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INFLUENCE OF FLOODING AND DIFFERENT TEMPERATURES OF THE SOIL ON GAS-FILLED POROSITY OF PEA, MAIZE AND WINTER WHEAT ROOTS

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A b s t r a c t. Development of gas-filled root porosity in response to various levels of oxygen supply was tested for *Pisum sativum* cv. I³owiecki, *Zea mays* cv. Alma F1, *Triticum aestivum* cv. Rosa and CZR 1406. Eight-day old seedlings were subjected to differentiated aeration conditions (control with pore water pressure of about 15 kPa and flood treatment) for 12 days at three soil temperatures (7, 15 and 25 ^{o}C). The above-ground parts of the plants were grown at the temperature of 25 ^{o}C, while the soil temperature was differentiated by keeping cylinders with the soil in the thermostated water of appropriate temperature. The results obtained suggest that plant adaptation in the form of aerenchyma formation is efficient in the case of winter wheat at the lowest temperature, and maize at 7 and 15 ^{o}C, when the respiratory activity is not too high. Pea plants are able to adapt in the entire temperature range under consideration. Aerenchyma formation in plant roots is connected with plant adaptation to environment and beneficially influences functioning of the ecosystem.

K e y w o r d s: aeration, aerenchyma, root porosity, flooding, temperature

INTRODUCTION

Supply of oxygen to plants is of fundamental importance to the growth of all species including the plants of aquatic habitats. Different species developed different strategies to be able to adapt to flooded areas. Genetic differences in the tolerance to waterlogging were reported for many plant species, e.g., Zea *mays* [9,24] and *Triticum aestivum* [4]. The plants tolerant to waterlogging have specific morphological and anatomical characteristics that enable them to survive and function under waterlogged conditions, such as aerenchyma formation and adventitious root development [7,12,15].

In the majority of cases, a successful strategy is a combination of morphological, anatomical and metabolic adaptations. A well-developed aerenchyma system of a plant would ensure an efficient exchange of gases between atmosphere and soil. An extensive internal aeration system allows for the transport of atmospheric oxygen to plant roots to avoid root anaerobiosis [26] and oxygenation of the rhizosphere.

Oxygen concentration in the root tissue is a function of plant and soil properties. Soil physical properties (i.e., water content, porosity, temperature, etc.) determine the rate at which oxygen can diffuse to the root surface. Many plant properties determine the rate of diffusion and consumption of oxygen by the root tissues. Properties affecting oxygen concentration in the roots include radial and longitudinal diffusivity of oxygen, membrane permeability, oxygen uptake rate, root diameter, and root porosity.

An increase in the aerenchyma formation in response to flooding has been reported by many authors [2,22,27].

Experimental data indicate that aerenchymous wetland plants have the potential to affect the neighbouring plants via soil oxygenation positively, but these effects combined with competition can alter the physical environment [3].

The aim of the present paper was to investigate the influence of oxygenation stress at various soil temperature levels on the air - filled porosity and penetration depth of the roots of 20-day old seedlings of two winter wheat species (cv. Rosa and CZR 1406), pea (cv. Iłowiecki) and maize (cv. Alma F1).

MATERIALS AND METHODS

The experiment was performed in the growth chamber. Brown soil developed from loess (Ortic Luvisol) containing 1.54% of organic matter, 25% of the 1-0.05 mm fraction, 70% of the 0.05-0.002 mm fraction and 5% of clay was used. The soil material from the Ap horizon was sieved through a 5 mm screen and then packed into glass cylinders. The cylinders were about 45 cm long and 6 cm in diameter. The bulk density of the soil in the cylinders was about 1.1 Mg m^{-3}. Seeds of *Pisum sativum* (cv. I³owiecki), *Zea mays* (cv. Alma F1) and *Triticum aestivum* (cv. Rosa and CZR 1406) were germinated in a thermostat chamber for about 5 days and then transplanted into the cylinders. A few days were allowed for the plants to establish their root system. Soil conditions were differentiated by changing two physical parameters, i.e., soil moisture and soil temperature. The temperature of both the roots and shoots was maintained at 25 ^{o}C for the first few days.

The 8-day old seedlings were subjected to differentiated aeration conditions (control with pore water pressure about 15 kPa and flooded) for 12 days at three soil temperatures (7, 15 and 25 ^{o}C). The shoots of the seedlings were grown at the temperature of 25 ^{o}C while the soil temperature was differentiated by keeping the cylinders with the soil in the thermostated water of appropriate temperature.

At the end of the treatment the measurements of root porosity, root and shoot length and biomass were taken. Soil and other foreign particles were carefully removed from the roots. Root porosity was measured by the pycnometer method [14] to quantify the fractional air space formation in the roots. Relative humidity was maintained at 40% and illumination at 100 Wm^{-2} lasted for 16 h per day for each experiment. The roots were examined visually to observe the effect of various treatments.

Redox potential (*Eh*) was measured using four platinum electrodes and a saturated calomel electrode (as the reference electrode) and a laboratory pH-meter (Radiometer PHM 64). The electrodes were placed at the depth of 2, 10 and 25 cm. The measurements were taken after stabilisation of the readings (usually 5 min). All the data were subjected to analysis of variance, using Statgraphics 5.

RESULTS AND DISCUSSION

Shoot mass of the control treatments (Fig. 1) increased with temperature within the entire range studied for all the investigated species. The increase of the shoot biomass of the control plants with temperature was distinct in the case of winter wheat (cv. Rosa) and of maize (6-7 fold in the range from 7 to 25 ^{o} C) and rather moderate for winter wheat cv. CZR 1406 and peas (about 2 fold for the temperature interval). Under flood conditions, shoot biomass was much lower as compared to the control and a significant positive effect of temperature on the shoot biomass of the flooded plants was visible only in the case of the pea plants. For other plants, only an insignificant increasing tendency occurred at 15 ^{o}C and then at 25 ^{o}C a decreasing tendency was observed. That indicates that the negative effect of oxygen deficiency was the most pronounced at the highest temperature levels.

The root biomass (Fig. 2) was significantly stimulated by the increase of temperature for the pea and maize plants under control conditions. In the case of winter wheat varieties, an increasing tendency towards root biomass growth with temperature was observed to 15 ^{o}C, while at 25 ^{o}C even a small decreasing tendency occurred. This would indicate that the increase of root biomass was decreased due to luxurious

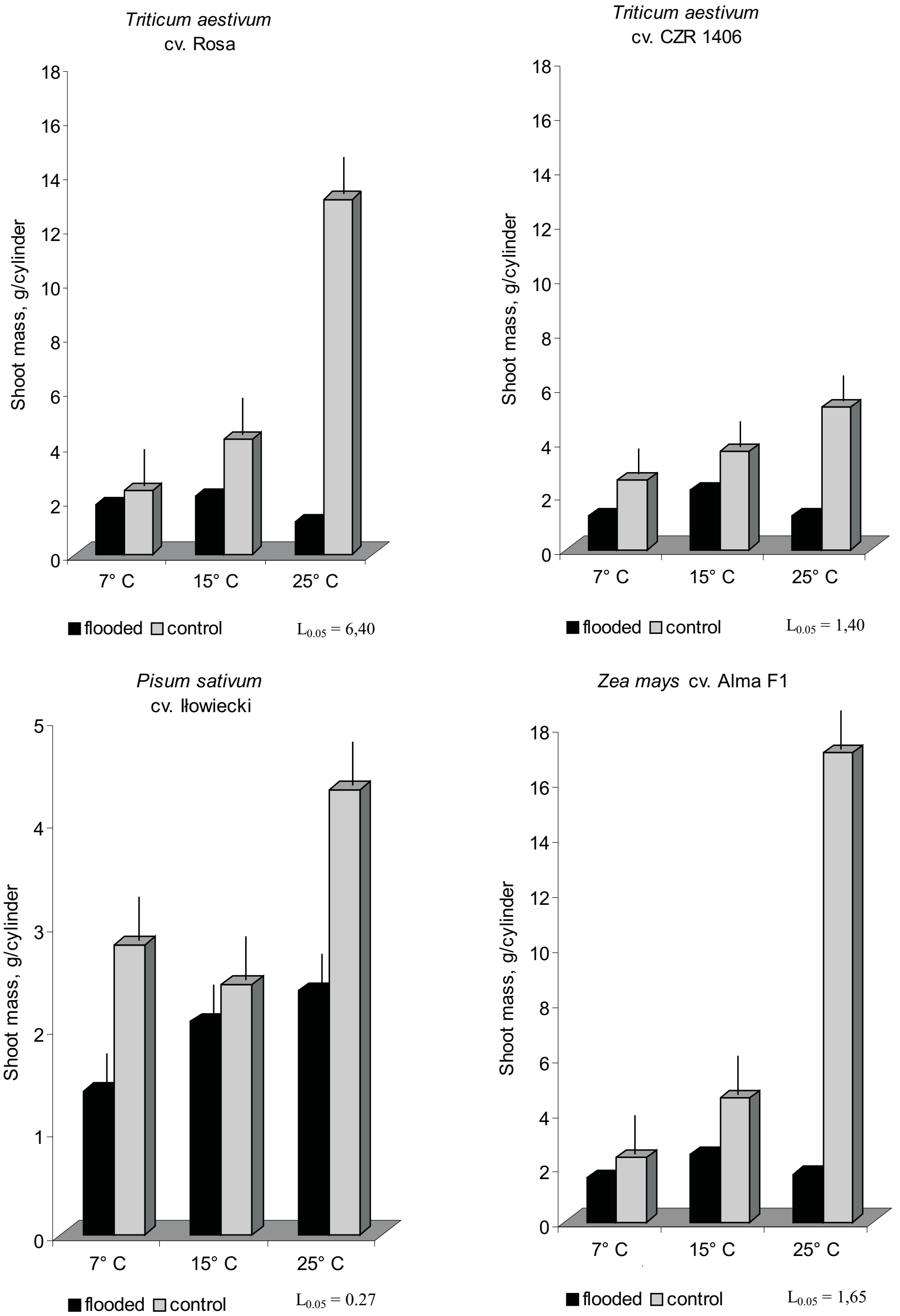

Fig. 1. Shoot biomass of two varieties of winter wheat, pea and maize plants under different experimental treatments. The bars denote 95% Tukey's half-intervals for the effect of temperature where significant differentiation occurred. The intervals related to the flood effect are indicated below the temperature axis as $L_{0.05}$.

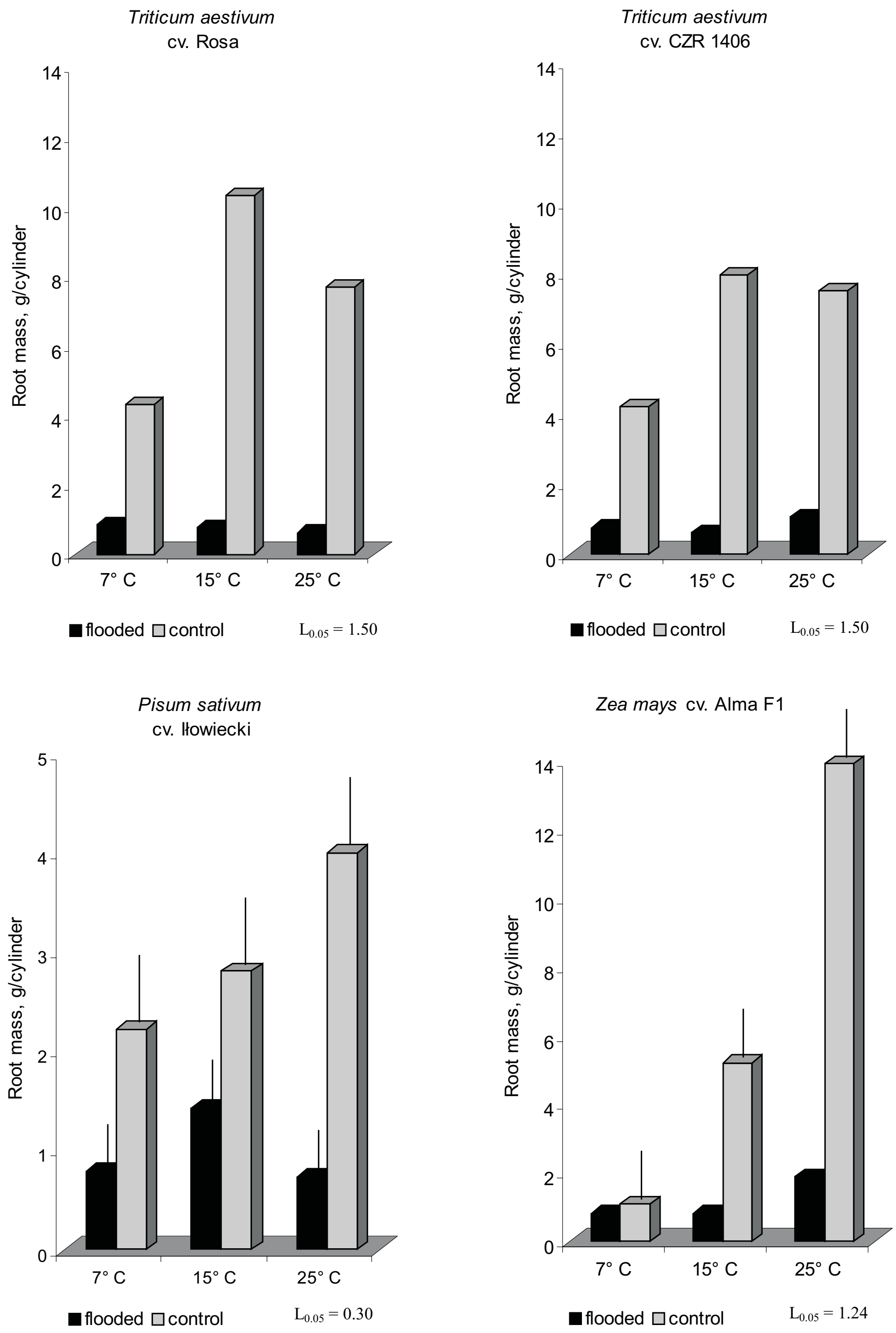

Fig. 2. Root mass of wheat, pea and maize under flood and control conditions at three different temperatures. Explanations as in Fig. 1.

respiration. Root flooding caused a decrease in the growth of the root biomass in all the plants. Under flood conditions the root mass was not related to temperature, with the exception of pea plants, which showed the highest root mass at 15 ^{o}C as compared to 7 and 25 ^{o} C.

The depth of root penetration (Fig. 3) of the control plants generally increased with temperature. Soil flooding caused a 2-10 fold decrease of the root penetration depth with respect to the control. Under flood conditions, the root penetration depth of pea and maize was not significantly differentiated in the entire range of temperature levels.

Root porosity of the control winter wheat plants (Fig. 4) was about 3-4 % and did not show any significant relation to temperature. In the case of the control pea and maize plants, an increase in the root porosity levels by 1-2 % with an increasing temperature was observed. The quality of winter wheat roots in the flooding treatments at 15 and 25 ^{o}C and of the maize roots at 25 ^{o}C was so bad that their porosities could not be estimated. Thus, flooding caused an increase in the root porosity where such observation was possible, i.e., in the entire temperature range for the pea at 7 and 15 ^{o}C for the maize, and only at 7 ^{o}C for both winter wheat cultivars. The results obtained suggest that the plant adaptation in the form of aerenchyma formation is efficient for wheat only at 7 ^{o}C, and for maize at 7 and 15 ^{o}C, when the respiratory activity is not too high. Pea plants can adapt in the entire temperature range under consideration.

The effect of the experimental treatments (flooding and soil moisture tension of 15 hPa) at three soil temperatures (7, 15 and 25 ^{o}C) on the shoot and root mass, root penetration depth and root porosity are presented in Table 1.

Many non-wetland plants have low gas-filled porosity when growing under adequate external aeration, but can produce roots with more porosity when aeration is insufficient [7]. Increased porosity is normally based on the lysis of cortical cells in the young roots at some distance from the root tip. Small changes in the gas-filled root porosity in the range 0-10 % (v/v) exerted a major effect on the distance at which the root can penetrate into a poorly aerated medium [6]. Development of gas filled root porosity in response to temporary low oxygen supply was tested by Van Noordwijk and Brouwer [23]. They showed, that the roots of maize had higher gas-filled porosity, when grown permanently in the non-aerated solution. In a second experiment, a comparison was made between high (20 kPa) and low (about 2 kPa) O_2 partial pressure in a recirculating nutrient solution. Young plants of wheat, sugar beet and cucumber had *Eg* in the range of 3-8 % (v/v), but in older plants these values ranged from 1 to 3%.

Some authors [8,19,20] proposed a hypothesis that an increase in the aerenchyma content can provide sufficient O_2 for aerobic root metabolism under hypoxic-anoxic conditions. However, despite the existence of an extensive aerenchyma system for O_2 supply, this system may be overwhelmed under extreme anaerobiosis. There are many occasions during the vegetation period when temperatures of the root zone remain low while shoots are subjected to much warmer conditions.

Aston [1] investigated some of the effects of such conditions on wheat. Plant roots were exposed to alternating day and night temperatures varying between 2 and 25 ^{o}C while shoot temperature was kept constant. He found that dry matter production and leaf expansion increased with an increasing root-zone temperature. Hay and Tunnicliffe Wilson [11] reported that the rate of leaf appearance in winter was controlled by the soil temperature. In addition, leaf extension rate was linearly related to the cumulative soil temperature.

Leaf extension seems to be controlled by the root-zone rather than shoot temperature in other grasses, such as *Hordeum vulgare L.* [10], *Lolium perenne L.* [21], and *Zea mays L.* [25].

While the root - zone temperature clearly influences plant growth, the physiological basis for this response has not been thoroughly investigated. Kaufmann [16] suggested that low root-zone temperature (0-5 ^{o}C) had an important

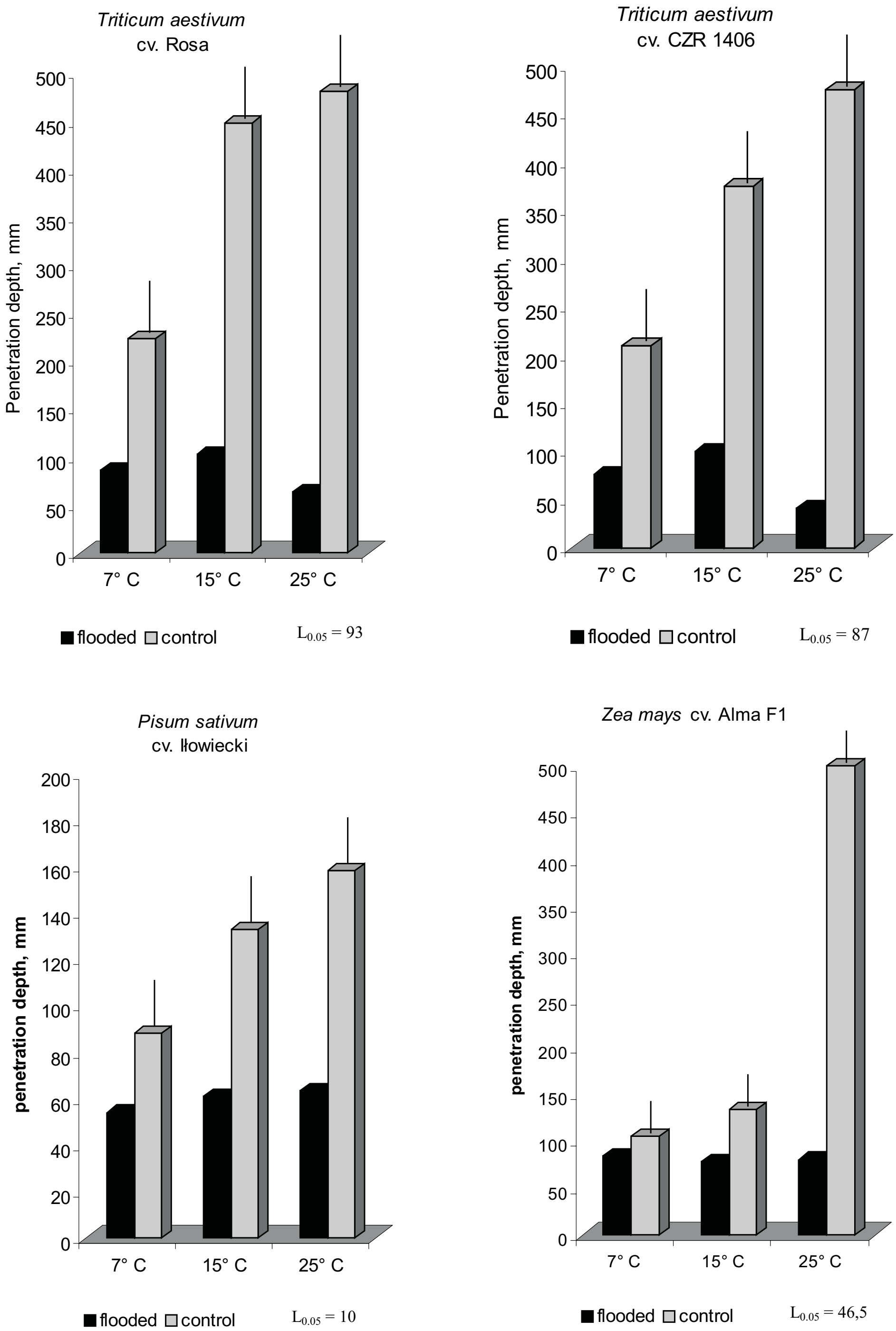

Fig. 3. Root penetration depth of the investigated plants under different experimental treatments. Explanations as in Fig. 1.

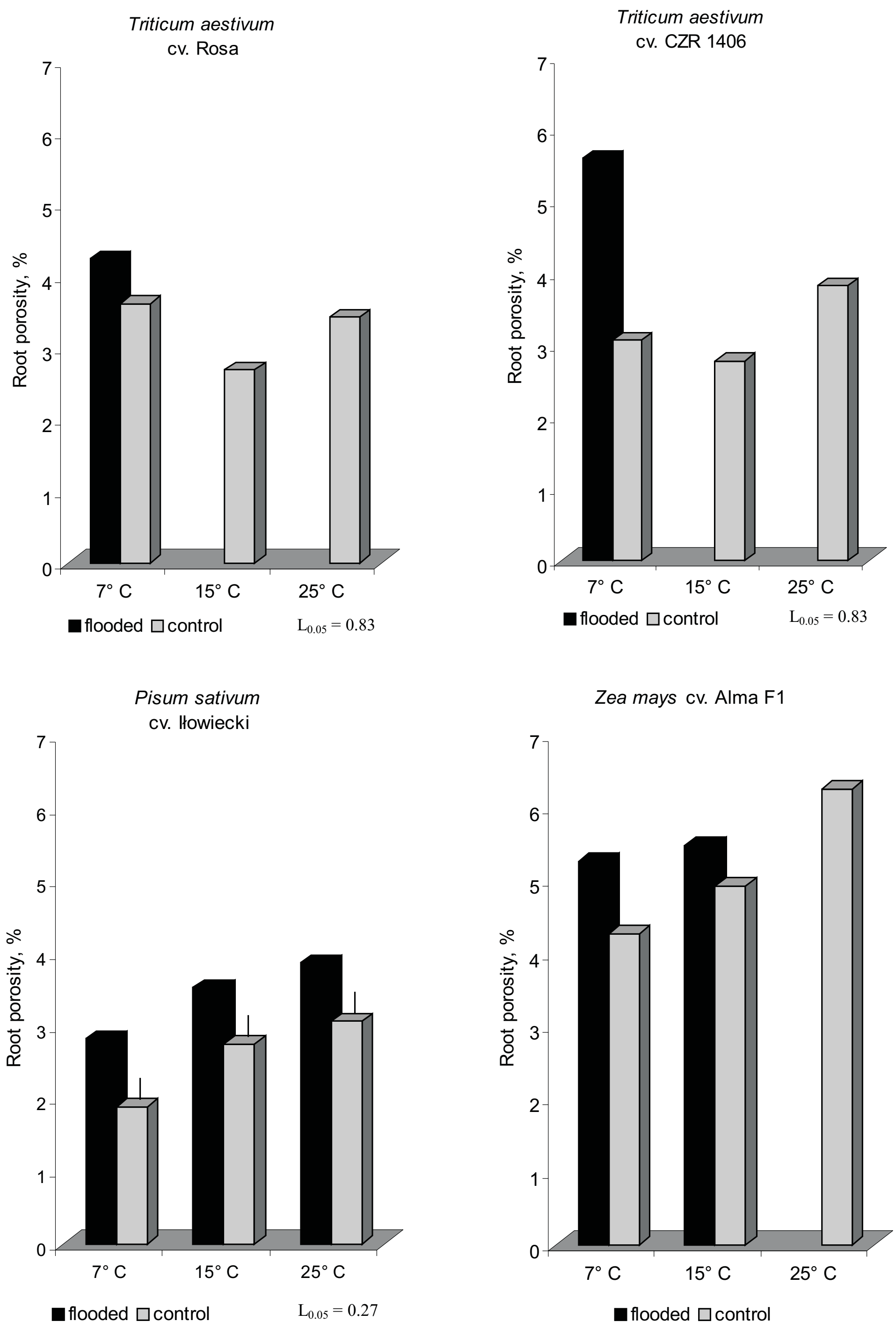

Fig. 4. Root porosity of wheat, pea and maize plants under different treatments. Explanations as in Fig. 1.

T a b l e 1. The effect of experimental treatments (flooding and soil moisture tension 15 hPa at three soil temperature 7, 15 and 25 ^{o}C) on the shoot and root mass, root penetration depth and root porosity

Treatment		Shoot mass	Root mass	Root penetration depth	Root porosity
		Winter wheat cv. Rosa			
Flooding		-	-	-	+
Temperature	control	+	+	+	0
	flooded	0	0	0	n.d.
		Winter wheat CZR 1406			
Flooding		-	-	-	+
Temperature	control	+	+	+	0
	flooded	0	0	0	n.d.
		Pea cv. Iłowiecki			
Flooding		-	-	-	+
Temperature	control	+	+	+	+
	flooded	+	-	0	+
		Maize cv. Alma F1			
Flooding		-	-	-	-
Temperature	control	+	+	+	+
	flooded	0	0	0	+

(+) significant increase at p=0.05, (-) significant decrease at p=0.05, (0) lack of significant effect, n.d. not determined.

effect on the reduction of water uptake by wheat. Manipulation in the water status of a plant could influence most physiological responses, which might be reflected in the plant growth response to the root-zone temperature.

The plants were grown under redox potential values varying from 400 to 480 mV. A decrease of redox potential under flooding conditions to 180, 145 and 69 mV at 7, 15 and 25 ^{o}C, respectively, was observed. Low redox potential conditions in the root zone could provide a more intense sink for O_2 diffusing from the atmosphere. In addition, plant growth could have decreased with a decrease in *Eh* as a result of inhibition of the nutrient uptake, which in turn could affect photosynthetic activity in plants [4] and as a result of accumulation of the potentially toxic substances, which could impair normal physiological functioning of plants.

The obtained results suggested that the amount of aerenchyma was sufficient to provide the root system with enough O_2 to support aerobic respiration at 7 and 15 ^{o}C under flooding conditions for maize plants, and for pea plants in the entire investigated range of temperature levels. A number of studies of wetland species showed an increase in the aerenchyma formation in response to flooding [2,22]. Root porosity of sunflower, corn and wheat were greatly increased in the full-flooded as compared to non-flooded conditions [27]. Formation of new roots under flooded conditions by tomato, corn and sunflower was observed by Kramer and Jackson [12,17].

Twenty-day old pea seedlings can survive flooding conditions lasting for 12 days at 7, 15 and 25 ^{o}C in the root zone, maize seedlings at 7 and 15 ^{o}C and winter wheat only at 7 ^{o}C.

CONCLUSIONS

1. Among the plant cultivars studied (winter wheat, maize and pea), the pea turned out to

be most flood resistant. The roots of pea survived flooding conditions lasting for 12 days in the entire temperature range. Their porosity increased by about 1-2 % of the root volume under flooded conditions as compared to the control treatments. Root penetration depth of the pea plants under control conditions increased with the increase of the soil temperature.

2. The roots of winter wheat plants grown at 7 °C survived flooding conditions lasting for 12 days. Their porosity increased by 1 % of the root volume for Rosa and 2.5% for CZR 1406 varieties under flood conditions. The root penetration depth under flood conditions increased with the increase of the soil temperature.

3. The maize plants suffered most from the flooding at 25 °C (the lowest root biomass and the quickest plant necrosis). Root porosity in the control treatments of the maize plants was within 4-6 % of the root volume and showed an increase in the entire investigated range of temperature levels.

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