Ecophysiological Interpretations on the Water Relations Parameters of Trees(V)[1]

Seasonal Changes in Tissue-Water Relations on the *Quercus grosseserrata* and *Quercus acutissima* Leaves-

Sang Sup Han[2] · Heung Seon Choi[2]

樹木의 水分特性에 관한 生理·生態學的 解析(V)[1]

－물참나무와 상수리나무 葉의 水分特性의 季節變化－

韓 相 燮[2] · 崔 興 善[2]

ABSTRACT

Seasonal changes of water relations parameters were obtained from p-v curves in leaves of *Quercus grosseserrata* and *Quercus acutissima*.

The osmotic pressure at full hydration, πo, and osmotic pressure at incipient plasmolysis, πp, were high in newly emerged leaves but decreased with leaf development in each of the species. Water deficit at turgor loss was 10 to 20% in each of the species during the growing season. Maximum bulk elastic modulus in cell walls at full turgor, Emax, rises rapidly with leaf development before senescence in each of the species. Seasonal change of number of osmoles solute in symplasm per dry weight, Ns/DW, was higher in *Quercus grosseserrata* leaves than *Quercus acutissima* leaves, while relative water content (Vp/Vo, RWC*, Vo/Vt) was relatively constant in each of the species.

Key words; seasonal changes; tissue-water relations; Quercus grosseserrata; Quercus acutissima.

要　　　約

물참나무葉과 상수리나무葉의 水分特性因子의 季節變化를 p－v曲線法에 의해 測定하였다. 兩樹種의 最大飽水時의 浸透壓 π_o와 初期原形質 分離點의 浸透壓 π_p는 生育初期에 높고 成熟葉이 되어 가면서 減少하였다. 全生育期間을 通해 兩樹種은 全水分量의 約 10～20%의 水分을 喪失할 때 膨壓이 0에 達했다. 兩樹種의 最大飽水時의 細胞의 彈性係數, Emax는 葉이 伸長함에 따라 增加하였으며, 硬葉化된 以後는 減少하였다. 오스몰수, Ns/DW 의 季節變化는 물참나무葉이 상수리나무葉보다 컸으며, 相對含水率(Vp/Vo, RWC*, Vo/Vt)은 비교적 季節變化가 작았다.

INTRODUCTION

The pressure-bomb technique (Scholander et al, 1965) can be applied to study the tissue-water relations of leaves. In essence Scholander's pressure-bomb technique involves the measurement of all or part of what is called a 'pressure-volume curve'. A leafy shoot is completely enclosed inside a pressure chamber except for the cut end of the stem which is protruded through an airtight seal into the open air. The gas pressure of the bomb is increased until sap water flows out of the leafy shoot; after a measured quantity has been expressed, the pressure is fixed until sap water neither flows in or out. This pressure is called the balancing pressure, P. The above process is repeated with the pressure increment. A plot is then constructed of l/p against the total volume expressed, Ve and this plot is called the 'pressure-volume curve (P-V curve)' (Tyree and Hammel, 1972).

Especially this p-v curve has been very useful in measuring the tissue-water relations parameters of leafy shoot of tree species (Cheung et al, 1975; Tyree et al, 1978; Han and Choi, 1983). These parameters obtained in p-v curves could also yield information relating to the ability of trees to withstand internal water stress (drought tolerance) (Tyree et al, 1978; Maruyama and Morikawa, 1983).

In addition, most of these parameters were different among the tree species (Cheung et al, 1975, 1976; Maruyama and Morikawa, 1983; Tyree et al, 1978) and have a marked seasonal variations in several tree species (Maruyama and Morikawa, 1984; Parker et al, 1982; Tyree et al, 1978).

However, it has been rarely discussed in water relations parameters in tissues related to seasonal variations except several reports (Han and Choi, 1983; Maruyama and Morikawa, 1984; Parker et al, 1982; Tyree et al, 1978). Therefore, it is of importance to investigate the seasonal variations of ontogenic ability of trees to cope with internal water stress.

The *Quercus grosseserrata* and *Quercus acutis-*

sima trees have a high growth rate and a wide natural range of geographic distribution in South Korea. New leaves of these species in Chuncheon, located in central part of Korea, usually emerge in late April. The leaves generally become fully mature in late June and become healthy and active through July and August. They turn to yellowish in mid-October and shedding in most of leaves in late October.

The present study was to investigate the seasonal changes of p-v parameters of leaves of *Quercus grosseserrata* and *Quercus acutissima*.

MATERIALS AND METHODS

The measurements were conducted on the leaves of *Quercus grosseserrata* and *Quercus acutissima* trees growing in the campus of the Kangwon National University. The sample leaves were collected in late afternoon (after 6 p.m.) when water deficits were relatively moderate. The leafy twigs used in the measurement were cut from a branch (about 60cm length) facing south and were immediately recut under water bath. The cut ends of the leafy twigs were then maintained under water bath and all of the leafy twigs were artificially hydrated to near full turgor pressure during over 12 hours before the experiments. The tissue-water relations parameters were measured with a pressure chamber (DIK-PC-40, Japan) using oxygen gas. In the pressure chamber technique, leaves (usually 1.0 to 2.0g) are completely enclosed inside a pressure chamber except for the cut end of twig, which protrudes through an airtight seal into the open air. Moistened filter paper was placed in the bottom of the chamber in order to increase the water vapor within the chamber and decrease transpiration from the samples.

The expressed water from the cut surface was collected with a preweighed polyethylene tube filled with dry tissue paper. The first balance pressure was 0.3 MPa and when the water efflux from the cut surface was not nearly dectable (i.e., less than 1 mg of change in weight), the pressure in the

chamber was progressively increased in 0.3 MPa intervals up to a maximum of 3.8 MPa. The experiments were performed at 22-25°C in a relatively constant temperature room and the measurements were monthly performed three times for each species (and the mean value was represented) from early May to October 1985. The fresh weight, FW, weight of the leaf at maximum turgor pressure was weighed before the experiment start; the dry weight, DW, was the weight of the leaf measured after it had been dried at about 80°C after 48 hours. The general procedures of the analysis of water relations parameters by the pressure-volume curve method were similar to those decribed by Cheung et al (1975), Han & Kim (1980), Tyree & Hammel (1972), Tyree et al (1978), Han & Choi(1983), and Maruyama & Morikawa(1984).

RESULTS AND DISCUSSION

The pressure-volume curve was described by the following equations (Tyree and Hammel, 1972):

$$1/p = V/ (RTNs - F(V)) = (Vo - Ve)/$$

$$(RTNs - F(V)) \quad \dots \dots \dots \dots \dots \dots 1$$

$$1/p = V/ RTNs = 1/\pi, \text{ when } F(V) = 0 \dots \dots 2$$

P is the balance pressure in the bomb, Vo is the original volume of symplasmic (osmotic) water, Ve is the volume of water expressed, V = Vo-Ve, RT is the gas constant times the obsolute temperature, Ns is the total number of osmoles of solute in all the living cells in the leaves, F(V)/V is the volume-averaged turgor (VAT) pressure of the cells in the leaves, π is the osmotic pressure. This p-v curve is normally curvilinear in shape as shown in Fig. 1. The nonlinear region of the p-v curve (equation 1) is a resultant of both turgor and osmotic pressure changes in the cells, whereas the linear region can apparently be attributed to the osmotic component alone (Cheung et al., 1976). The above equation 2 indicates the linear region in Fig. 1.

In Fig. 1, the original volume of osmotic water, Vo, can be obtained by extrapolating the straight-line portion of the p-v curve to the abscissa, and original osmotic pressure, πo, can be obtained by
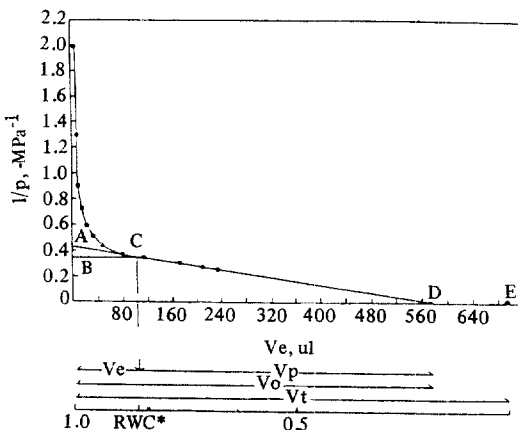

Fig. 1. A typical pressure-volume curve on *Quercus grosseserrata* leaves in October, 1985. Ve is the expressed water volume; A is the inverse of the original bulk osmotic pressure, πo; B is the inverse of the osmotic pressure at incipient plasmolysis, πp; C is the incipient plasmolysis point; D is the original symplasmic water volume, Vo; D-C is the symplasmic water at incipient plasmolysis, Vp; E is the total water volume, Vt.

extrapolating the straight-line portion of the p-v curve to the ordinate. The πo equals RTNs/Vo, πo = RTNs/Vo (Cheung et al., 1975). The osmotic pressure, πp and osmotic water volume, Vp, can be obtained by cross point between non-linear region and linear region in this p-v curve. The volume-averaged turgor (VAT) pressure, F(V)/V can be rewritten from equation 1 as following equation 3:

$$\frac{F(V)}{V} = \frac{RTNs}{Vo - Ve} - P \quad \dots \dots \dots \dots \dots \dots 3.$$

The relative water content at incipient plasmolysis, RWC* was calculated by using the equation:

$$RWC* = \frac{Vt - Ve(tlp)}{Vt} \quad \dots \dots \dots \dots \dots 4.$$

Where Vt is the total water volume (symplasmic and apoplastic water) of sample leaves and Ve(tlp) is the expressed water volume of sample leaves at turgor loss point. The bulk elastic modulus of cell walls at maximum turgor, Emax, was calculated after Cheung et al. (1976) as:

$$E_{max} = \frac{dP_{vat}}{dF} \quad \ldots\ldots\ldots\ldots\ldots 5.$$

where P_{vat} = volume-averaged turgor pressure near maximum turgor and $F = (V_o-V_e-V_p)/V_p$.

The seasonal changes of the original osmotic pressure at maximum turgor, π_o, and osmotic pressure at incipient plasmolysis, π_p, obtained from p-v curve were shown in Fig. 2. π_o was decreased rapidly from late April to early June, then there was a little change until October. These results of seasonal progression of π_o and π_p in Fig. 2. were similar to the sugar maple leaves (Tyree et al., 1978). The π_o in *Quercus grosseserrata* leaves was 0.1 to 0.4 MPa higher than that of *Quercus acutissima* leaves during the growing season. The seasonal variation of π_p of the each species generally followed the seasonal pattern of π_o, but the π_p was 0.2 MPa to 0.4 MPa lower than π_o (Fig. 2). The π_o seems to be a parameter having ecological importance, for it directly indicates the amount of osmotic solutes which a leaf contains per unit volume of symplasmic water (Cheung et al., 1975). A decrease of π_o during the growing season would increase drought tolerance by increasing the water potential gradient from the soil to the leaf (Teskey et al., 1984) because a low value of π_o could allow cell elongation to persist under conditions of water stress (Cheung et al., 1975). Therefore, under conditions of high water stress, the low osmotic potentials in both species during the growing season probably allow plant metabolic process such as photosynthesis to function more efficiently
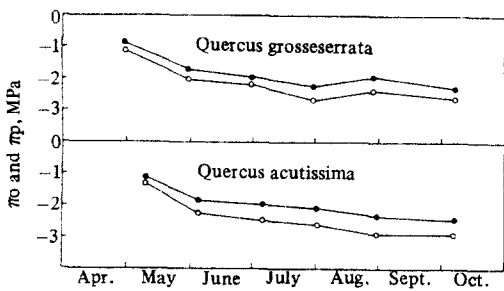
(Parker et al., 1982). The seasonal decreases in π_p were probably due to leaf area expansion and increases in internal plant resistance to water flow during plant development (Carter and Sheaffer, 1983). The results of Fig. 2. suggest that the summer leaves may process physiological and biophysical adaptations to water stress reflected in lower π_o and π_p. Additionally, seasonal differences in π_p were evident, indicating the prescence of leaves with greater cell rigidity during August (Monson and Smith, 1982).

The volume of osmotic water at incipient plasmolysis per symplasmic water volume, V_p/V_o, indicated the effect of tissue elasticity on the relative water content at which turgor loss occured (Fig. 3.). The values of V_p/V_o in *Quercus grosseserrata* slightly increased from May to July, then decreased until September, ranging from 80 to 88%, but progressively decreased in *Quercus acutissima*
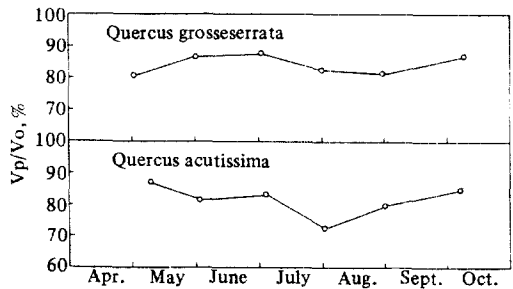
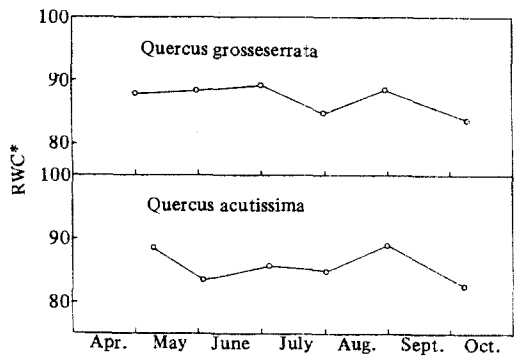Fig. 3. Saesonal changes of relative water content, V_p/V_o at incipient plasmolysis.

Fig. 4. Seasonal changes of relative water content at incipient plasmolysis, RWC*.

Fig. 2. Seasonal changes of original osmotic pressure, π_o and osmotic pressure at incipient plasmolysis, π_p in each species. ●, π_o; ○, π_p.

from May to September, ranging from 87 to 72%. By leaf fall the Vp/Vo increased again in both species. During the period of leaf maturation, the Vp/Vo of *Quercus grosseserrata* showed higher value than that of *Quercus acutissima*. The leaves, which have higher value of Vp/Vo than 80%, show a superior osmoregulation (or water conservation) by means of their cell wall properties (Cheung et al., 1975; Han et al., 1985).

Relative water content at incipient plasmolysis, RWC*, remained somewhat constant during the study period retaining relatively high (more than 80%) values (Fig. 4.). The high relative water contents are further evidence that an amply supply of water was available and easily conducted to the leaves (Kapos and Tanner, 1985). There was no significant shift in RWC* associated with season. Water deficit at turgor loss was 10 to 20% in each species during the growing season. The low values of RWC* such as mockernut hickory suggest a low competitive ability on xeric sites and may account for the stunted form of this species (Parker et al., 1982). The RWC* of *Quercus grosseserrata* and *Quercus acutissima* leaves in Fig. 4. was similar to the result of *Quercus crispula* and *Betula ermani* leaves (Maruyama and Morikawa, 1984), but it was relatively higher than 77% of *Cryptomera japonica* shoot (Yahata, 1979) or about 70% of morkernut hickory leaves (Parker et al., 1982).

The seasonal changes of symplasmic water volume at full hydration (Vo), and the number of osmoles of solute(Ns) are both presented on a dry weight basis in Fig. 5. Seasonal trends in Vo/DW and Ns/DW for the two species reflected physiological and morphological changes in the tissue of leaves. In *Quercus grosseserrata*, the Vo/DW and Ns/DW were low at early growth phase and steadily increased until July, reflecting continued dry matter accumulation after expansion of the foliage had ceased (Teskey et al., 1983), then decreased again until leaf fall. In *Quercus acutissima* Vo/DW declined progressively until October and Ns/DW slightly increased from early May to early July, then decreased. The Vo/DW and Ns/DW were
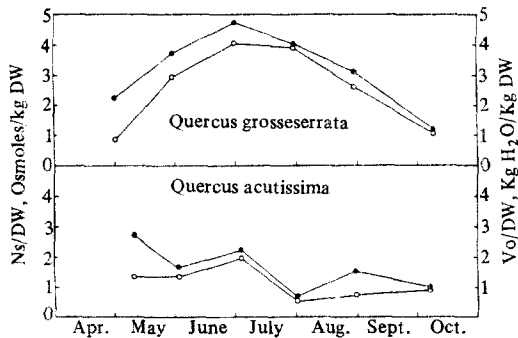

Fig. 5. Seasonal changes in number of osmoles per dry weight, Ns/DW and volume of symplasmic water per dry weight, Vo/DW in each species. o, Ns/DW; ●, Vo/DW.

generally higher in *Quercus grosseserrata* than in *Quercus acutissima* during the study period. however, the decline in Vo/DW is not caused by an actual decline in Vo since Vo increases with maturing leaves. It is probably due to a disproportionate increase in the dry weight as the secondary wall is laid down. The early increase in Vo/DW may have been caused by an inability of cell wall growth to keep pace with expansion. The later disproportionate increase in dry weight which lowers Vo/DW may also be the reason for the decline in Ns (Tyree et al., 1978). The actual solute content in the leaf tissue varies inversely with πo. As a consequence, while solute content varied over the growing season with πo, Ns/DW remained at relatively stable leavels after leaf maturation (Tyree et al., 1978). As leaves matured and dry matter content in the leaves increased, values of Vo/DW and Ns/DW decreased, and subsequently remained low and relatively stable over the growing season (Parker et al., 1982: Maruyama and Morikawa, 1984).

The maximum bulk elastic modulus, Emax, is an indication of the ability of the cells to change volume with decreasing water potential (Nilsen et al., 1983) (Fig. 6.). In *Quercus grosseserrata*, the Emax rised rapidly from early May to early July to a maximum value of about 12 MPa, but by leaf fall in October Emax has dropped back to about 4 MPa. The Emax in *Quercus acutissima* either
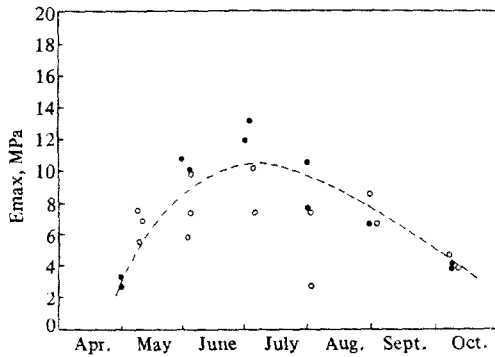
Fig. 6. Seasonal changes of the bulk elastic modulus at maximum turgor, Emax, in *Quercus grossesrrata* and *Quercus acutissima* leaves. ●, *Quercus grosseserrata*; o, *Quercus acutissima*.

remained relatively constant or generally increased showing maximum value of about 10 MPa, and was lower than in *Quercus grosseserrata* over the study period. Plants can adapt to seasonal water stress through osmotic adjustment (Maruyama and Morikawa, 1984) or by alternations in the bulk elastic modulus, which is an indication of cell wall elasticity (Tyree and Hammel, 1972; Cheung et al., 1976; Roberts et al., 1981). The larger the bulk elastic modulus, E, the smaller the cell elasticity. A low E value exhibits a high wall extensibility. The low value of Emax may better correlate with the thin walls one would expect to fine in leaves before secondary wall thickening is complete (Tyree et al., 1978). The Emax values obtained for a plant material can indicate the ability of a plant to osmoregulate or conserve water. A leaf with a higher Emax will be able to decrease its water potential more rapidly with water loss than one with a lower Emax (Cheung et al., 1975, 1976). A cell with a low E will increase more in volume and in surface area than a cell with a high E (Zimmermann et al., 1976). Turgor potential can be maintained at low leaf water content either by an adjustment of cell volume through cellular elasticity or an adjustment of osmotic potential (Nilsen et al., 1983). The Emax is often used as an indication of possible adjustment cell elasticity, but there are many reasons why this value may contain consider-

able variability and error (Cheung et al., 1976; Roberts et al., 1981).

Water in leaves is distributed between the symplasm (protoplasm and vacuole of all the cells) and the apoplast (cell wall, xylem, and intracellular water). The seasonal trends of symplasmic water volume per total leaf water (fresh weight - dry weight), Vo/Vt, are plotted in Fig. 7. The percentage of Vo/Vt in *Quercus grosseserrata* increased steadily about 62 to 88% from May to October. In *Quercus acutissima*, the Vo/Vt remained high ranging from about 85 to 90% until August, then declined to 72% by October. Decreases in Vo/Vt accompanying leaf senescence observed in *Quercus acutissima* were probably a result of increased membrane permeability. Senescence in plant tissues is accompanied by increased apparent free space and a loss in capacity to retain solutes. Consequently, apparent symplasmic volume would be reduced as membrane integrity and semipermeability declined (Parker et al., 1982). Seasonal trends of Vo/Vt were somewhat variable over the growing season but the Vo/Vt of *Quercus acutissima* was higher than that of *Quercus grosseserrata* at early May. The proportion of Vo/Vt may not directly correlated with drought resistance, however the leaves with higher Vo/Vt may be considered that retains superior capacity recovering from water stress through more osmotic water relating to osmotic potential (Han et al., 1985).
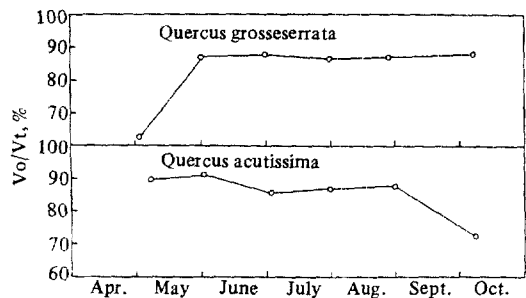

Fig. 7. Seasonal changes of Vo/Vt in each species. Vo is the volume of symplasmic water at full hydration and Vt is the total leaf water at full hydration.

The seasonal patterns of the relationship between leaf water potential, ψL and volume-averaged turgor pressure, Pvat, were shown in Fig. 8. The relationship between ψL and Pvat showed nearly linear and corresponded results of other reports (Han, 1985; Maruyama and Morikawa, 1983). The leaf water potential, ψL, when the turgor pressure first becomes zero, were about 1.0 to 2.0 MPa from May to July and 2.3 MPa to 2.6 MPa after leaf maturity in *Quercus grosseserrata*. The Pvat of *Quercus acutissima* leaves were generally higher than that of *Quercus grosseserrata*, which seem to be more advantageous to water stress since rapid loss of turgor would cause stomatal closure and this would result in conserving water. Many important physiological and morphological processes such as leaf enlargement and associated photosynthesis are directly affected by the reduction of leaf turgor potential which accompanies the loss of water from leaf tissue. Generally the leaves maintained high water potential at incipient turgor loss point seem to be more ontogenically advantageous to internal water stress (drought resistance). The ability of a plant to maintain high turgor potential in cells is therefore an important adaptation to water deficits (Jones and Turner, 1978).
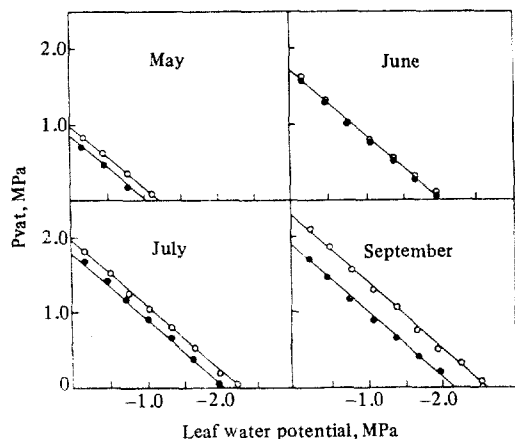
The results of this study indicate that capacity

of trees to internal water stress is reflected in its water potential components. The low values of πo and πp, Emax and high values of Vo/DW and Ns/DW, Vp/Vo, Vo/Vt exhibited by *Quercus grosseserrata* and *Quercus acutissima* indicated a superior capacity to sustain stomatal opening and water uptake from soil and to maintain relatively high values of RWC* when water potential declined. These characteristics is similar to other drought-tolerating species (Parker et al., 1982; Roberts and Knoerr, 1977), and may at least partially explain the wide natural distribution and high growth rate of *Quercus grosseserrata* and *Quercus acutissima* trees in Korea.

Further study of these water relations parameters relating to soil water content and stomatal behavior are necessary.

LITERATURE CITED

1. Carter, P. R. and C. C. Sheaffer. 1983. *Alfalfa* response to soil water deficits II. Plant water potential, leaf conductance, and canopy temperature relationships. Crop. Sci. 23:676-680.

2. Cheung, Y. N. S., M. T. Tyree, and J. Dainty. 1975. Water relations parameters on single leaves obtained in a pressure bomb and some ecological interpretations. Can. J. Bot. 53: 1342-1346.

3. Cheung, Y. N. S., M. T. Tyree, and J. Dainty. 1976. Some possible sources of error in determining bulk elastic moduli and other parameters from pressure volume curves of shoots and leaves. Can. J. Bot. 54: 758-765.

4. Han, S. S. 1985. Effects of water stress on the photosynthesis, respiration, and transpiration rates of leaves in Korean white pine trees. The Journal of Science and Technology, Kangweon National Univ. 22: 118-131.

5. Han, S. S. and K. R. Kim. 1980. Ecophysiological interpretations on the water relations parameters of trees. I. The diagnosis of tolerant to drought by the pressure chamber technique. J. Kor. For. Soc. 50: 25-28.

Fig. 8. Volume-averaged turgor pressure (Pvat) versus leaf water potential in *Quercus grosseserrata*(●) and *Quercus acutissima* (o).

6. Han, S. S., D. S. Cheun, and H. S. Choi. 1985. A study on the drought tolerance of trees. Res. Bull. of the Experiment Forests, Kangweon Nat'l. Univ. 5: 3-7.

7. Han, S. S. and H. S. Choi. 1983. Ecophysiological interpretations on the water relations parameters of trees. II. Seasonal changes in tissue-waeter relations parameters obtained from p-v curves on the *Pinus koraiensis* and *Abies holophylla* shoots. J. Kor. For. Soc. 61: 8-14.

8. Jones, M. M. and N. C. Turner, 1978. Osmotic adjustment in leaves of *Sorghum* in response to water deficits. Plant Physiol. 61: 122-126.

9. Kapos, V. and E. V. J. Tanner. 1985. Water relations of Jamaican upper montane rain forest trees. Ecology. 66(1): 241-250.

10. Maruyama, Y. and Y. Morikawa. 1983. Measurement of leaf water relations using the pressure-volume technique. J. Jap. For. Soc. 65(1): 23-28.

11. Maruyama, Y. and Y. Morikawa. 1984. Seasonal changes of several water relations parameters in *Quercus crispula, Betula ermani,* and *Abies homolepis.* J. Jap. For. Soc. 66: 499-505.

12. Monson, R. K. and S. D. Smith. 1982. Seasonal water potential compenents of Sonoran Desert plants. Ecology. 63: 113-123.

13. Nilsen, E. T., M. R. Sharifi, P. W. Rundle, W. M. Jarrel, and R. A. Virginia. 1983. Diurnal and seasonal water relations of the desert phreato-phyte *Prosopis Glandulosa* (honey mesquite) in the Sonoran Desert of California. Ecology. 64(6): 1381-1393.

14. Parker. W. C., S. G. Pallardy., T. M. Hinckley, and R. O. Teskey. 1982. Seasonal changes in tissues water of three woody species of the *Quercus Carya* forest type. Ecology. 63(5): 1259-1267.

15. Roberts S. W., B. R. Strain, and K. R. Knoerr. 1981. Seasonal variation in leaf tissue elasticity in four forest species. Physiological Plantrum. 52: 245-250.

16. Scholander, P. F., H. T. Hammel, E. D. Bradstreet, and E. A. Hemmingsen. 1965. Sap pressure in vascular plants. Science 148: 339-346.

17. Teskey, R. O., C. C. Grier, and T. M. Hinckley. 1984. Change in photosynthesis and water relations with age and season in *Abies amabilis.* Can. J. For. Res. 14: 77-84.

18. Tyree, M. T. and H. T. Hammel. 1972. The measurement of the turgor pressure and water relations of plants by the pressure-bomb technique. J. of Exp. Bot. 23(74): 267-282.

19. Tyree, M. T., Y. N. S. Cheung., M. E. Macgregor, and A. J. B. Talbot. 1978. The charaterstics of seasonal and ontogenetic changes in the tissue water relations of *Acer, Populus, Tsuga,* and *Picea.* Can. J. Bot. 56: 635-647.

20. Yahata, H. 1979. Water relations parameters of leaves of *Cryptomeria japonica.* pp. 114-125. in H. Miyajiima, ed. Characteristics of native clonal cultivars of *Cryptomeria japonica* in Kyushu. Fac. Agr., Kyushu Univ.

21. Zimmermann, U., E. Steudle, and P. I. Lalkes. 1976. Turgor pressure regulation in *Valonia Utricularis.* Plant Physiol. 58: 608-613.