 cm	0–5 cm	5–10 cm	10–15 cm
Barley 11–12 d old										
–	5	342^{b}	308^{ab}	280^{ab}	2460^{b}	2290^{b}	2100^{b}	16.9^{a}	16.2^{a}	15.4^{a}
Barley 58–61 d old										
0% O_2	2, 3*	286^{ab}	253^{a*}	293^{a}	2200^{ab}	1960^{b*}	2090^{b}	16.3^{a}	14.7^{a*}	14.1^{ab}
2% O_2	4	309^{ab}	251^{a}	289^{a}	2490^{b}	2310^{b}	2370^{b}	18.9^{a}	20.3^{a}	18.4^{abc}
10% O_2	3	399^{b}	362^{ab}	254^{a}	2820^{b}	2800^{b}	2540^{b}	18.4^{a}	19.5^{ac}	23.3^{c}
20% O_2	6	392^{b}	335^{ab}	309^{ab}	2620^{b}	2560^{b}	2610^{b}	16.4^{a}	18.5^{a}	22.0^{c}
Open pot	8	206^{a}	265^{a}	274^{a}	1810^{a}	2190^{b}	2410^{b}	16.4^{a}	17.9^{ab}	20.3^{bc}

[A] Means denoted with a different letter on the same row or column differ significantly ($P < 0.05$); n = number of replicate pots.

[B] Dry bulk density 1.39 Mg m^{-3}, air-filled porosity in open pots 18–25%, in all others 13–19%. Soil was continuously flushed with a gas stream of known O_2 concentration beginning from 11–12 d after sowing. Open pots received no gas flow.

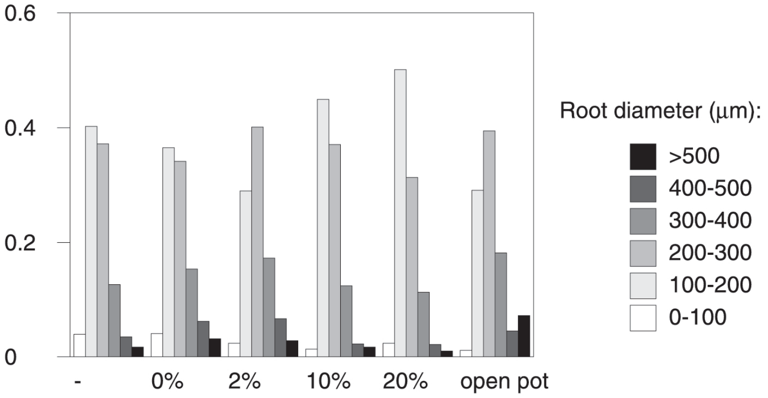

Fig. 1. Root width distributions of barley in the surface layer (0–5 cm depth) of the loose soil (1.39 Mg m^{-3}) at the various treatments. The proportion of roots in the different diameter classes is expressed as a fraction of the total root length (– = 11–12 d old plants harvested just before starting the aeration treatments; 0–20% = 58–61 d old plants grown in the soil aerated with gas stream of a known O_2 concentration; open pot = 58–61 d old plants grown in soil that received no gas flow but the surface of which was open to the atmosphere).

was nearly unaffected by soil hypoxia is readily explained by the much reduced growth of roots that alone radically lessened their possibilities for any adaptive changes. Consequently, the morphological properties of the roots reflected mainly the soil conditions before hypoxia. The growth of shoots and roots in these experiments are discussed in detail by Simojoki (2000b). The results on the specific volume of roots in the deepest soil layer (Table 3) further suggest that low O_2 concentrations in soil air not only reduces the root growth but also prevents the formation of aerenchyma. This result is supported by the observations in solution culture studies that at very low O_2 concentrations the formation of aerenchyma is insensitive to the stimulated ethylene production, as aerenchyma fails to develop even in the presence of exogenous ethylene (Jackson et al. 1985). Total anoxia prevents the biosynthesis of ethylene and the formation of aerenchyma (Drew et al. 1979, He et al. 1994).

In the airtight pots the roots were mainly seminal ones, as the growth of adventitious roots emerging from the lower parts of the stem was much hampered by sealing the lids. In the open pots on the contrary, root growth was unimpeded, and thus the greater proportion of thick adventitious roots in the uppermost soil layer may explain why no differences in root width between the soil depths were observed (Fig. 1, Table 2).

Conclusions

The changes in various root morphological parameters of barley in response to hypoxic and mechanical impedance stresses in soil were quantified by image analysis. The hypothesis that these stresses would induce changes indicating more inefficient use of photosynthates for constructing the roots was found to be only partly correct.

Most morphological changes in the barley roots were probably a reaction to increased soil mechanical impedance, such as the increase of the root width by compaction. Further, the roots near the surface in the well-aerated loose soil were thinner, and of higher specific length or of lower specific volume, than those at the deepest soil layer, which may also be attributed to dissimilar mechanical impedance in the layers. Compaction and hypoxia were expected to affect root morphology in a similar manner, as the production of ethylene in roots is promoted by both of them. However, root morphology was nearly unchanged (without any signs of e.g. aerenchyma formation) where root growth was prevented by hypoxia. The results suggest that severe hypoxia lessens the possibilities of roots to adapt to hypoxic soil by reducing root growth and by preventing the formation of aerenchyma.

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SELOSTUS

Maan tiivistämisen ja hapensaannin muutosten vaikutukset ohran juurten morfologiaan

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Biologinen stressi voidaan määritellä miksi tahansa ympäristötekijäksi, joka voi aiheuttaa eliöitä vaurioittavia kemiallisia ja fysikaalisia muutoksia niiden fysiologiassa. Maaperässä fysikaaliset ja kemialliset stressit voivat esimerkiksi muuttaa juurten kasvua ja morfologiaa, mikä voi heikentää kasvien veden ja ravinteiden ottoa sekä juurten hapensaantia. Viljelymaan tiivistyminen on yleinen ongelma Suomessa ja muualla olosuhteissa, joissa maa on kylvö- ja sadonkorjuuaikoina märkää. Tiivistyneen maan suurentunut mekaaninen vastus ja heikentynyt ilmavuus voivat rajoittaa juurten kasvua.

Tässä tutkimuksessa kvantifioitiin maan tiivistämisen ja hapenpuutteen vaikutuksia kasvien juurten morfologisiin ominaisuuksiin kuva-analyysimenetelmällä. Muiden tutkimusten perusteella voitiin olettaa, että nämä stressit lisäävät endogeenisen etyleenin tuotantoa kasvissa. Siksi niiden odotettiin aiheuttavan sellaisia juurten morfologisia muutoksia, joita suurten etyleenipitoisuuksien tiedetään aiheuttavan, ja jotka osoittavat yhteytystuotteiden käytön tehokkuuden heikkenemistä juuriston rakentamisessa, kuten esimerkiksi juurten ominaispituuden väheneminen. Tämä ajatus osoittautui vain osittain oikeaksi.

Maan tiivistämisen ja hapenpuutteen aiheuttamia muutoksia juurissa tutkittiin astiakokeessa, jossa ohraa kasvatettiin hietamaassa. Pääosan ohran juurten morfologisista muutoksista aiheutti todennäköisesti maan mekaanisen vastuksen kasvu, esimerkiksi maan tiivistäminen lisäsi juurten paksuutta, ellei maa ollut märkä. Samoin hyvin ilmastetun (10–20 % O_2 maan ilmassa), löyhän maan syvimmässä kerroksessa juuret olivat paksumpia ja ominaispituudeltaan lyhyempiä tai ominaistilavuudeltaan suurempia kuin pintakerroksessa, mikä epäilemättä johtui syvimmän kerroksen suuremmasta mekaanisesta vastuksesta. Löyhässä, kosteassa maassa (ilmahuokoisuus >12 %) hapenpuute (0–2 % O_2 maan ilmassa) esti juurten kasvun mutta ei muuttanut juurten morfologiaa.