Enhanced tolerance of high-p plants to environmental stresses is related to primary root diameter and potential root hydraulic conductivity for water and nutrient uptake

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Abstract

Glasshouse and field experiments were conducted over a period of 8 years to understand the mechanism of tolerance to environmental stresses, particularly in response to increased soil phosphorus concentration. Studies included factorial experiments on white clover, cotton, and wheat subjected to frequent defoliation, water deficit and/ or waterlogging stresses in different agro-climatic conditions. Morphological, physiological and anatomical measurements indicated importance of root growth and root activity, particularly the potential root hydraulic conductance of basal primary roots and associated uptake of water and nutrient under environmental stresses. An increased supply of soil phosphorus above adequate amounts appears to increase the potential root hydraulic conductance per unit leaf area as a result of substantial increases in the number and size of xylem vessels. Under adverse environmental conditions, high-P supply also appears to increase the leaf expansion rate, size of the cell, and the size and number of vacuoles in each cell to store more solutes and water.

Key words

Root hydraulic conductance, water uptake, environmental stress, phosphorus, xylem vessel.

Introduction

Evidence in the literature suggests that the tolerance of many crop and pasture species to environmental stresses is enhanced by increased phosphorus supply (1,2,3,4). For example, Singh *et al*. (4) reported that increased P supply for white clover plants improved the soil-plant water relations and extraction of water from a severely drying soil compared with the low-P plants. In subsequent experiments, Singh and Sale (5) noted thicker primary roots for the high-P plants compared with the low-P plants, particularly under dry conditions. Similarly, O'Toole and Chang (6) found drought resistant rice varieties to have longer roots that were thicker in diameter than those of susceptible varieties. They concluded that these roots supplied essential water during drought. In support, Radin and Eidenbock (1) reported that there was an increased capacity of the root system to transport water from dry soil to the shoots of high-P cotton plants, as compared to low-P plants.

An increase in root diameter, however, also suggests a wider stele with more xylem vessels in the high-P roots. Any change in the diameter of xylem vessels has a profound effect on the potential hydraulic conductance of that vessel, given that the hydraulic conductance of a narrow vessel is proportional to the fourth power of the vessel radius for ideal capillaries (Hagen-Poiseuilles law) (7). In this study we aim to examine whether increased root thickness and/ or changes in xylem diameter and density of primary roots can explain the beneficial effects of high P levels on tolerance of plants to environmental stresses.

Methods

Numerous experiments were conducted under control or field conditions between 1994 and 2002. Treatments included the factorial combination of various P levels, defoliation frequency, and soil water regimes. It should be noted that low-P plants by no means were P-deficient plants. The soil-P level for the low-P plants was always >10 Olsen-P (mg P/kg soil, bicarbonate extraction), and the low-P plants never showed any P-deficiency symptoms. Treatments in each experiment were provided with adequate levels of other major and minor plant nutrients. Key measurements were made of the biomass, water uptake, leaf area and leaf expansion rate, thickness of basal primary roots, size and density of xylem vessels (as noted from the cross section of the thickest nodal root for white clover and wheat, or the tap root for cotton). The potential hydraulic conductance of basal primary roots was estimated from the mean diameter and mean number of xylem vessels in the primary roots (Hagen-Poiseuilles law) (7). The experimental design, treatment combinations, growing conditions and measurement details of some experiments have been described in the following publications (5,8,9,10).

Results

An enhanced P supply markedly increased (*P*<0.05) the biological yield, water and nutrient (P) uptake for various plants subjected to environmental stresses compared with the low-P plants (Table 1). In particular, morphological studies indicated that basal primary root diameter of white clover and cotton subjected to dry soil conditions, and the thickness of adventitious nodal roots for wheat under waterlogging, increased (*P*<0.05) with increasing P supply (Table 1).

Table 1. Effect of P supply on the means of root diameter, xylem number, water uptake and biomass yield, for white clover plants subjected to frequent defoliation and dry soil, for cotton plants subjected to dry soil, and for wheat under waterlogged conditions. Different letters indicate that values are significantly different (*P*<0.05).

Plant species	Stress	Treat.	Root diameter (mm)	No. of xylem vessels	Water uptake (kg)	Biomass (g)	Nutrient (P) uptake (mg)
W. clover	Def &	Low-P	1.2a	231a	1.2a	1.2a	0.18a
	Water	High-P	1.8b	551b	4.2b	9.1b	2.55b
Cotton	Water	Low-P	12.5a	870a	39.4a	67.0a	16.08a
		High-P	15.7b	615b	67.8b	122.0b	42.70b
Wheat	O_2	Low-P	1.4a	-	0.2a	0.23a	-
		High-P	2.2b	-	0.5b	0.87b	-

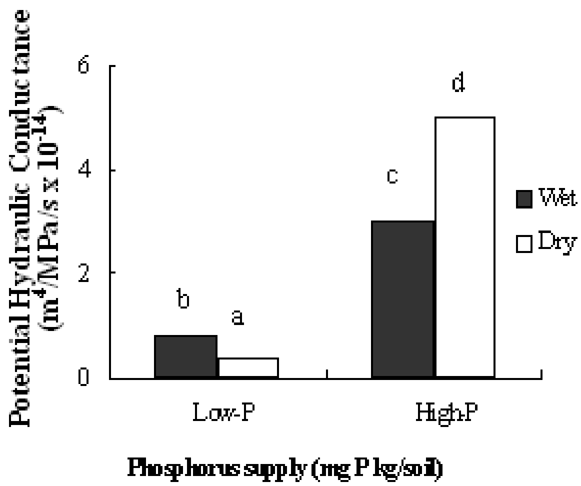

Figure 1: Effect of P supply and soil water treatments on the potential hydraulic conductance, estimated from the mean number and diameter of xylem vessels in primary roots of frequently defoliated white clover plants (9). Different letters indicate that values are significantly different (*P*<0.05)

Anatomical studies further highlighted the influence of xylem density and size on the potential hydraulic conductance, which increased many folds between low and high-P treatments (Fig. 1). The hydraulic conductance per unit leaf area increased by 2.6 fold with increased P supply, which also had a more marked effect on the stele of the root compared to the cortex (9). The development of extra vascular tissue in high-P plants contributed to an increase in the cross sectional area of roots in high-P plants. It is also important to note that the size of the xylem vessels appears to be dependent on the plant species and root thickness. For example, the very thick tap-root of a cotton plant had xylem vessels with much larger diameters (80 μm) than those in nodal roots of white clover (30 μm) (Plate 1, Table 1).

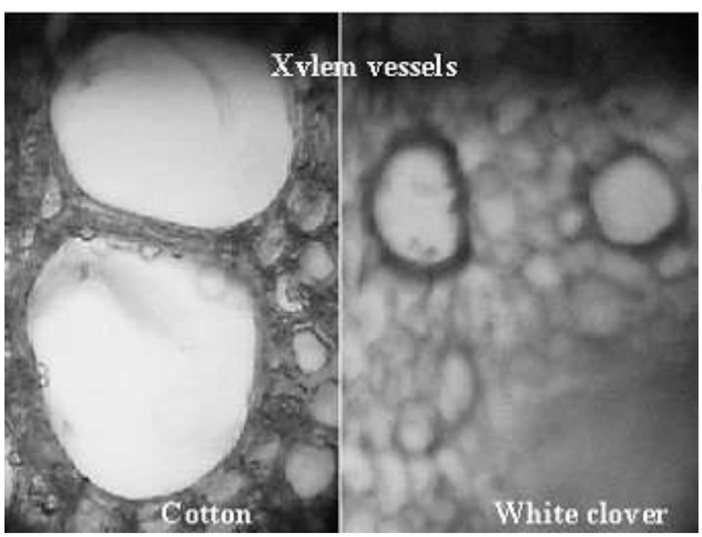

Plate 1. Micrograph showing comparative sizes of a typical group of the largest xylem vessels in the roots of high-P cotton (80 μm in diameter) and high-P white clover plants (30 μm in diameter) at the same magnification, 90x.

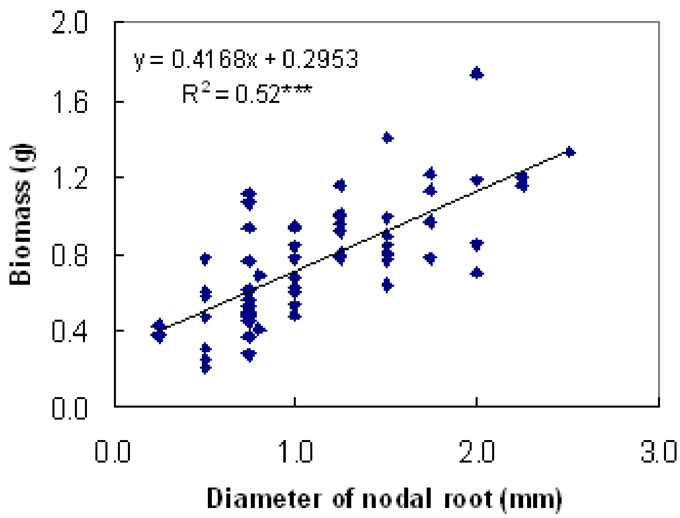

Figure 2: Relationship between total plant biomass and diameter of the thickest adventitious nodal root, across eight wheat and one triticale cultivars subjected to control or waterlogged conditions (for details please see paper 188 in this conference).

Physiological studies have indicated that, compared to low-P plants, high-P plants have larger cell sizes with distinct vacuoles, indicating a greater cell-wall expansion, and an increased storage capacity for water and solutes required for expansive leaf growth (10). There is also a highly significant positive relationship between hydraulic conductance and leaf area, and between hydraulic conductance and the rate of water uptake (9). A strong relationship between the thickest adventitious nodal root and biomass has also been noted (Fig. 2) from a recent experiment on “Screening of tolerant and susceptible wheat varieties to waterlogging” (see paper 188 in this conference). This particular study included six spring and two winter wheat varieties, which were compared with a line of triticale tolerant to waterlogging. In our context, Christopher *et al*. (11) (in lucerne) reported that at the end of the flooding period, seedlings provided with banded-P were larger than the flooded, no-P controls.

Conclusion

Increasing the P supply for the plants under environmental stresses increased the primary root diameter and the size and density of xylem vessels compared with the low-P plants. There was a proportionally greater increase in the potential hydraulic conductance of roots with that of total leaf area with increased P supply,such that potential conductance per unit of leaf area was greater for the high-P roots compared with the low-P roots (8). This study clearly demonstrates the thickness and associated potential root hydraulic conductance of the primary roots as important factors contributing to the tolerance of high-P plants to environmental stresses. The increased capacity of the primary roots of high-P plants to conduct water might generate additional suction to extract water and nutrients from a drying soil. This would further assist the high-P plants in tolerating adverse soil conditions, as they had less likelihood of conductivity constraints in meeting the increased transpirational demand from their larger leaf areas. Radin and Eidenbock (1) noted that differences in hydraulic conductance due to low-P supply clearly preceded any effects on leaf area development, and concluded that hydraulic conductance limited the leaf expansion by restricting water transport.

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