

## Sap Temperature Distribution of the Xylem and Leaf Water Status of Apple Trees in Relation to Soil Oxygen Diffusion Rates

Hee-Myong Ro

Department of Horticultural Environment, National Horticultural Research Institute, RDA,  
Suwon 440-310, Korea

Received March 14, 2000

A pot-lysimeter experiment was conducted with 3-year-old 'Tsugaru' apple (*Malus domestica* Borkh.) trees to examine the changes in oxygen diffusion rate (ODR) with lateral flow velocity of water through soil. The influence of lateral water flow velocity on water relations and elemental content in leaf, and sap temperature distribution patterns of the xylem of trees were also determined. Trees were grown under four soil water regimes: (1) fast laterally flowing (FWT,  $2.50 \times 10^{-4}$  cm s<sup>-1</sup>), (2) slow laterally flowing (SWT,  $0.25 \times 10^{-4}$  cm s<sup>-1</sup>), and (3) stagnant water table (WLT) at 60-cm, and (4) drip-irrigation at -40 kPa of soil matric potential as a control. The rate of O<sub>2</sub> diffusion converged near  $2 \times 10^{-3}$  g m<sup>-2</sup> min<sup>-1</sup> for FWT and control soils, but decreased below  $1 \times 10^{-3}$  g m<sup>-2</sup> min<sup>-1</sup> 40 days after treatment (DAT) for WLT soils. For SWT soils, however, the ODR at 15 cm below the soil surface was similar to that of control, but at 45 cm below the soil surface, ODR was similar to that of the WLT treatment. Leaf water potential of FWT and SWT plants was similar to that of control plants, but the values for SWT plants declined by 98 DAT. Leaf water potential of WLT plants decreased from -1.86 MPa (9 DAT) to -2.41 MPa (59 DAT) and finally down to -2.70 MPa. The sap temperature measured at 1100-hr was lowest at top and highest at bottom for FWT and control plants, but this pattern of SWT and WLT plants was disturbed from 29 DAT. However, for SWT plants, such thermal disturbance of sap temperature disappeared from 63 DAT.

**Key words:** leaf water status, oxygen diffusion rate, oxygen flux density, sap temperature.

Either a high water table or waterlogged condition developed in orchard soils may cause deficient aeration unfavorable to plant growth in terms of oxygen availability. When the soil O<sub>2</sub> is depleted, it must be replaced by the atmospheric O<sub>2</sub> lest it should inhibit root growth and functioning in soils. The availability of O<sub>2</sub> to plant roots and soil biota strongly depends on the transport rate of O<sub>2</sub> through the soil.<sup>1,2)</sup> The transport of O<sub>2</sub> through the soil occurs primarily by the gaseous diffusion, which can be facilitated to some extent by the advective transport of O<sub>2</sub> caused by differences in total air pressure. The rate of O<sub>2</sub> diffusion in soils depends largely on the pore space geometry resulting from soil texture and structure, and it decreases as saturation of soil with water advances. Other factors influencing the rate of O<sub>2</sub> diffusion are available in the literature.<sup>3)</sup> Attempts have been made to measure the ODR to roots using a platinum electrode<sup>4,5)</sup> However, techniques using bare Pt microelectrodes have raised much controversy. McIntyre<sup>6)</sup> identified some major problems of the techniques derived by Letey and Stolzy<sup>4)</sup> to measure oxygen diffusion rate.

Reduced aeration in the soil can occur inherently by lack of sufficient non-capillary pore space for adequate gas exchange but practically by high water tables or actual soil saturation due to low solubility and slow O<sub>2</sub> diffusion in water.<sup>7)</sup> The most severe case of reduced aeration in the soil can occur when the soil is waterlogged. The resultant O<sub>2</sub> deficit in such soil is attributable to the sustained soil saturation that greatly blocks O<sub>2</sub> diffusion.

Injury from such conditions usually develops sequentially during a period of several days or more and has been extensively discussed. Wilting is likely to be the first symptom of O<sub>2</sub> stress if atmospheric conditions are favorable for transpiration and death of plants is final. If sufficient O<sub>2</sub> for root respiration is available, however, even the prolonged saturated soil conditions are not harmful to root growth.<sup>8)</sup> The reduction in leaf turgor potential that accompanies the loss of water from leaf tissue directly affects many important morphological and physiological processes.<sup>9)</sup> However, many plant species adjust to water deficits and maintain leaf turgor potential by lowering leaf osmotic potential as leaf water potential declines.<sup>10)</sup>

In particular, high water tables of either flowing or stagnant water often occur in poorly drained orchard soils. As plants do not tend to develop root systems below water table, the fluctuation in the height of water table and its duration and season in relation to O<sub>2</sub> concentration has been treated much in the literature.<sup>11,12)</sup> However, little attention

Phone: 82-31-240-3716; Fax: 82-31-240-3556  
E-mail: hmro@unitel.co.kr

**Abbreviations:** CTL, control; DAT, days after treatment; Eh, redox potential; FRP, fiber-reinforced plastic; FWT, fast laterally flowing; ODR, oxygen diffusion rate; OM, organic matter; SWT, slow laterally flowing; WLT, stagnant water table.

has been paid to the effect of lateral flow velocity of water through the soil.

From a physical point of view, transpiration can be viewed as a temperature control process in the plant by evaporating water vapor from the canopy.<sup>13</sup> Temperature in the plant is regulated in several ways, and the most effective way is utilization of excess heat in the evaporation of liquid water. The moment the rate of root uptake of soil moisture falls below transpiration, the plant itself must begin to lose moisture. This imbalance cannot continue for any length of time without resulting in loss of turgidity and hence in wilting of the plant. Concurrently, the upward negative thermal gradient along the xylem conduits is more likely to be disturbed. However, such thermal disturbance has seldom been reported in the literature. Considering the interest in the rate of O<sub>2</sub> diffusion, vertical distribution pattern of sap temperature of the plant was of another major concern. The objectives of this study were: (1) to measure the rate of O<sub>2</sub> diffusion in soil as influenced by the lateral flow velocity of water through the soil, and (2) to examine the vertical temperature distribution pattern of the experimental plant under such conditions.

## Materials and Methods

**Pot-lysimeters and trees.** This study was conducted under a transparent glass rain shield (5 m above ground) using a sandy loam soil (coarse, loamy, mesic family of Typic Dystrichrepts). The soil had a pH of 4.5, redox potential (Eh) of +490 mV, saturated hydraulic conductivity of  $3.5 \times 10^{-4}$  cm s<sup>-1</sup>, 6.5 g organic matter (OM) kg<sup>-1</sup>, 0.0 and 5.5 mg kg<sup>-1</sup> water-soluble Fe<sup>2+</sup> and Mn<sup>2+</sup>, respectively, and CEC of 10.6 cmol<sub>c</sub> kg<sup>-1</sup>. Twelve aboveground pot lysimeters were constructed with fiber-reinforced plastic (FRP) resin. Each pot with an internal dimension of 1.5-m width, 1.5-m length, and 1.2-m depth was packed with soil to a bulk density of 1.3 Mg m<sup>-3</sup>. Tap water was circulated around each pot lysimeter to minimize abrupt changes in soil temperatures.

Twelve 3-year-old 'Tsugaru' apple trees grafted on M.26 rootstock were transplanted individually into twelve pots during the spring of 1993. Trees in the pot lysimeters were randomized in two ways at a spacing of 1.5 m in the row and 3.0 m between rows, so that trees did not overlap. Trees were grown under four soil water regimes: A, FWT ( $2.50 \times 10^{-4}$  cm s<sup>-1</sup>); B, SWT ( $0.25 \times 10^{-4}$  cm s<sup>-1</sup>); C, WLT at 60-cm; and D, drip-irrigation at -40 kPa of soil matric potential (CTL) as a control.

Drip-irrigated lysimeter plots employed tensiometers to schedule irrigation. Each water table treatment was attained by laterally flowing tap water via a peristaltic pump through sandy loam soil employing the method of Sadeghi and Starr.<sup>14</sup> A steady-state condition with respect to lateral water flow was established. Soil water treatments in triplicate were started from July 18 to October 30, 1993. Irrigation was

provided to each drip-irrigated lysimeter system. The recommended N-P-K fertilization rates of 200-100-200 kg ha<sup>-1</sup> for apple trees were chosen to maintain optimum concentrations in leaves.

### Pt-electrode installation and ODR measurements.

Platinum-electrodes were constructed using the method of Cogger *et al.*<sup>15</sup> Prior to use, all electrodes were soaked in distilled water for several days and tested for precision in distilled water. Electrodes varying no more than 15 mV from the mean in distilled water were chosen for the measurements. Following the procedure of Phene,<sup>16</sup> the surface area of each electrode was measured in a 3% bentonite clay suspension equilibrated with atmospheric O<sub>2</sub>. Each electrode was placed in a hole pre-drilled with a metal rod of the same diameter as the electrode body to a depth of approximately 2 cm above the measuring point and then pushed the final 2 cm through soil. The triplicate electrodes were installed at 15- and 45-cm depths in each pot lysimeter unit. After anodes were stabilized in contact with the soil of their respective lysimeters, polarograms were constructed using one cathode of a group of replicates at the same depth by applying the stepwise increase of potential.<sup>17</sup> Five minutes were allowed for the electrical current to be stabilized to a quasi-steady state. Applied voltages were chosen from the plateau on the polarograms. Measurements were made from July 22 to October 30, using a Ag-AgCl half cell reference electrode via KCl-saturated agar-agar gel salt bridge and a portable multi-channel oxygen flux meter, omitting the first 2 measurements (July 22 and 29) due to the instability of the ensuing current of bad electrodes.

### Measurements of leaf water potential and content.

From July 22 to October 30, leaf water potential was measured periodically on a fully expanded, mature leaf of each test plant using a pressure chamber (DIK 7000, Daiki Rika Kogyo, Co., Ltd., Tokyo, Japan). At every measurement, five leaves in the middle were sampled per plant between 1000- and 1200-hr. The leaf was cut at the petiole base and immediately placed in the pressure chamber with approximately 0.5 cm of the cut end of the petiole protruding through the soft silicone stopper used to seal the chamber. At the same time, a duplicate leaf was sampled for the determination of leaf water content. The pressure in the chamber was gradually increased by applying compressed N<sub>2</sub> gas until the sap returned to the cut end of the main xylem vessels, monitored with a magnifying lens. The pressure at which the sap appeared was recorded and released before the leaf was removed.

### Ambient air temperature and sap temperatures.

Ambient air temperatures 2.5 m above ground were measured hourly from August 1 to October 10, 1993 using a copper-constantan thermocouple probe connected to the datalogger (21XL, Campbell Scientific Inc., USA). The thermocouple probe in air was shaded by placing in the middle of a styrofoam cup. During the measurement period, sap temperatures along the xylem conduits were measured

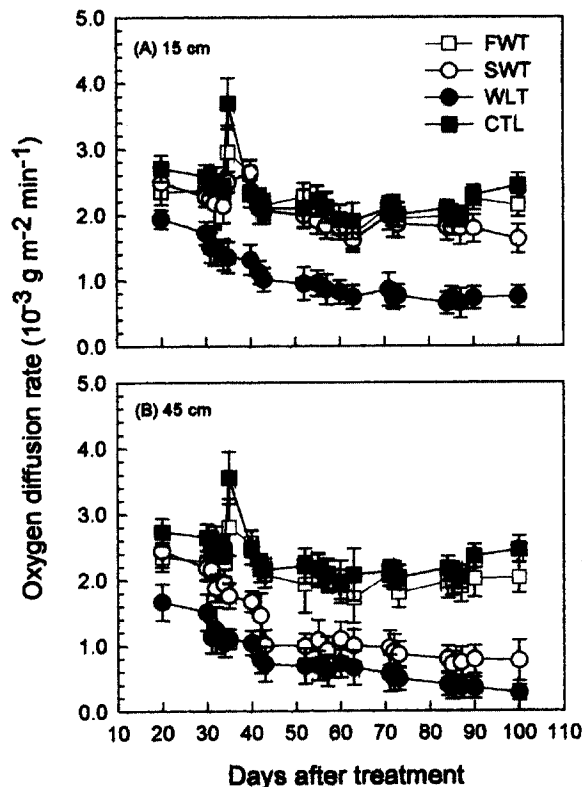
using copper-constantan thermocouple probes. At the end of experiment, tree canopies were expanded to a modified prolate ellipsoid of 1.7 m high and 1.2 m wide. During the same period, tree-trunk circumferences measured at 0.1 m above the graft union increased from 7.52 to 8.93 cm. Net radiation was measured using a silicon pyranometer (LI200S, Licor Inc., USA). The scanned temperature data via multiplexer (AM416, Campbell Scientific Inc., USA) and solar radiation were collected using a datalogger (21XL, Campbell Scientific Inc., USA). Three thermocouple probes per tree were installed at three different elevations from main stem (0.1 m above the graft union), via oblique branch (0.9 m above the graft union), to the petiole of terminal leaf (1.5 m above the graft union). Each thermocouple probe was inserted in a pinhole made along the xylem and then insulated with silicone. Preliminary optical microscopic observations of the wounded petiole, branch, and trunk of the additional trees indicated that thermocouples were in xylem and the wounded zones were healed after 2 weeks.

**Chemical analyses.** Soil samples (15-45 cm) were collected from each unit on selected dates. Each sample was a mixed composite of cores taken from three randomly selected locations. Twelve composite samples were collected from the entire plot, representing all the replicates at each analysis. The moist soil samples were analyzed for determination of water-soluble  $\text{Fe}^{2+}$  and  $\text{Mn}^{2+}$ , following standard colorimetric methods.<sup>18)</sup> Leaf samples used for determination of leaf water content were taken for nutrient analysis. Oven-dry leaf samples were ground and wet digested using ternary solution. Standard methods were used for analysis of K, Mg, Fe, and Mn with an atomic absorption spectroscopy (3300, Perkin-Elmer, USA).

## Results and Discussion

The ODR at 15 cm of planted pot-lysimeters peaked at August 22 and thereafter was maintained around  $2 \times 10^{-3} \text{ g m}^{-2} \text{ min}^{-1}$  in all treatments except for WLT treatment (Fig. 1A). Such increase on August 22 was attributed to the sustained drop of air temperature that causes soil  $\text{O}_2$  to dissolve more, thus giving a higher  $\text{O}_2$  concentration in the soil solution. At the end of experiment, however, the ODR of SWT treatment began to decrease with a concurrent reduction in leaf water potential of the plants without adjusting to  $\text{O}_2$  deficit, compared to that of control (Fig. 2A). The figure  $2 \times 10^{-3} \text{ g m}^{-2} \text{ min}^{-1}$  appeared so often to be a critical oxygen diffusion rate for root growth in the measurements where a certain amount of hydrogen in addition to oxygen was reduced,<sup>4)</sup> as identified by McIntyre.<sup>6)</sup>

Similar variations in ODR at 45 cm of pot-lysimeters were observed in FWT and control treatments, while those in SWT and WLT treatments were similar (Fig. 1B). However, the ODR in SWT soils was higher than that in WLT soils. The ODR values at 15- and 45-cm depths for WLT soils



**Fig. 1.** Temporal variations in soil oxygen diffusion rates at (A) 15- and (B) 45-cm depths of planted soils. Vertical bars denote standard error. Lack of bars indicates low standard error.

decreased to  $1.4$  and  $1.0 \times 10^{-3} \text{ g m}^{-2} \text{ min}^{-1}$  at 40 DAT, and approached  $8.0$  and  $3.0 \times 10^{-4} \text{ g m}^{-2} \text{ min}^{-1}$  at the end of the study, respectively.

The voltage at which  $\text{H}^+$  reduction begins is dependent on the pH of the solution surrounding the electrode as well as the oxygen content.<sup>19)</sup> Solution chemistry indicates that the pH has little effect on decomposition voltage of  $\text{H}^+$  until the pH decreases to about 4.0.<sup>6)</sup> McIntyre<sup>6)</sup> also concluded that voltage of 0.4 or 0.45 V would be better than the often-used voltage of 0.65 V to prevent the reduction of  $\text{H}^+$  in acid soils, but under anaerobic conditions some  $\text{H}^+$  reduction may occur even at these voltages. Blackwell<sup>17)</sup> stated that low pH and low  $\text{O}_2$  concentration could allow the reduction of water at greater than 0.4 V.

On the other hand, dissolved oxygen concentrations of soil solutions at 15- and 45-cm depths in WLT pot-lysimeters measured on September 1, September 22, October 5, and October 18 were invariably lower than  $6.0 \text{ mg L}^{-1}$  (data not shown). Ro *et al.*<sup>11)</sup> showed that the sustained DO concentration below  $6.0 \text{ mg L}^{-1}$  in the surface region of sandy loam soil is enough to cause rapid decrease in leaf water potential and root activity of Tsugaru apple tree, otherwise such physiological symptoms were not observed.

The pattern of daily variations in leaf water potential of plants in FWT and SWT was close to that of control plants throughout the experiment, but the values for SWT plant became lower from 72 DAT (Fig. 2). Leaf water potentials of

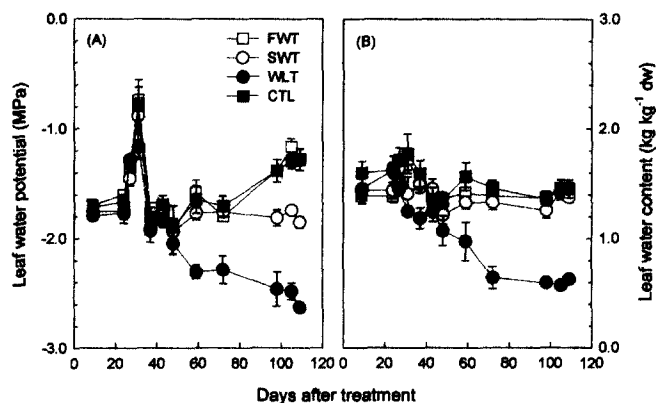


Fig. 2. Temporal variations in (A) leaf water potential and (B) leaf water content measured at 1100-hr. Vertical bars denote standard error. Lack of bars indicates low standard error.

WLT plant did not differ from control plants during the first 43 days, but began to decline gradually from -1.86 to -2.41 MPa on September 10 (59 DAT) and finally down to -2.70 MPa, which was 1.41 MPa below that of control plant. For SWT plants, leaf water potential decreased to -1.84 MPa by 98 DAT, while leaf water content did not.

Daily variation pattern of leaf water content calculated from its dry weight was similar to that of leaf water potential with smaller fluctuation, but the values for plants in FWT and SWT decreased abruptly on August 30 (48 DAT) but recovered shortly to control levels. Unlike leaf water potential, leaf water content of plant in SWT at the end was not lowered appreciably compared to that of control plant. For plants in WLT, a noticeable reduction in leaf water content followed several days behind the occurrence of reduction in leaf water potential. Zhang and Archbold<sup>20</sup> revealed that the plant maintains to some extent its leaf turgor potential as leaf water potential declines. Leaves of WLT plants showed signs of wilting approximately 59 days after treatment, indicating that water uptake was impaired. The leaf water content ( $1.44 \text{ kg kg}^{-1} \text{ dw}$ ) of stressed plants

decreased to  $0.62 \text{ kg kg}^{-1} \text{ dw}$  at the end. A noticeable retardation in shoot growth or even cessation of growth was found in 3-year-old 'Fuji'/M.26 apple trees grown under stagnant water table at 0.45 m below the surface (unpublished data).

Leaves were sampled and analyzed 12 times, but mid-season (August 25, 43 DAT) and final (October 26, 105 DAT) data were chosen for comparison (Table 1). Foliar K concentration of treated plants at the final sampling time was lowered appreciably compared to that in mid-season, while that of control plants was not. In particular, foliar K concentration in WLT plants was significantly lower than in control plants. During depletion of  $\text{O}_2$  from soil, lowering of either foliar- or root-K concentration was found.<sup>8,21</sup> With increasing time, foliar Ca concentration of FWT, SWT, and control plants increased, while that of WLT decreased. However, foliar Ca concentration at the final sampling time was significantly lower in SWT and WLT plants than in FWT and control plants. Compared to foliar K, foliar Ca concentration of both treated and control plants was lowered, but that of WLT was still significantly different. Foliar Fe concentration at the final sampling time increased slightly in the treated plants compared to that during mid-season, while that of control plants decreased. However, foliar Fe was significantly different in WLT plants. In particular, virtually little increase in foliar Fe of WLT plants even under persisting high soil  $\text{Fe}^{2+}$  condition (28 at 50 DAT and 55  $\text{mg kg}^{-1}$  at 84 DAT) indicated that nutrient absorption capacities of roots may be severely impaired after 43-day exposure to anaerobic conditions. Foliar Mn concentration in FWT, SWT, and control plants at the final sampling time increased with a minimum increase in SWT, while that of WLT did not vary. Temporal comparison of foliar Mn suggested that roots of SWT plants may be impaired due in part to high levels of soil  $\text{Mn}^{2+}$  ( $25 \text{ mg kg}^{-1}$  at 38 DAT) associated with soil  $\text{O}_2$  deficiencies.

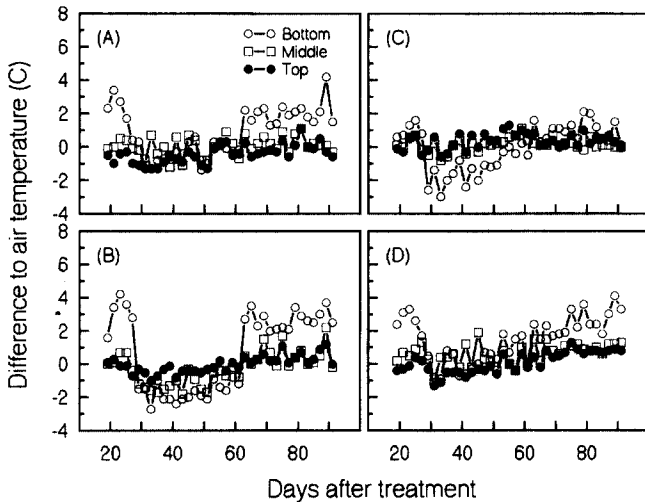
From the scanned diurnal temperature data, those measured at 1100-hr were chosen for comparison. Sap

Table 1. Selected elemental concentration in leaves of 'Tsugaru'/M.26 apple trees during mid-season and at the end of experiment.

Sampling period <sup>#</sup>	Treatment	Element				
		K	Ca	Mg	Fe	Mn
MID	FWT	3.24 <sup>a</sup>	3.59 <sup>a</sup>	1.50 <sup>a</sup>	2.35 <sup>ab</sup>	9.65 <sup>a</sup>
	SWT	2.97 <sup>ab</sup>	2.45 <sup>b</sup>	1.47 <sup>a</sup>	2.38 <sup>ab</sup>	2.84 <sup>b</sup>
	WLT	2.00 <sup>b</sup>	2.67 <sup>ab</sup>	1.28 <sup>b</sup>	1.90 <sup>b</sup>	5.80 <sup>ab</sup>
	CTL	3.40 <sup>a</sup>	3.34 <sup>ab</sup>	1.54 <sup>a</sup>	3.21 <sup>a</sup>	9.10 <sup>a</sup>
END	FWT	2.78 <sup>ab</sup>	4.20 <sup>a</sup>	1.19 <sup>a</sup>	2.66 <sup>a</sup>	11.83 <sup>ab</sup>
	SWT	2.05 <sup>ab</sup>	2.84 <sup>b</sup>	1.10 <sup>ab</sup>	2.43 <sup>ab</sup>	3.60 <sup>b</sup>
	WLT	1.40 <sup>b</sup>	2.65 <sup>b</sup>	0.79 <sup>b</sup>	2.04 <sup>b</sup>	5.17 <sup>ab</sup>
	CTL	3.42 <sup>a</sup>	3.62 <sup>ab</sup>	1.12 <sup>a</sup>	2.35 <sup>ab</sup>	13.65 <sup>a</sup>

<sup>#</sup>MID corresponds to August 25 and END denotes sampling at October 26.

Different letters within column denotes significant differences between means using Duncan's multiple range test,  $P \leq 0.05$ .



**Fig. 3.** Temporal variations in sap temperatures at three different elevations in terms of difference to ambient air temperature in (A) fast-, (B) slow-, and (C) stagnant-water table, and (D) control plants.

temperatures at three different elevations were presented in terms of difference to ambient air temperature (Fig. 3). In general, sap temperature of the petiole of terminal leaf varied with air temperature for FWT, SWT, WLT, and control plants. The overall pattern of sap temperature in control plants was high at bottom, intermediate at middle, and low at top, indicating that thermal gradient along with sap flow in xylem was undisturbed (Fig. 3D). Similar results were obtained for FWT plants (Fig. 3A), but not for SWT and WLT plants. For SWT plants, this pattern of temperature gradient was disturbed from 30 DAT but recovered shortly (63 DAT) to control pattern (Fig. 3B). However, WLT plants did not show signs of recovery even at 63 DAT (Fig. 3C). By this time, leaf water potential of WLT plants had dropped to  $-2.28$  MPa and the corresponding water content was  $0.64$  kg kg<sup>-1</sup> dw (Fig. 2). Overall, the stressed WLT plants showed thermal disturbance pattern during and after reduction in leaf water content.

Sap temperature in the xylem would be a reflection of energy balance of the tissue. From the principles of physics, this is a reflection of the net radiation received by the tissue and how this is dissipated either as sensible heat, latent heat, or stored heat<sup>13)</sup>. Moreover, the flow of sap solution through tissue may influence its temperature depending on whether the water is a source or sink for heat. In general, the mass flow rate of xylem sap resulting from individual leaf transpiration rates varies in accordance with solar radiation under well-watered conditions; however, it declines when stress occurs.<sup>22)</sup> The sustained reduction in transpiration may cause an energy imbalance along the xylem conduits, thus resulting in heat accumulation, even though it is only one contributing component. However, since no measure of the mass flow rate of sap or net radiation experienced by the tissues at different elevations was made, this study lacks

supporting information to explain the effect of O<sub>2</sub> limitation on water conduction and the significance of the pattern of sap temperatures.

As this study measures the ODR in soils induced by the lateral flow velocity of water table and its influence on the pattern of sap temperature, the energy balance of the tissues is not of major concern, even though it is important in interpreting the temperature of the tissues. In addition, soil redox variables, i.e., redox potential, pH, and dissolved oxygen concentration, were monitored, but not shown here.

Thermal disturbance in the pattern of sap temperature began to occur in stressed SWT and WLT plants as the values of ODR in soils decreased (Fig. 1). However, this disturbance did not always lead to a considerable reduction in leaf water content (Fig. 2). Depending on the duration of the disturbance, for instance, leaf water content of WLT plants decreased considerably, while that of SWT plants was maintained to control levels. This phenomenon is to some extent related to O<sub>2</sub> status in soils. The WLT soils exhibited low ODR values less than  $1 \times 10^{-3}$  g m<sup>-2</sup> min<sup>-1</sup> at 15- and 45-cm depths, while SWT soils exhibited adequate values at 15-cm and low values at 45-cm. Since the pH of the medium was maintained greater than 4.0, as indicated by McIntyre,<sup>6)</sup> this pH condition did not allow the reduction of water at the chosen voltages greater than 0.4 V. However, since no measure of rooting distribution was made, this study also lacks supporting information to explain how the plant roots contribute to the pattern of the rate of O<sub>2</sub> diffusion. This study also lacks convincing the effects of oxygen limitation on water conduction in roots.

Nevertheless, the results of this study show that the lateral velocity of water table would influence the rate of O<sub>2</sub> diffusion through soils and the reduced ODR would disturb the pattern of thermal sap temperature of the plants. However, it should be noted that the results from this study show the short-term effects of the rate of O<sub>2</sub> diffusion in soils induced by the lateral flow velocity of water table at fixed depth on sap temperature distribution of plant. The long-term effects of the fluctuation in the height of water table besides its speed and its duration and the effects of soil texture and structure need further study.

## References

1. Refsggaard, J. C., Christensen, T. H. and Ammentorp, H. C. (1991) A model for oxygen transport and consumption in the unsaturated zone. *J. Hydrol.* **129**, 349-369.
2. Wilson, G. V., Thiesse, B. R. and Scott, H. D. (1985) Relationships among oxygen flux, soil water tension and aeration porosity in a drying soil profile. *Soil Sci.* **139**, 30-36.
3. Ouyang, Y. and Boersma, L. (1992) Dynamic oxygen and carbon dioxide exchange between soil and atmosphere: I. Model development. *Soil Sci. Soc. Am. J.* **56**, 1695-1702.
4. Letey, J. and Stolzy, L. H. (1964) Measurements of

- oxygen diffusion rates with the platinum microelectrode: I. Theory and equipment. *Hilgardia* **35**, 545-554.
5. Armstrong, W. (1979) Aeration in higher plants. *Adv. Bot. Res.* **7**, 226-332.
  6. McIntyre, D. S. (1970) The platinum microelectrode method for soil aeration measurement. *Adv. Agron.* **22**, 235-283.
  7. Grable, A. R. (1966) Soil aeration and plant growth. *Adv. Agron.* **18**, 57-106.
  8. Ro, H. M., Park, J. M. and Kim, K. Y. (1995) Effect of dissolved oxygen on the leaf water potentials, leaf nutrient compositions, root activities of Tsugaru apple tree and the chemical environment of rhizosphere. *J. Kor. Soc. Hort. Sci.* **36**, 493-499 (in Korean).
  9. Hsiao, T. C. (1973) Plant responses to water stress. *Annu. Rev. Plant Physiol.* **24**, 519-570.
  10. Morgan, J. M. (1984) Osmoregulation and water stress in higher plants. *Annu. Rev. Plant Physiol.* **35**, 299-319.
  11. Dziejowski, J. E., Rimmer, A. and Steenhuis, T. S. (1997) Preferential movement of oxygen in soils. *Soil Sci. Soc. Am. J.* **61**, 1607-1610.
  12. Wesseling, J. (1974) Crop growth in wet soils. In *Drainage for Agriculture*, van Schilfgaarde, J. (ed.) pp. 3-37, Agron. Monogr. 17. ASA, Madison, WI.
  13. Merva, G. E. (1975) In *Physioengineering Principles*, pp. 5-6, The AVI Publishing Company Inc., Westport, CT.
  14. Sadeghi, A. M. and Starr, J. L. (1992) Transport in a horizontal flow chamber. *Soil Sci. Soc. Am. J.* **56**, 600-603.
  15. Cogger, C. G., Kennedy, P. E. and Carlson, D. (1992) Seasonally saturated soils in the Puget lowland: II. Measuring and interpreting redox potentials. *Soil Sci.* **154**, 50-58.
  16. Phene, C. J. (1982) Oxygen electrode measurements. In *Methods of Soil Analysis*, Klute, A. (2nd ed.) pp. 1137-1150, Part 1, ASA and SSSA, Madison, WI.
  17. Blackwell, P. S. (1983) Measurements of aeration in waterlogged soils: some improvements of techniques and their application to experiments using lysimeters. *J. Soil Sci.* **34**, 271-285.
  18. Page, A. L., Miller, R. H. and Keeney, D. R. (1982) In *Methods of Soil Analysis*, Klute, A. (2nd ed.) Part 2, ASA and SSSA, Madison, WI.
  19. Armstrong, W. (1967) The relationship between oxidation-reduction potentials and oxygen diffusion levels in some waterlogged organic soils. *J. Soil Sci.* **18**, 27-34.
  20. Zhang, B. and Archbold, D. D. (1993) Water relations of a *Fragaria chiloensis* and a *F. virginiana* selection during and after water deficit stress. *J. Am. Soc. Hort. Sci.* **118**, 274-279.
  21. Rosen, C. J. and Carlson, R. M. (1984) Influence of root zone oxygen stress on potassium and ammonium absorption by *Myrobalan* plum rootstock. *Plant Soil* **80**, 345-353.
  22. Steinberg, S. L., Zajicek, J. M. and McFarland, M. J. (1991) Water relations of hibiscus following pruning or chemical growth regulation. *J. Am. Soc. Hort. Sci.* **116**, 465-470.