Combined Soil Physical Stress of Soil Drying, Anaerobiosis and Mechanical Impedance to Seeding Root Growth of Four Crop Species

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Abstract: Soil compaction often creates combined physical stresses of drought, anaerobiosis, and mechanical impedance in field soil. This paper aims to analyze the effect of combined and independent soil physical stresses on crop root growth to find out the species-specific response to the physical stresses, which has not been reported before. Drying stress without the increase of mechanical impedance was evaluated in a very loose pot soil environment. This drying stress did not modify the root elongation rates of rice and pea by the 48 h exposure to the stress environment. For maize and cotton, however, mild drying stress (−80 kPa Ψₘ) enhanced root elongation by 17-18%, but severe drying stress (−900 kPa Ψₘ) reduced it by 17-21% as compared with the control environment (−10 kPa Ψₘ). The combined stress of drying and mechanical impedance nearly stopped the root elongation in all the species, while that of anaerobiosis and mechanical impedance did not stop the elongation of rice and cotton; cotton elongated about 32% of control environment. In maize, root diameter was reduced by the severe drying stress due to the reduction in the number of cortical cell layer and diameters of both central cylinder and xylem vessel. In contrast, cotton showed a significant increment of cortex diameter, although overall diameter was not statistically increased by the severe drying stress. The ability of cotton to continue elongation under anaerobic and mechanical stress implied the higher penetration ability to the hard pan layer under the anaerobic condition just after the heavy rainfall.

Key words: Cotton, Drought, Maize, Oxygen diffusion rates, Pea, Rice, Soil compaction, Waterlogging.

Agricultural field soils often offer unfavorable physical environment to crop roots. For example, soil compaction by the usage of heavy agricultural machinery usually creates combined physical stresses of drought, anaerobiosis, and mechanical impedance (Iijima and Kono, 1991, 1992). When the soil is very wet, e.g. just after a heavy rainfall, the decreased soil pore space by soil compaction produces an anaerobic environment together with higher mechanical impedance for root growth. In contrast, after several days of no rain, the soil becomes dry producing a drought environment plus high impedance to root growth.

Although there are many studies on the combined soil physical stresses in agricultural fields or artificial pot environments (e.g. Agnew and Carrow, 1985; Engelaar et al., 2000; Trautner and Arvidsson, 2003), few investigators have studied the root growth responses to different levels of combined soil physical stresses. Among them, Eavis (1972) used the pea radicle grown in a sandy loam soil under different levels of soil water potential and soil bulk density, and measured the length and diameter of the radicle as the criteria of the combined stresses under different levels of soil water, air and impedance status. Although he examined the threshold of three major stresses, he evaluated the aeration of the soil only by the air-filled porosities, which will serve different thresholds for different soil textures. Since he analyzed only the response of pea, the legume species, as the test plant, the threshold values to restrict root growth in his work may differ from that in the major cereal species such as maize and rice. Moreover, only the changes in root length and diameter were evaluated, and the responses of anatomical structures of roots to the combined stresses were not studied.

The effect of soil drought (and/or short-term soil drying) stress on plant root growth has been examined extensively, but few studies addressed the associated soil mechanical stress. Soil mechanical impedance usually increases as the soil become drier (Iijima and Kono, 1991, 1992). The extent of the increase of the mechanical stress depends on the soil bulk density, soil particle size distribution, soil structure, and so on. Therefore, the response of crop roots to drought (and/or soil drying) stress should be carefully evaluated by considering the increase of the associated mechanical stress, which depends on the soil physical properties.
used in the experiments.

In the present study, the root growth responses of four different major crop species to the combined and independent soil physical stresses of soil drying (short-term drought), anaerobiosis, and soil mechanical impedance were analyzed to examine whether the response differs among the species. We tried to separate the soil drying and mechanical stress, and evaluated the effects of drying and mechanical impedance, independently. Here, we used the oxygen diffusion rates for the quantification of anaerobic environment so as to acquire better criteria for the comparison of root growth in different texture of soil. Moreover, the anatomical response was also examined together with the root growth response to get deeper understanding of the root response to the combined soil physical stresses.

Materials and Methods

1. Physical analysis of soil

Air-dried loamy sand soil (sand 87.0%, silt 9.6%, clay 3.4%) was sieved through 2 mm mesh and packed in plastic cylinders, 50 or 100 mm in diameter and 50, 100, or 150 mm in height, at the bulk density of 1.00 (loose), 1.30 (lightly compact), 1.40 (compact) and 1.50 Mg m\(^{-3}\) (heavily compact). Physical environments were measured at various levels of soil water potential (\(\Psi_w\)) ranging from −1 (wet), −3, −5 (mild wet), −10 (field capacity), −20, −80 (mild dry), −900 (dry) kPa. Soil water – tension characteristics were measured by the pressure plate (Soil pF meter, DIK-3420) method at the range of 0\(\sim\)−120 kPa, and by the psychrometry (Dew Point Microvoltmeter HR-33T) using a cylinder 50 mm in diameter. Oxygen diffusion rates (ODR) was measured by the platinum electrode method (soil oxygen diffusion meter, DIK 5100) using a 100 mm diameter cylinder. The changes of ODR values as a function of soil water potential (\(\Psi_w\)) ranging from −1 (wet), −3, −5 (mild wet), −10 (field capacity), −20, −80 (mild dry), −900 (dry) kPa. Soil water – tension characteristics were measured by the pressure plate (Soil pF meter, DIK-3420) method at the range of 0\(\sim\)−120 kPa, and by the psychrometry (Dew Point Microvoltmeter HR-33T) using a cylinder 50 mm in diameter. Oxygen diffusion rates (ODR) was measured by the platinum electrode method (soil oxygen diffusion meter, DIK 5100) using a 100 mm diameter cylinder. The changes of ODR values as a function of soil water potential were continuously monitored from −6.0 kPa to 0.0 kPa. Soil mechanical impedance was measured using a developed penetrometer device with a 0.98 mm diameter metal probe, which has the relieved shaft, pushed into the soil at the rate of 1 mm min\(^{-1}\) (Iijima et al., 2003b). The penetrometer resistance (\(Q\)) was calculated as \(Q = F/A\), where \(F\) is the penetration force and \(A\) is the cross-sectional area of the probe. Three to six replicate cores were used for measurement of each soil physical characteristic.

2. Crop growth

Maize (Zea mays L., popcorn, cv. Robust 80-71) and rice (Oryza sativa L., upland rice, cv. IRAT 109) were used as the model crops of the cereal species, and pea (Pisum sativum L., cv. Narikoma 30 days) and cotton (Gossypium hirsutum L., upland cotton, cv. dwarf cotton) were used as the model crops of legume and dicotyledonous species, respectively. The seeds of each species were surface-sterilized by immersion in a 1% solution of calcium hypochlorite for 15-20 min. They were then washed several times with distilled water and placed on filter paper moistened with distilled water in a Petri dish, in darkness, at 28°C for 72 h for rice and 36 h for other species. Seedlings with a straight seminal (tap) root, 10 to 15 mm long, were used in all experiments. Germinated seedlings were planted on the surface of soil cores packed into plastic cylinders, 50 mm in diameter and 50, 100, and 150 mm in height, at the three levels of soil bulk density in section 1 (loose, lightly compact, and heavily compact) and five levels of soil water potentials (wet, mild wet, field capacity (as control), mild drying, drying). Loose soil at the level of wet and mild wet were not prepared because the soil became naturally compacted by adding water to adjust the required \(\Psi_w\). The cylinder with a 150 mm height was used for maize because the maximum root length exceeded 100 mm (the maximum root elongation within the experimental period plus 10-15 mm root length at planting). The root axis was held vertically and anchored rigidly behind the zone of elongation with a small quantity of plaster of Paris (Iijima et al., 2000, 2003b) to avoid the buckling of the root axis when penetrating into the compact soil, and the whole seedling was covered loosely with the wetted soil. One seedling was transplanted into each soil core and allowed to grow at 20°C (65% relative humidity) in a growth chamber with a 12h photoperiod. In
total, four to five replicate plants were grown in each combination of soil physical environment. At 48 h after the transplanting, roots were sampled and the increment of seminal root length during the experimental period was measured. The root diameter was measured at the center point of each root segment used for anatomical analysis under the light microscope.

3. Anatomical analysis
Five mm root segment, whose center was one fifth length position from the base of the 48 h elongation to the root tip, was cut from the seminal roots, and preserved in FAA (formalin: acetic acid: 70% ethanol = 1:1:18 parts per volume) solution for anatomical evaluation. When the root elongation during 48h was less than 3.2 mm, the 5-mm root segment from the root tip was used. After the series of ethanol dehydration, the samples were embedded in hard paraffin, and eight µm thickness of cross section was made with a rotary microtome. The root sample was stained with erythrotin. The image of the cross section under a light microscope was taken with a digital camera and recorded in a personal computer. The diameter of each tissue such as cortex, central cylinder and xylem vessel, and the numbers of cortex cell tiers and xylem vessels were measured.

4. Statistical analysis
The interaction between two factors was analyzed by two way ANOVA. The difference between the two average values was subjected to t-test. The smoothing line method was used for curve fitting in all figures.

Results

1. Soil physical stresses
Fig. 1 (upper) shows the relationship among oxygen diffusion rates (ODR), water potential ($\Psi_w$), and bulk density of the soil. As the $\Psi_w$ increased (wetter), ODR decreased in all the bulk density treatments. Soil with a higher bulk density showed much a lower ODR within the measured range of soil water status. Fig. 1 (lower) shows the relationship between penetrometer resistance and $\Psi_w$ at three levels of bulk density treatments. In loose soil, penetrometer resistance is always nearly 0 (from 0.000 to 0.031 MPa). In lightly compact, the soil penetrometer resistance increased sharply between −5 kPa and −10 kPa of $\Psi_w$, but it increased only slightly in a much drier water status (less than −20 kPa). In heavily compact soil (1.5 Mg m$^{-3}$), the soil penetrometer resistance increased as the soil water potential decreased to less than −5 kPa $\Psi_w$. 

Fig. 2. Root elongation rates as affected by the combinations of soil water, air, and mechanical impedance. Soil bulk density in each compaction treatment is 1.00 (loose), 1.30 (lightly compact) or 1.50 (heavily compact) Mg m$^{-3}$. Vertical bars indicate standard error. Four to five replicates were used in each combination of soil physical environment.
2. Root elongation and diameter

In rice and pea, root elongation rate in loose soil was relatively constant in the soil water potential range of −10 to −900 kPa (Fig. 2). In contrast, maize and cotton showed a different trend; mild drying stress at −80 kPa $\Psi_w$ increased root elongation of maize and cotton by 17.1 and 18.4%, respectively, but severe drying stress at −900 kPa reduced them by 20.8 and 17.0%, respectively, as compared with the control environment (−10 kPa $\Psi_w$). The anaerobic stress at −1 kPa $\Psi_w$, reduced the root elongation rates in both lightly and heavily compact soils, and the reduction was severer in maize and pea than in rice and cotton. The root elongation of maize and pea under the combined stress environment of anaerobiosis and mechanical stress (−1 kPa $\Psi_w$, heavily compact) showed only 9.1 and 16.1% of the highest elongation in mild dry–loose soil, respectively. The roots of rice and cotton, however, elongated slightly better than other three species; it elongated 11.8% of the control environment (mild dry, loose) followed by 5.7% in cotton, and 4.1–4.2% in maize and rice, respectively.

3. Root anatomical response

The cross sections of roots under different soil water status. The combined soil stress of higher mechanical impedance and drying (−900 kPa $\Psi_w$, heavily compact) significantly reduced the root elongation in all the species as compared with another combined stress of anaerobiosis and mechanical stress. The pea root, however, elongated slightly better than other three species; it elongated 11.8% of the control environment (mild dry, loose) followed by 5.7% in cotton, and 4.1–4.2% in maize and rice, respectively.

The root diameter increased as the compaction level increased from loose to heavily compact (Fig. 3). In loose soil, maize root became significantly thinner as $\Psi_w$ decreased (P < 0.01 by one way ANOVA), although the root diameter of rice and pea was not influenced by the decrease in $\Psi_w$. Under the combined stress of soil drying and mechanical impedance (at −80 and −900 kPa $\Psi_w$ in heavily compact soil) root diameter increased significantly in all the species except for rice at −900 kPa $\Psi_w$. Under combined stress of anaerobic and mechanical impedance (−1 kPa $\Psi_w$, heavily compact), cotton showed the slight increase in root diameter, although other species did not.
combinations of soil physical stresses clearly indicate anatomical modification of crop roots by the stresses (Fig. 4). In particular, changes in the thickness of cortical cell layers together with the number and size of cortical cells can be observed in the figure. The cortical cell diameter tended to be modified similarly to overall root diameter indicated in Fig. 3. Sole drying stress can be quantified statistically by comparing (a) and (b), where roots were grown under field capacity \( \Psi_w \), and dry conditions, respectively, in loose soil. Anaerobic stress and mechanical impedance alone will be evaluated by the comparison of (c) and (d), and (b) and (e). The size of each tissue was changed according to the intensity of the stress, and the relative values to the respective values in the control environment (b/a for drying, c/d for anaerobiosis, and e/b for mechanical impedance) are summarized in Table 1.

The effect of soil-drying stress, on root elongation
Table 1. Root growth and anatomy as affected by soil physical stresses. Values are the ratio of each stress treatment to the respective control.

|                      | Root elongation rates | Root diameter | Thickness of cortex | Number of cortical cell tiers | Diameter of central cylinder | Number of xylem vessel | Diameter of xylem vessel |
|----------------------|-----------------------|---------------|---------------------|-------------------------------|-----------------------------|------------------------|--------------------------|
| Drying               |                       |               |                     |                               |                             |                        |                          |
| Maize                | 0.79*                 | 0.91*         | 0.97                | 0.96*                         | 0.90*                       | 1.00                   | 0.88*                    |
| Rice                 | 0.93                  | 1.03          | 1.02                | 1.05                          | 0.95                        | 0.96                   | 0.95                     |
| Pea                  | 1.03                  | 0.96          | 0.98                | 0.99                          | 0.90*                       | 1.06                   | 0.85*                    |
| Cotton               | 0.83*                 | 1.08          | 1.18*               | 1.05                          | 0.99                        | 1.14                   | 0.95                     |
| Anaerobiosis         |                       |               |                     |                               |                             |                        |                          |
| Maize                | 0.22*                 | 1.02          | 1.01                | 0.98                          | 1.02                        | 1.02                   | 0.96                     |
| Rice                 | 0.45*                 | 1.02          | 1.12                | 1.00                          | 0.99                        | 1.09*                  | 0.93                     |
| Pea                  | 0.09*                 | 0.94          | 0.95                | 1.08                          | 0.96                        | 1.01                   | 0.90                     |
| Cotton               | 0.54*                 | 0.97          | 1.01                | 0.96                          | 0.92                        | 0.94                   | 0.96                     |
| Mechanical impedance |                       |               |                     |                               |                             |                        |                          |
| Maize                | 0.06*                 | 1.80*         | 2.10*               | 1.20*                         | 1.40*                       | 0.98                   | 1.32*                    |
| Rice                 | 0.05*                 | 1.10          | 1.09                | 1.00                          | 1.11                        | 1.11                   | 1.09                     |
| Pea                  | 0.12*                 | 1.51*         | 1.63*               | 1.17*                         | 1.29*                       | 1.08                   | 1.29*                    |
| Cotton               | 0.08*                 | 1.44*         | 1.54*               | 1.15*                         | 1.25*                       | 1.08                   | 1.05                     |

Drying, the ratio of the values in dry-loose (−900 kPa \(\Psi_w\), 1.0 Mg m\(^{-3}\)) to those in field capacity-loose (−10 kPa \(\Psi_w\), 1.0 Mg m\(^{-3}\)); Anaerobiosis, the ratio of the values in wet-lightly compact (−1 kPa \(\Psi_w\), 1.3 Mg m\(^{-3}\)) to those in field capacity-lightly compact (−10 kPa \(\Psi_w\), 1.3 Mg m\(^{-3}\)); Mechanical impedance, the ratio of the values in dry-heavily compact (−900 kPa \(\Psi_w\), 1.5 Mg m\(^{-3}\)) to those in dry-loose (−900 kPa \(\Psi_w\), 1.0 Mg m\(^{-3}\)). *, statistically significant at \(P<0.05\) by t-test as compared with the respective control. Four to five replicates were used in each combination of soil physical environment.

and radial expansion growth varied with the species. Only maize and cotton showed the statistical reduction of root elongation in response to soil drying stress, and rice and pea did not, as described in the previous section. The severe drying stress did not always reduce the growth rates within the 48 h duration. In maize, root diameter was also reduced due to the reduction of the number of cell tiers and the diameter of both central cylinder and xylem vessel. Pea showed the similar trend of diameter reduction in the tissue level, although the root diameter was not changed. In cotton, however, the thickness of cortex layer increased in response to drying stress, although root diameter was not significantly modified by the severe drying stress.

In the response to the other two individual stresses of anaerobiosis and mechanical impedance, species-specific difference was not clearly observed except for the rice radial expansion growth under mechanical stress. Anaerobiosis generally reduced root elongation but did not modify the radial expansion growth in the species examined. Mechanical impedance reduced root elongation more clearly than the other two physical stresses in all crops. It significantly increased root diameter by increasing the number of cortical cells and thickness of cortex layer. In rice, radial expansion growth was not significantly increased.

Table 2 shows the interaction of the two factors, soil bulk density treatments and soil water treatments. The loose soil treatment was not used for the statistical evaluation due to the lack of the wetted treatments (−1 and −5 kPa \(\Psi_w\)). As for the root elongation rates and root diameter, the interaction of the two stress factors was significant except for rice. This indicated that the growth reduction under the combined soil physical stresses of soil drying, anaerobiosis and mechanical impedance was exhibited differently in the three species. Moreover, the individual diameter of cortex, central cylinder, and xylem vessel in rice was not significantly changed by increase in bulk density. This also indicated that the stress intensity in lightly compact soil in rice was not so small that the radial expansion growth was not statistically significant between the lightly and heavily compact soils. This may cause no significance in interaction between the two factors (soil bulk density and drying) in rice species. As for the anatomical response, maize and cotton showed the significant interactions in some of the parameters, however, rice and pea mostly did not.

**Discussion**

In this study, the effects of combined and individual soil physical stresses on the growth of four major crop species were examined using 13 levels of soil water, aeration, and mechanical status. Soil drying and mechanical stress was thoroughly separated using unimpeded and heavily compacted soils, and evaluated sole drying stress without the soil mechanical stress. The results indicated that there are some species-specific response to the soil physical stresses in root
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elongation and anatomical modification of each tissue.

1. Soil physical stresses

Oxygen diffusion rates (ODR) mainly indicates the speed at which soil oxygen diffuses within the water films formed on the surface of wet soil particles (Phene, 1986). This is considered to be the most reliable measure of the anaerobic environment for the plant roots (Erickson, 1982), because the plant roots absorb soil oxygen through the water films formed on the root epidermal surface when the soil is wet. In general, when the ODR is higher than 40 (×10^{-8} g cm^{-2} min^{-1}) soil aeration status will not inhibit plant growth (Stolzy and Letey, 1964). The soil used in this experiment exceeded this value at −4 kPa Ψw under lightly compact soil (1.30 Mg m^{-3}), and at −6 kPa Ψw in heavily compact soil (1.50 Mg m^{-3}). This indicates that roots in the compact soil, such as hard pan layer, require a lower soil water potential (drier condition) for their favorable growth under the relatively wet environment. This result agrees with the general trends of relative diffusion coefficient (D/D₀) in a clay loam soil (Currie, 1984) and ODR in a silt loam soil (Agnew and Carrpw, 1985).

Penetrometer resistance is the most reliable measure to indicate mechanical impedance in the crop field although it shows two to eight times higher values than the actual resistance plant roots experience (Iijima et al., 2003b). In general, penetrometer resistance increases as the soil moisture decreases due to the increase in soil frictional resistance between soil particles and between metal probes and soil particles. The soil used in this experiment also showed this trend (Fig. 1 lower). Therefore, drought (and/or short term soil drying) stress in the agricultural field soil would be often associated with the higher mechanical impedance to the root growth. In this experiment, very loose soil without compaction was carefully prepared to create the treatment without mechanical impedance to root growth. This situation is observed only in the very loosely prepared nursery bed and/or in the continuous cracks in the actual field soils, which is big enough not to disturb the root growth. The difference of mechanical impedance in the loose soil throughout the wide range of soil water status was not detected by the needle-type slowly moving penetrometer device used. The mechanical impedance would be in the range of negligible resistance to plant root growth (Iijima et al., 2004). When the soil was heavily compacted, the difference between the wet and dry soil was quite large, which agrees with the results in the former studies (Iijima and Kono, 1991, 1992).

2. Root elongation and diameter

As discussed above, loose soil treatment can offer the sole drying stress to the root growth. As mentioned in materials and method, loose soils at −1 and −5 kPa Ψw were not prepared because the soil became naturally compacted by adding water to adjust the Ψw to this level. Although mild drying stress is known to promote plant root growth (Sharp and Davies, 1979), we found the inter-specific difference in the response to the

|                   | Root elongation rates | Root diameter | Thickness of cortex | Number of cortical cell tiers | Diameter of central cylinder | Number of xylem vessel | Diameter of xylem vessel |
|-------------------|-----------------------|---------------|---------------------|-----------------------------|----------------------------|------------------------|------------------------|
| Maize  | BD | *** | *** | *** | *** | * | * | NS |
|        | Ψw | *** | *** | *** | *** | *** | NS | ** |
| Interaction | BD | *** | * | NS | NS | NS | NS | NS |
| Rice   | Ψw | *** | *** | * | * | * | NS | NS |
| Interaction | BD | NS | NS | NS | NS | NS | NS | NS |
| Pea    | Ψw | *** | *** | *** | NS | * | ** | NS |
| Interaction | BD | *** | *** | * | NS | NS | NS | NS |
| Cotton | Ψw | *** | *** | *** | *** | * | NS | NS |
| Interaction | * | *** | *** | * | NS | NS | NS | NS |

BD, two levels of soil bulk density, 1.3 and 1.5 Mg m^{-3}, are tested here due to the lack of the wetted treatments in the 1.0 Mg m^{-3} bulk density treatment. Ψw, five levels of soil water treatments, −1, −5, −10, −80, and −900 kPa Ψw. *, **, and ***, indicate statistical significance at P <0.05, 0.01, and 0.001, by two-way ANOVA, respectively. NS, not significant at P > 0.05. Four to five replicates were used in each combination of soil physical environment.
stress; \(-80\) kPa \(\Psi_w\) (mild drying stress) in very loose soil, enhanced root elongation of maize and cotton but not that of rice and pea. The reason for this species-specific response is unknown so far. Clear inter-specific difference was also observed in the response to the combination of anaerobic stress and mechanical stress; maize and pea nearly stopped root elongation under wet treatment in both heavily and lightly compact, however, rice and cotton did not (Fig. 2). Although the penetrometer resistance was not so high under the wet soil condition, roots must be exposed to relatively higher mechanical disturbance during the penetration into the compacted soil due to the limited soil pore space. The force required to move the compacted soil particles during root penetration into wet soil, need to be carefully evaluated to prove the actual level of resistance root experienced under the very wet environment, because metal-prove penetration (penetrometer resistance) is quite different from that in roots (Iijima et al., 2003b). As rice is known to form the aerenchyma structure in cortical cell layer (see for example Fig. 4), which will serve the passage of aeration to the root meristem, rice plants are tolerant to submerged soil environment. Although heavily compact soil offered some extent of mechanical stress to root elongation, the mechanical impedance alone under the wet environment would be not too high to stop root elongation in rice. The combined soil stress of higher mechanical impedance and drying, nearly stopped root elongation, although pea showed slightly better elongation (12% of the highest elongation), followed by cotton (6%), as compared with other two species (4%). Pea and cotton are widely used for the study on soil mechanical impedance, and are known as relatively strong species to the soil mechanical stress (Materechera et al., 1991). Cotton showed a relatively high rate of root elongation in the wide range of soil water status from anaerobiosis to soil drying including mechanical disturbance of soil, as compared with the major cereal and legume species tested in this experiment (Table 1). These results indicated that cotton would have the overall tolerant abilities to the soil and combined soil physical stresses tested in this study.

As for the changes in root diameter, the combined stress of soil drying and mechanical impedance showed the increase trend in all the species except for rice (Fig. 3). Probably the mechanical impedance in heavily compact soil would be so severe for rice that it would even restrict the radial expansion growth under the stress environment imposed. The overall trend of growth response of maize and cotton to the wide range of soil physical environment was similar to that of pea reported by Eavis (1972). The trend in pea in this study, however, showed a slightly different trend, which may be attributed to the difference of cultivar used and/or environmental difference such as used soil.

3. Root anatomical response

Species-specific difference was found in the modification of tissue diameter by the soil-drying stress (Table 1). The reason for the difference may be related to the production of endogenous ethylene or other growth regulators. Plant roots often exhibit symptoms of exposure to ethylene under the soil physical stresses such as rapid soil drying, excess soil moisture (oxygen deficiency) and mechanical impedance (Morgan and Drew, 1997). In this experiment, the soil-drying stress increased the diameter of cortex layer in cotton, which is the typical morphological change induced by endogenous ethylene, but on the contrary, it reduced the radial expansion growth of each tissue in maize and pea. In rice, the diameter of each tissue was unchanged. The intensity of drying stress to enhance the ethylene production and the level of shrinkage caused by the desiccation in very dry rhizosphere soil may be different among the four species examined. Thus, the level of radial expansion growth would be differently expressed within 48 h of experimental period. Further study on endogenous plant growth regulator under each stress is necessary to find the reason for the species-specific response in the growth and anatomical modification observed in this study.

4. Implication of the present results

Soil physical environment of agricultural soils changes through time depending on the soil water status. The intensity of soil drying and excess moisture will be much stronger in the compacted soil than in the loose soil. Although no-tillage is an effective sustainable cropping system to prevent soil erosion (Iijima et al., 2003a, 2005), it often affects crop root development due to the higher mechanical impedance to root elongation (Izumi et al., 2004). Water uptake under such a restricted soil physical environment will also be modified by rooting in shallow soil layer (Zegada-Lizarazu et al., 2006a; Iijima et al., 2007). Deep rooting (Araki and Iijima, 2005; Zegada-Lizarazu et al., 2006b, 2007) will offer the chance for the crop to survive under the drought environment by acquiring the water resources in the deep soil layer. In this experiment, cotton showed relatively stable root elongation under the combined soil physical stress of anaerobiosis and mechanical stress. The ability of cotton roots to continue their growth under such condition implies that cotton roots can penetrate hard pan and/or compacted soil layer when the mechanical impedance becomes lower due to the temporal wet condition just after the heavy rainfall. The characteristics of cotton roots to penetrate the impeded soil layer should be further studied to acquire the basic information of deep rooting habit of crop species.
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