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Effect of soil water content on the gravitropic behavior of nodal roots in maize

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Abstract

The direction of root growth is an important factor that determines the spatial distribution of roots in the soil. The influence of soil water content on the direction of growth of maize nodal roots was studied both in the field and in the greenhouse. In the field experiment, the one plot was regularly irrigated (I-plot) and the other non-irrigated (N-plot). In the greenhouse experiment, three water treatments were conducted on plants grown in pots: continuously wet (CW), early drying (ED), and late drying (LD). The direction of root growth was quantified by the angle from the vertical, measured at 1 cm intervals for 10 cm from the first five internodes. Nodal roots grew more vertically in the N-plot and ED treatment than those in the I-plot and CW treatment. This was due to the decrease of the initial angle and/or the liminal angle. It is therefore thought that two events regulate the growth direction of nodal roots under dry soil conditions: gravitropic bending at root emergence from the stem and the later establishment of the angle of growth. Nodal roots appearing after rewatering in the ED treatment grew in a similar direction as those in the CW treatment. It follows from this that the water content of the surrounding soil has a direct effect on the direction of growth. Nodal roots that emerged in rapidly drying soil in the LD treatment ceased growing after showing negative gravitropism. The possible mechanisms determining the growth direction of nodal roots in drier soils are discussed.

Introduction

The growth of maize nodal roots is plagiogravitropic: most nodal roots of field-grown plants adopt a non-vertical orientation. The growth direction of nodal roots, somewhat horizontal at emergence from the stem, is settled in due course of time in an angle from the vertical, the liminal angle. The growth direction depends on the position of the internode from which nodal roots emerge; namely, the nodal roots from upper internodes have smaller liminal angles and grow more vertically (Yamazaki and Kaeriyama, 1982). The pattern of root distribution in the soil, which affects the water and nutrient availability of the plant, is determined by the growth direction of nodal roots from successive internodes (Nakamoto et al., 1991). Despite its importance to root morphology and ecology, little attention has been given to the growth direction of nodal roots.

Both genetic and environmental factors affect the growth direction of maize nodal roots (Chaudhary and Prihar, 1974; Jordan, 1987; Nakamoto et al., 1991; Tardieu and Pellerin, 1990, 1991). However, it remains unknown whether or how soil water, one of the most influential factors on the root distribution, affects the growth direction of individual roots. It is reported that osmotic stress enhances the gravitropic response of primary roots in maize (Leopold and LaFavre, 1988) and in wheat (Oyanagi et al., 1992). These results from laboratory experiments suggest the possibility that the gravitropic control of plant roots responds to the surrounding water status. Deeper rooting caused by soil water deficits (Mayaki et al., 1976; Newell and Wilhelm, 1987) may be involved with the downward change of the growth direction of nodal roots. The objective of this study is to examine the details of the growth direction of maize nodal roots paying special attention to soil water content.

Materials and methods

The experiments were conducted at the Experimental Farm, Faculty of Agriculture, The University of Tokyo, Japan, in 1992.

Field experiment

The soil was volcanic ash of the Kanto loam type, Humic Andosol. Soil bulk density was $0.68\,g\,cm^{-3}$ and soil strength, measured with a penetrometer (25°20′ cone, strength of spring $1.96 \times 10^3\,Nm^{-1}$), was less than 0.5 MPa in the topsoil (0–30 cm). Volumetric water content of the soil was about 0.50 at field capacity. A piece of land 8 × 4 m was moated to prevent the inflow of surface water and roofed at a height of 3 m with a transparent PVC sheet to shelter it from the rain. Chemical fertilizer, 4.8 g N, 7.2 g P_2O_5, 6.4 g K_2O per m^2, was applied to the soil surface before sowing. On April 26, maize seeds, *Zea mays* L. cv. Nagano 1, were sown at a depth of 5 cm, in rows 70 cm apart, with hills spaced at 20 cm intervals. Plenty of water was applied for a week after sowing. The field was then divided into two plots. One half (I-plot) was irrigated twice a week and the other half (N-plot) was non-irrigated. Volumetric soil water content was measured at depths of 5, 10, and 20 cm. Sixty-one days after planting (DAP) plants were sampled from the middle of each plot to measure the growth direction the nodal roots.

Greenhouse experiment

Surface soil of the experimental farm was collected, air-dried, sieved through a 3 mm mesh screen, and mixed with chemical fertilizer at a rate of 0.06 g N, 0.09 g P_2O_5 and 0.08 g K_2O per kg. Plastic pots, 25 cm in diameter, were filled with the soil to a depth of 25 cm. The soil bulk density was $0.79\,g\,cm^{-3}$. One seed of maize cultivar Nagano 1 was sown into each pot at a depth of 3 cm. To study the effect of soil water content on the growth direction of nodal roots, the pots were divided into three groups according to water content.

1. Continuously wet (CW): the soil was watered every day and volumetric soil water content was adjusted to about 0.45
2. Early drying (ED): the soil was watered until 10 DAP, unwatered to 35 DAP, and then watered again, keeping water content at about 0.45
3. Late drying (LD): the soil was watered until 23 DAP and then left to dry.

Volumetric soil water content was obtained by weighing the pots. It was approximately 0.51 at field capacity and 0.20 at the wilting point. Plants were occasionally sampled to determine the time of nodal root emergence from successive internodes. On 56 DAP plants were sampled to measure the growth angle of the nodal roots.

Measurement of the growth direction of nodal roots

Plants were carefully excavated and washed with tap water so that the nodal roots were visible. The nodal roots were trimmed to about 10 cm from stem and branch roots were removed. The plant was then suspended vertically and left for about half an hour for air-drying. Since nodal roots have form elasticity, they regained their original three-dimensional trajectories, at least within the basal 10 cm. The trajectory of a nodal root was, as a rule, on the vertical plane including the plant axis. A projection of trajectory on the vertical plane was obtained by tracing it on a transparent sheet. Preliminary studies showed no significant difference between trajectories obtained by this procedure and those traced on

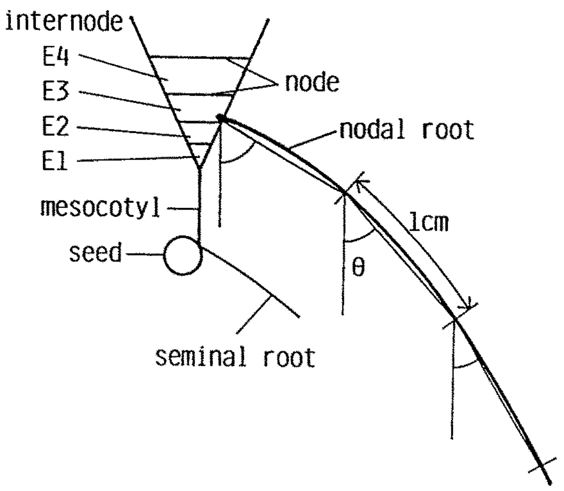

Fig. 1. The growth angle of nodal roots. The angle of growth (θ), degrees of deflection from the vertical, is measured for each 1 cm length of a nodal root.

intact soil profiles. The trajectory was digitized with a step of about 2 mm on a computer assisted digitizer with a resolving power of 0.01 mm. The angle between the vertical and the tangent to the root axis, the growth angle, was calculated for each 1 cm length of basal 10 cm of the nodal root (Fig. 1).

Nodal roots were measured on plants without injured seminal or nodal roots, since any injured root might influence the growth of others. All nodal roots from the first five internodes were studied (Table 1). The internodes and the nodal roots were numbered acropetally, 1, 2, . . . , *i*, and designated as E_1, E_2, . . . , E_i and E_i roots (Picard et al., 1985). The growth angle was calculated as a mean of the nodal roots from each internode on the plant. The number of plants measured was five for the N- and I-plots in the field experiment, ten for the CW, and five for the ED and LD treatments in the greenhouse experiment.

Results

Field experiment

While the soil water profile of the irrigated plot (I-plot) was almost steady throughout the experiment, that of the non-irrigated plot (N-plot) reached a steady state at about 21 DAP (Fig. 2). Although shoot growth of the N-plot plants was retarded (12 leaves on 61 DAP compared 14 leaves in the I-plot), E1–E5 roots appeared in both plots. E1–E5 roots in the I-plot emerged and grew under the soil water conditions shown in profile I. On the other hand, E2–E5 roots in

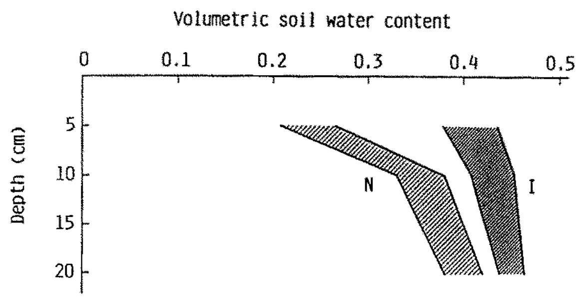

Fig. 2. The soil water profile from 21 to 61 days after planting in the field experiment. Volumetric soil water content in the irrigated plot (I) and in the non-irrigated plot (N) remained within the range of the hatched area.

Table 1. Mean number of nodal roots emerging from successive internodes in maize

Treatment	Internode				
	E1[a]	E2	E3	E4	E5
Field experiment					
Irrigated (I–plot)	3.8	3.8	2.8	5.4	6.8
Non-irrigated (N-plot)	4.0	3.6	2.6	4.0	5.8
Greenhouse experiment					
Continuously wet (CW)	4.4	4.1	4.4	6.2	8.3
Early drying (EW)	4.6	4.2	3.6	4.0	4.0
Late drying (LD)	—	—	3.0	0.0	0.0

Data are from five plants except for ten plants for CW.
[a] E1 is the internode between coleoptile and the first leaf.

the N-plot, which emerged after 21 DAP, grew in drier soil as shown by profile N. E1 roots in the N-plot experienced decreasing soil water from profile I to N. There was no significant difference in soil temperature between I- and N-plot. Mean maximum and minimum temperature during the experiment at a depth of 5 cm were 26°C and 18°C, those at a depth of 10 cm were 22°C and 18°C.

E1–E5 roots grew more vertically in N-plot than in I-plot, as the angle of growth was smaller in N-plot (Fig. 3). This was mainly because the initial angle, the growth angle measured at the most basal part of nodal roots, was significantly smaller in N-plot. E2–E5 roots in both plots did not seem to attain the liminal angle at 10 cm. However, the asymptotic change of the angle of these roots suggested that the liminal angle was smaller in N-plot than in I-plot. E3 roots in the N-plot showed negative gravitropism and the growth angle at 10 cm was larger than the initial angle.

Greenhouse experiment

Figure 4 shows the volumetric soil water content and dates of the emergence of nodal roots in each treatment. In the CW treatment, E1–E5 roots appeared at intervals of about eight days. In the ED treatment, E1 roots emerged soon after the cessation of watering and grew in rapidly drying soil. E2 and E3 roots grew under very dry conditions. The ED plants, having stopped growing and wilted by 35 DAP, developed E4 and E5 roots after rewatering. In the

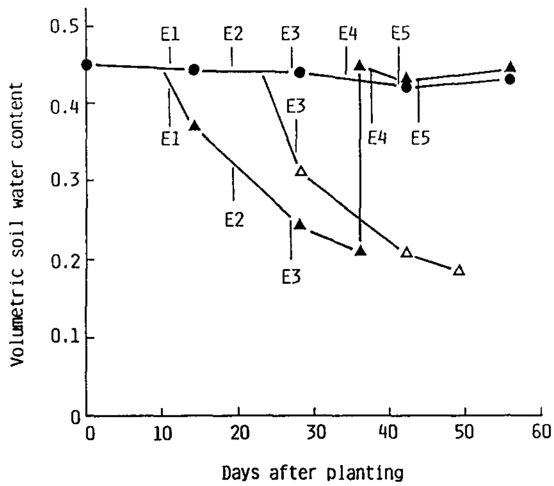

Fig. 4. Volumetric water content of the soil in the CW (circle), ED (triangle), and LD (open triangle) treatments of the greenhouse experiment. Vertical *bars* indicate the approximate time of nodal root emergence.

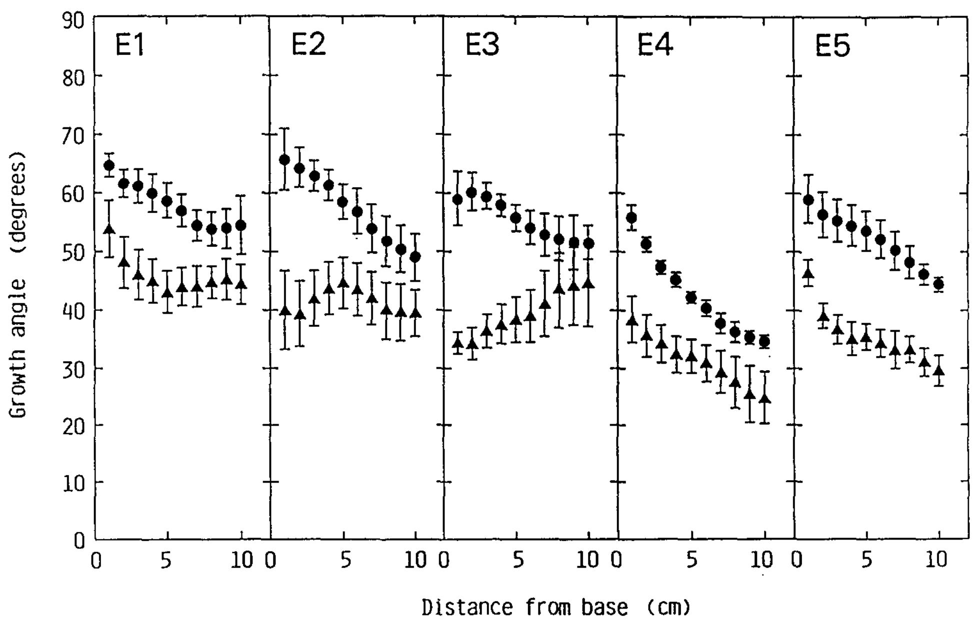

Fig. 3. The growth angle of nodal roots from the 1st to 5th internode (E1–E5) in the irrigated plot (circle) and in the non-irrigated plot (triangle) of the field experiment. Data with standard error are the mean of five plants.

LD treatment, E3 roots appeared when the soil water content declined rapidly after drying began. E4 roots did not appear in LD. The mean maximum and minimum soil temperatures at a depth of 5 cm in the CW treatment were 27°C and 18°C, respectively. The mean maximum temperature was about one degree higher in the ED and LD treatments.

E1–E3 roots of the CW treatment showed typical plagiogravitropic growth and had more or less a constant growth angle from base to 10 cm, suggesting a liminal angle (Fig. 5). The growth angle decreased with distance from root base discernibly in E4 roots and conspicuously in E5 roots of CW.

While the initial angle of E1 roots in the ED and CW treatments did not differ, that of E2 and E3 roots were significantly smaller in ED than in CW. E1–E3 roots in ED showed an asymptotic change in the growth angle and attained a liminal angle at 10 cm. The liminal angle of these roots was smaller than that of CW. Because of the smaller initial angle and/or the smaller liminal angle, the growth angle of E1–E3 roots was, as a whole, smaller in the ED treatment than in the CW treatment. That is, the nodal root in the dried soil of the ED treatment grew more vertically than the roots in CW. In this connection, it must be noted that there was an overall increase in the growth angle of E2 and E3 roots in ED, which means that these nodal roots showed negative gravitropic response; the growth direction, more vertical at emergence, was adjusted toward the horizontal in due course of time. Despite the difference in soil water history from 10 to 35 DAP, the nodal roots of the ED treatment appearing after rewatering, E4 and E5 roots, showed a quite similar growth angle to that of E4 and E5 roots in the CW treatment, respectively.

In the LD treatment, E3 roots ceased growing at about 8 cm. These roots started growing more vertically than those in CW but changed their growth direction upwards. The angle of growth attained by the end of growth was much larger than the liminal angle in the CW treatment.

Discussion

The growth of the nodal roots of cereal plants is referred to as plagiogravitropic (Oyanagi et al., 1993) because the nodal roots elongate nearly straight from plant retaining their initial angle,

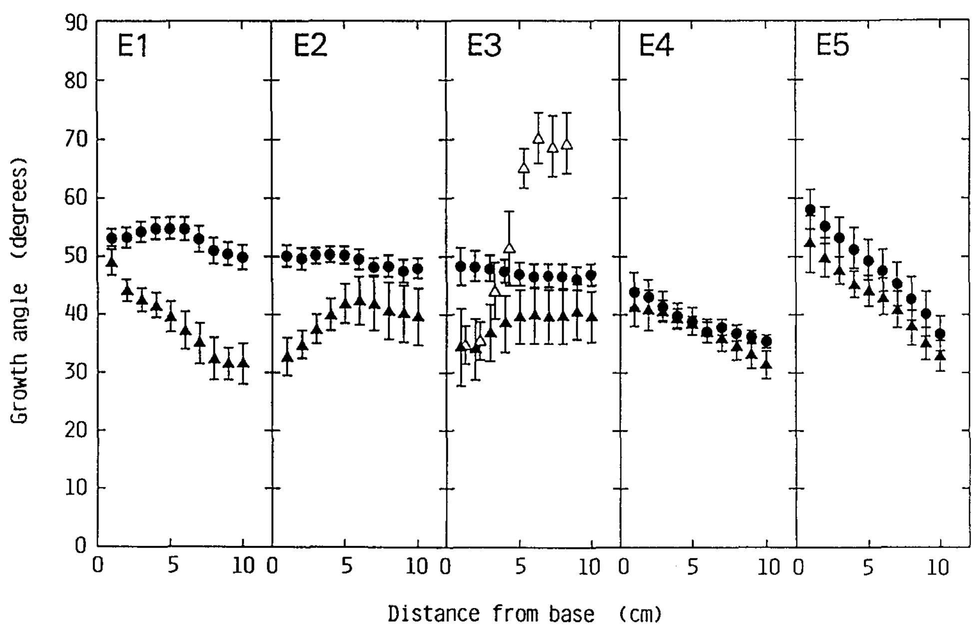

Fig. 5. The growth angle of nodal roots from the 1st to 5th internode (E1–E5) in the greenhouse experiment. CW (circle), ED (triangle), and LD (open triangle) treatments. Data with standard error are the mean of ten (CW) or five (ED, LD) plants.

or establish a liminal angle if they respond to gravity. One noteworthy result of this study is that soil with low water content induces a decrease in both the initial angle and the liminal angle. While the initial angle is easy to measure, it is rather difficult to estimate the liminal angle unless the angle of root growth is constant or asymptotical. The liminal angle, when it can be estimated by measuring the basal 10 cm of the root, does not seem to be closely correlated with the initial angle of the same root: the liminal angle can be smaller or larger than the initial angle accordingly as the root displays positive or negative (e.g. E2, E3 roots in the ED treatment in Fig. 5) gravitropism. The environment at the site of root emergence, where physical properties of the surrounding air, leaf sheaths and soil affect root growth, may be quite different from the soil environment the root tip experiences at later stages. From our results, the initial angle seems to be more sensitive to low soil water content than the liminal angle. However, the liminal angle may be more decisive of the global spread of a root system because it controls the orientation of remote plant roots.

The direction of root growth is influenced by both intrinsic and extrinsic factors. We can indicate an intrinsic control on the growth angle from the results from the CW treatment (Fig. 5). Nodal roots from different internodes grow in different directions depending on internode position, even if they grow under similar soil water conditions. This suggests the existence of an internal control within the plant on the direction of root growth, which enables nodal roots to grow in various directions and to explore soil effectively. On the other hand, the smaller growth angles of the N-plot (Fig. 3) and of the ED treatment (Fig. 5) make it clear that low soil water content, an external factor, induces nodal roots to grow more vertically. The question arises, however, whether water stress has a direct effect on the growth zone of root tips or whether it influences the growth direction of roots indirectly through changes in the internal control mentioned above. The observation that E4 and E5 roots in the ED treatment appearing after rewatering show similar trajectories to those in the CW treatment (Fig. 5) supports the hypothesis that the surrounding water status directly affects the growth direction of the root tip. This result is in agreement with results from laboratory experiments on the enhancing effect of a low water potential on the gravitropic response (Leopold and LaFavre, 1989; Oyanagi et al., 1992). There seems to be no rational attempt to explain the influence of water on the direction of root growth except the 'water theory' (Kutschera, 1983), which stems from field observations as well as physiological experiments. According to the theory, the difference in water uptake between the upper and lower side of the root, interacting with the asymmetry of the root cap, causes bending of the root. It is worth noting that this theory partly explains the establishment of the growth angle, which is the last of a series of events in gravitropism but has yet to be thoroughly studied (Jackson and Barlow, 1981).

As for the drought habit of maize roots, high soil temperature is also an important extrinsic factor influencing the gravitropic behavior of nodal roots. The growth direction of maize seminal roots is the most horizontal at 17°C and became more vertical as the soil temperature increases up to 30°C (Onderdonk and Ketcheson, 1973). In our greenhouse experiment, the maximum soil temperature was higher by one degree in the drying treatments (ED, LD) than in the CW treatment. The more vertical growth of nodal roots observed in ED and LD may, therefore, be partly caused by high soil temperature. Since soil temperature depends on the extent of drought, its effect on the growth direction must be studied further. Other factors influencing gravitropic behavior are a temperature gradient and a water potential gradient. Both thermotropism (Fortin and Poff, 1991) and hydrotropism (Takahashi and Scott, 1991) interact with the gravitropic curvature of maize primary roots. In our field experiment, the temperature gradient between depths of 5 and 10 cm was no greater than 1°C/cm at daytime and seemed to be too weak to cause a thermotropic response. On the other hand, it is quite usual for a positive water gradient to exist in drying soil. Although the gradient strength required for a hydrotropic response is not known, hydrotropism could be involved in the marked decrease in the growth angles shown by E1 roots of the ED treatment (Fig. 5).

E3 roots in the LD treatment grew in a somewhat curious manner (Fig. 5). Although the initial angle seemed to be the same as in the ED treatment, the roots stopped growing after showing marked negative gravitropism. One explanation for this may be as follows. Due to the water history, the plants of LD were not as well adapted to drought as those of ED at the stage of E3 root emergence. The roots, having lost their ability to respond to gravity, due to physiological or morphological changes in dried tissue, could not penetrate downwards into the soil and were forced to grow more horizontally by the mechanical resistance of soil. There is much room for argument on this point. The physical nature of root-soil interaction influencing gravitropism remains to be studied.

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