

## Ecophysiological Interpretations on the Water Relations Parameters of Trees(II)<sup>1</sup>

- Seasonal Changes in Tissue-Water Relations Parameters Obtained from P-V Curves on the *Pinus koraiensis* and *Abies holophylla* Shoots -

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## 樹木の水分特性에 관한 生理·生態學的 解析(II)<sup>1</sup>

- P-V 曲線에 의한 잣나무와 잣나무枝葉의 水分特性 因자의 季節變化 -

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### ABSTRACT

This study was to diagnose the ontogenetic ability of drought tolerance in trees, and was to investigate the seasonal changes in tissue-water relations parameters,  $\pi_o$ ,  $\pi_p$ ,  $E_{max}$ ,  $N_s/DW$ ,  $V_o/W_s$  and  $RWC_{(t1p)}$ , obtained from P-V curves on the *Pinus koraiensis* and *Abies holophylla* shoots. The results obtained are as follows: 1) Seasonal changes of original osmotic pressure at maximum turgor,  $\pi_o$ , were -1.2 to -1.6 MPa in *Pinus koraiensis* and -1.4 to -1.7 MPa in *Abies holophylla*. 2) Seasonal changes of osmotic pressure at incipient plasmolysis,  $\pi_p$ , were -1.8 to -2.1 MPa in *Pinus koraiensis* and -1.6 to -2.1 MPa in *Abies holophylla*. 3) Seasonal changes of relative water content at incipient plasmolysis,  $RWC_{(t1p)}$ , were 70 to 77% in *Pinus koraiensis* and 69 to 85% in *Abies holophylla*. 4) Seasonal changes of maximum bulk modulus of elasticity at maximum hydration,  $E_{max}$ , were 2.2 to 6.3 MPa in *Pinus koraiensis* and 3.1 to 7.9 MPa in *Abies holophylla*. 5) Seasonal changes of number of osmoles of solute in symplasm versus dry weight,  $N_s/DW$ , were 0.5 to 1.3 in *Pinus koraiensis* and 0.3 to 1.0 in *Abies holophylla*. 6) Seasonal changes of original osmotic water volume versus total water volume (symplasmic and apoplasmic water),  $V_o/W_s$ , were 55 to 65% in *Pinus koraiensis* and 40 to 65% in *Abies holophylla*. Consequently, as the comparative values of  $\pi_o$ ,  $\pi_p$ ,  $E_{max}$ ,  $N_s/DW$ ,  $V_o/W_s$ , and  $RWC_{(t1p)}$ , it might be suggested that *Abies holophylla* shoot could have more or less a greater ability of drought tolerance as compared with *Pinus koraiensis* shoot.

*Key words:* *Pinus koraiensis*; *Abies holophylla*; seasonal change; tissue-water relations parameters.

### 要 約

樹木에 있어서 耐乾性的 크기를 診斷하기 위하여 P-V 曲線法에 의해 얻은 잣나무와 잣나무枝葉(shoot) 內的 水分特性因子  $\pi_o$ ,  $\pi_p$ ,  $E_{max}$ ,  $N_s/DW$ ,  $V_o/W_s$ ,  $RWC_{(t1p)}$  등의 季節變化를 測定考察하였다. 그 結果는 다음과 같다. 1) 잣나무枝葉의 最大飽水時의 浸透壓  $\pi_o$ 는 -1.2~-1.6 MPa, 잣나무枝葉의  $\pi_p$ 는 -1.4~-1.7 MPa의 季節變化를 나타냈다. 2) 初期原形質分離點에 있어서 잣나무枝葉의 浸透壓  $\pi_p$ 는 -1.8~

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-2.1 MPa, 잣나무枝葉의  $\pi_p$ 는 -1.6~-2.1 MPa의 季節變化를 나타냈다. 3) 初期原形質分離點에 있어서 잣나무枝葉의 相對含水率  $RWC_{(tip)}$ 는 70~77%, 잣나무枝葉의  $RWC_{(tip)}$ 는 69~85%의 季節變化를 나타냈다. 4) 最大膨脹時의 잣나무枝葉細胞群의 彈性係數  $E_{max}$ 는 2.2~6.3 MPa, 잣나무의  $E_{max}$ 는 3.1~7.9 MPa의 季節變化를 나타냈다. 5) 잣나무枝葉의 乾物重에 대한 osmol 數  $N_s/DW$ 는 0.5~1.3, 잣나무枝葉의 경우는 0.3~1.0의 季節變化를 나타냈다. 6) 잣나무枝葉의 總含水量(symplasmic 과 apoplastic water의 合計)에 대한 總浸透水量  $V_o/W_s$ 는 55~65%, 잣나무枝葉의  $V_o/W_s$ 는 40~65%의 季節變化를 나타냈다. 以上の  $\pi_o$ ,  $\pi_p$ ,  $E_{max}$ ,  $N_s/DW$ ,  $V_o/W_s$ ,  $RWC_{(tip)}$  값의 特性을 考察할 때 잣나무枝葉이 잣나무枝葉보다 耐乾性이 약간 강한 樹種임을 알았다.

## INTRODUCTION

Water is the commonly limiting factor for tree growth and distribution (Kramer & Kozolowski, 1979) because the growth is restricted to some extent by either too much or too little water (Hinckley *et al.*, 1978). It is clear that the internal water deficits in forest trees play more a dominant role in growth and survival than water excess. The internal water deficits in tissues frequently develop that can impair such processes as cell elongation, photosynthesis, respiration, transpiration, and the other biosynthesis (Brix, 1979; Beadle, *et al.*, 1978, 1979; Han, 1982; Hinckley *et al.*, 1978; Lange *et al.*, 1976). Especially the critical water stress as plasmolysis or stomatal closure is of importance to tree growth and survival (Brix 1979; Beadle *et al.*, 1978).

In internal response of tree to drought resistance the tree is generally divided into two types, drought avoidance and drought tolerance (Levitt 1972). The drought avoidance in a given genotype is indicated by the capacity to maintain a relatively high internal water potential such as xylem or leaf water potential in spite of a low external water potential i.e., increasing soil or atmospheric moisture deficit (Parker *et al.*, 1982; Blum & Ebercon 1981). The drought tolerance implies that a tree can survive periods of low water potential, and must be attributable in part to inherent properties of the protoplasm (Parker *et al.*, 1982). Also drought tolerance is manifested by the relative ability of the plant tissue to sustain a smaller reduction in physiological or metabolic activity as its water potential decreases (Blum & Ebercon, 1981). Those resistances often

appear to be correlated with a specific combination of drought avoidance and drought tolerance (Parker *et al.*, 1982).

There are abundantly reported capacities in drought resistances with leaves in relation to photosynthesis, respiration, and transpiration (Beadle *et al.*, 1979; Brix, 1979; Han, 1982; Levitt, 1972; Pereira & Kozlowski, 1978; Zavitkovski, 1970). But most of the cited reports were more conducted with leaves of trees to drought avoidance capacity than drought tolerance capacity. Especially it has rarely been discussed in internal water relations parameters in tissues as related to drought tolerance of tree except several reports (Cheung *et al.*, 1975; Han & Kim, 1980; Maruyama & Morikawa, 1983; Levitt, 1972, Tyree *et al.*, 1978; Yahata, 1979).

In many regions of South Korea, early summer drought is common and results in limited tree growth and survival. Therefore, it is of importance to diagnose the ontogenetic capacity of drought tolerance for tree growth and survival. The objective of this study is intended to elucidate the seasonal changes of internal water relations parameters as related to drought tolerances in *Pinus koraiensis* and *Abies holophylla* shoots obtained from the pressure-volume curve (P-V curve), though the measurements studied here might not be enough for this kind of research.

## MATERIALS AND METHODS

*Pinus koraiensis* and *Abies holophylla* shoots with root parts removed were collected from 4-year-old seedlings growing on the nursery of the Kangweon National University. The sample shoots were collected at a time (after 7 p.m.) when water deficits

were relatively low. The cut surfaces of the stem ends were usually recut underneath the water bath and were artificially hydrated to near maximum turgor pressure (about 0.1 MPa) over 12 hours during the night. The recut shoot of 1.0-3.0g was immediately weighed and was placed in pressure chamber (DIK-PC-40, Japan) that inserted in a wet tissue paper. The balance pressure in the chamber by the oxygen gas was applied until water efflux from the cut surface of the shoot was not nearly detectable i.e., less than 2.0mg of increase in weight of the collecting water. The balance pressure was increased in steps of 0.3-0.4 MPa over the previous balance pressure. The pressure was always started at 0.3-0.5 MPa.

The expressed water from the cut surface of the shoot was absorbed by a preweighed polyethylene tube (about 5-cm-long) stuffed with dry tissue paper, and polyethylene tubes were exchanged at frequent intervals. The absorbed polyethylene tube was weighed at ten minute intervals in order to fine out the water efflux cease. The excised materials in this experiment were always used within 48 hours. For comparison of the water relations parameters and speed up water equilibrium in the chamber, the experiments were done at 22-25°C in a relatively constant temperature room. The fresh weight, FW, was the weight of the shoot at maximum turgor pressure; the dry weight, DW, was the weight of the shoot measured after it had been dried at about 80°C over two days. For investigation of seasonal changes of water relations parameters, the measurements were monthly performed from late May 1981 to late January 1982. The general procedures and analyses of water relations parameters for the pressure-volume curve (P-V curve) method were similar to those described by Cheung *et al.* (1975), Han & Kim (1980), Tyree & Hammel (1972), Tyree *et al.* (1978), and Yahata (1979).

## RESULTS AND DISCUSSION

New shoots of *Pinus koraiensis* and *Abies holophylla* in Chuncheon, located in central part of

Korea, generally emerge in mid-April and elongate slowly. The emerged new needles of *Pinus koraiensis* may be taken over a period of two months in mature, whereas the new needles of *Abies holophylla* may fully elongate within a month. Especially the needles of *Pinus koraiensis* were usually yellowish in color until early June. The newly emerged shoot in April was not done since yellowish shoot was too small and too soft to be used.

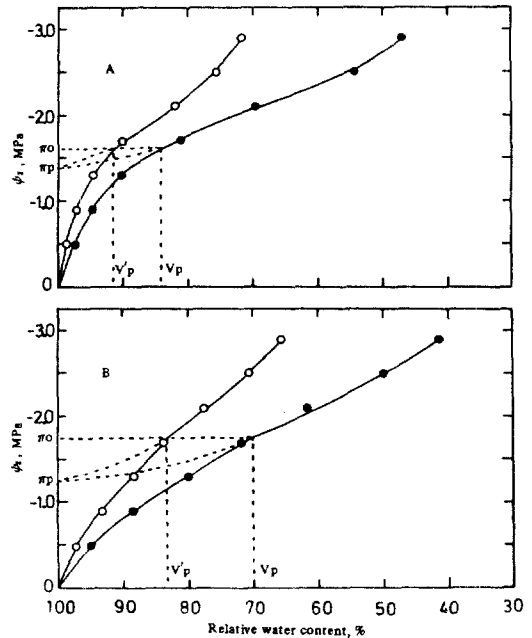


Fig. 1. Relation between shoot water potential ( $\psi_2$ ) and relative water content obtained from a P-V curve in May 1981.  $\pi_0$  is the original osmotic pressure;  $\pi_p$  is the osmotic pressure at incipient plasmolysis;  $V_p$  is the osmotic water volume at incipient plasmolysis, respectively. The open and closed circles indicate the RWC\* and RWC(tlp), respectively. A is the *Abies holophylla*; B is the *Pinus koraiensis*.

The relationship between shoot water potential and relative water content obtained from the pressure-volume curve in May is summarized in Fig. 1. The plotted RWC's in Fig. 1 are both presented on the  $V_e/V_0$  and  $V_e/W_s$  basis. The shoot water potential decreases for a given amount of water loss

were consistently smaller in *Pinus koraiensis* than in *Abies holophylla*. The greater degree of water potential decrease in *Abies holophylla* was due to a higher  $\pi_0$  together with more rigid cell walls (Cheung *et al.*, 1975). The *Abies holophylla* shoot showed rather extensive losses of osmotic water even at relatively high RWC as compared with *Pinus koraiensis* shoot in Fig. 1. The RWC(tlp) ( $=V_p/V_0$ ) for the symplasmic water volume at  $\pi_p$  was about 14% lower in *Pinus koraiensis* than in *Abies holophylla* in spite of the osmotic pressure,  $\pi_p$ , at incipient plasmolysis was approximately similar. In here, the  $V_p/V_0$  equals RWC(tlp) as:

$$RWC_{(tlp)} = \frac{V_0 - V_e(tlp)}{V_0}$$

where  $V_e(tlp)$  is expressed water volume by the sample at incipient plasmolysis and  $V_p$  is the symplasmic water volume remaining at incipient plasmolysis,  $V_0 - V_e(tlp)$ . The RWC\* ( $=V'_p/W_s$ ) for the *Pinus koraiensis* at incipient plasmolysis was about 82%, whereas for the *Abies holophylla* it was about 92%. In here, the  $V'_p/W_s$  equals RWC\* as:

$$RWC^* = \frac{W_s - V_e(tlp)}{W_s}$$

where  $W_s$  is the total water volume, symplasmic and apoplasmic water.

The differences of  $V_p/V_0$  and  $V'_p/W_s$  between two species are probably due to the relatively lower dehydration rate in tissue of *Pinus koraiensis* shoot as its water potential decreases. Especially the plant which has a low value of RWC(tlp) suggest a low competitive ability on xeric sites (Parker *et al.*, 1982) and has a low recoverable ability when osmotic pressure declined until over zero turgor pressure. A plant which has a low value of RWC(tlp) can show a high resistance of tissue-water flow. When resistance is based on the cross-sectional area of the conducting tissue, values of resistances for conifers are about five times greater than those for diffuse-porous deciduous trees and herbaceous plant (Hinckley *et al.*, 1978; Hellkvist *et al.*, 1974).

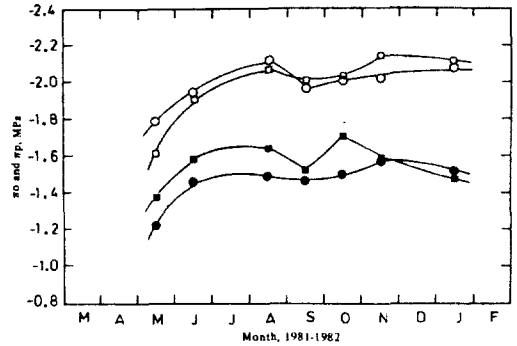


Fig. 2. The seasonal changes of original osmotic pressure,  $\pi_0$ , and osmotic pressure at incipient plasmolysis,  $\pi_p$ , in *Pinus koraiensis* and *Abies holophylla* shoots. The open circles and open squares are  $\pi_p$  values. The closed circles and closed squares are  $\pi_0$  values. The open and closed circles indicate the *Pinus koraiensis*. The open and closed squares indicate the *Abies holophylla*.

The seasonal changes of  $\pi_0$  and  $\pi_p$  obtained from the P-V curve were shown in Fig. 2. There was a general increase in  $\pi_0$  and  $\pi_p$  from May to August: then they remained approximately constant until next January. Whereas  $\pi_0$  in *Pinus koraiensis* was lower than in *Abies holophylla* throughout the growing season the  $\pi_p$  in *Pinus koraiensis* was slightly higher after August. The general trend of seasonal change for  $\pi_0$ , the osmotic pressure at maximum turgor was similar to the change for  $\pi_p$ , the osmotic pressure at incipient plasmolysis. This result was similar to other reports (Parker *et al.*, 1982; Tyree *et al.*, 1978).

The seasonal changes of maximum bulk modulus of elasticity,  $E_{max}$ , were shown in Fig. 3. The  $E_{max}$  was calculated after Cheung *et al.* (1976) and Tyree *et al.* (1978) as:

$$E_{max} = \frac{dP_{vat}}{dF}$$

where  $P_{vat}$ =volume-averaged turgor pressure at maximum turgor and  $F=(V_0-V_e-V_p)/V_p$ . The  $E_{max}$  in *Pinus koraiensis* has a tendency to gradually increase from 2.2 MPa in May to 6.3 MPa in November, then to decrease 2.4 MPa in next January. In contrast, the  $E_{max}$  in *Abies holophylla* decreased

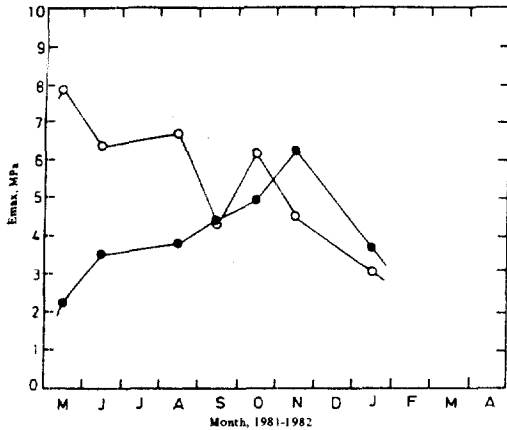


Fig. 3. The seasonal changes of the bulk modulus at maximum turgor,  $E_{max}$ , in *Pinus koraiensis* and *Abies holophylla* shoots. The open circles indicate the *Abies holophylla*; the closed circles indicate the *Pinus koraiensis*.

gradually from 7.9 MPa in May to 3.1 MPa in next January. The  $E_{max}$ 's were usually higher in *Abies holophylla* than in *Pinus koraiensis* during the growing season but they were *vice versa* during the non-growing season as shown in Fig. 3. Though the bulk moduli,  $E_{max}$ , obtained for a leaf or shoot can indicate the ability of a plant to osmoregulate or conserve water as related to drought resistance, drought avoidance and drought tolerance, its quantitatively accurate estimation might be difficult (Cheung *et al.*, 1976; Tyree *et al.*, 1978). If a plant with a higher  $E_{max}$  has a much drought tolerance than with a smaller  $E_{max}$ , *Abies holophylla* shoot may be more exhibited in drought tolerance than *Pinus koraiensis* shoot because a shoot with a higher  $E_{max}$  will be able to decrease its water potential more rapidly with water loss than one with a smaller  $E_{max}$  (Cheung *et al.*, 1976).

The seasonal changes of symplasmic water volume at maximum turgor ( $V_o$ ) versus total water volume ( $W_s$ ), symplasmic and apoplastic water, and the number of osmoles of solute ( $N_s$ ) versus dry weight ( $DW$ ) were shown in Fig. 4A,B. The  $V_o/W_s$  and  $N_s/DW$  were generally higher in *Pinus koraiensis* than in *Abies holophylla*. The  $V_o/W_s$  usually reached peak during the early growing season and then there were a gradual in *Pinus koraiensis* or rapid in

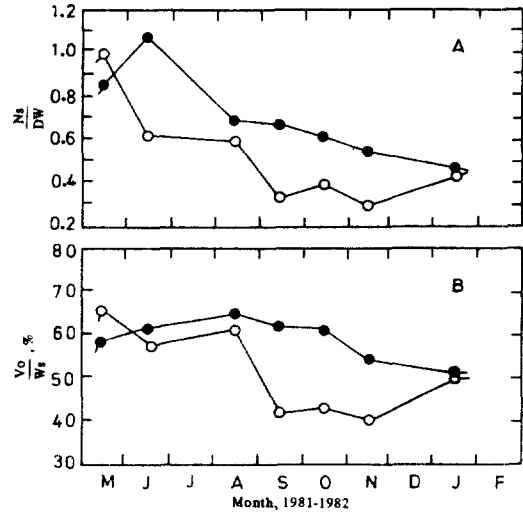


Fig. 4. The A figure is the seasonal changes of the number of osmoles of solute in symplasm,  $N_s$ , on the dry weight,  $DW$ , basis.  $N_s$  was calculated by the equation  $N_s = \pi_o V_o / (RT)$  where  $R$  is the universal gas constant and  $T$  is the Kelvin temperature. The B figure is the seasonal changes of the original osmotic water volume,  $V_o$ , on the total water volume (symplasmic and apoplastic water),  $W_s$ , basis. In A and B figures the open circles indicate the *Abies holophylla*; the closed circles indicate the *Pinus koraiensis*.

*Abies holophylla* decline until November. The similar trend was observed in *Acer* and *Populus* by Tyree *et al.* (1978). The high values of  $N_s/DW$  might be correlated with high values of  $\pi_o$  (negative) (Tyree *et al.*, 1978). The high value of  $\pi_o$  could allow cell elongation to persist under conditions of water stress, and usually some xerophytes would have a high  $\pi_o$  (Cheung *et al.*, 1975). As shown in Fig. 4, symplasmic water,  $V_o$ , made up about 40 to 65% in *Abies holophylla* and 55 to 65% in *Pinus koraiensis* of the total water volume,  $W_s$ . These values are lower than 60 to 95% in several leaves of broad-leaved trees (Cheung *et al.*, 1975) and 73% in *Cryptomeria japonica* (Yahata, 1979). However, the percentages of original osmotic water on total water volume basis,  $V_o/W_s$ , were consistently lower in a shoot than a leaf. This is probably due to the relatively greater volume of apoplastic water in a

Table 1. The seasonal changes of RWC(tlp), RWC\*, and Ws/DW in *Pinus koraiensis* and *Abies holophylla* shoots.

| Species                 | Month | RWC(tlp), % | RWC*, % | Ws/DW, % |
|-------------------------|-------|-------------|---------|----------|
| <i>Pinus koraiensis</i> | 5 '81 | 70.1        | 82.5    | 283.2    |
|                         | 6     | 74.8        | 84.5    | 295.3    |
|                         | 8     | 72.5        | 82.1    | 202.1    |
|                         | 9     | 74.8        | 84.4    | 181.2    |
|                         | 10    | 75.8        | 85.2    | 162.1    |
|                         | 11    | 76.5        | 87.3    | 156.1    |
|                         | 1 '82 | 72.5        | 85.9    | 140.3    |
| <i>Abies holophylla</i> | 5 '81 | 84.6        | 91.7    | 286.5    |
|                         | 6     | 83.8        | 90.9    | 164.8    |
|                         | 8     | 80.0        | 87.9    | 146.9    |
|                         | 9     | 75.6        | 89.8    | 128.6    |
|                         | 10    | 81.2        | 91.9    | 130.5    |
|                         | 11    | 73.8        | 89.5    | 113.8    |
|                         | 1 '82 | 69.3        | 83.5    | 129.4    |

woody tissue in the shoots (Cheung *et al.* 1975). In Fig. 4, the Ns/DW increased to a maximum early in leaf maturation and then declined to a more or less stable value. The early increase in Ns/DW may have been caused by inability of cell wall growth to keep pace with expansion. In Fig. 4, decreases in Ns/DW and Vo/Ws accompanying leaf senescence observed in *Pinus koraiensis* and *Abies holophylla* shoots were probably a result of increased membrane permeability. Apparent symplasmic water volume would be reduced as membrane integrity and semipermeability declined because senescence in plant tissue is accompanied by increased apparent free space and a loss in capacity to retain solutes (Parker *et al.*, 1982). Ns could have remained unchanged or even increased, but the large increase in DW would have reduced Ns/DW (Tyree *et al.*, 1978).

In the other hand, the seasonal values of RWC(tlp), RWC\*, and Ws/DW were presented in Table 1. The values of RWC(tlp) were between 70 to 77% in *Pinus koraiensis* and 69 to 85% in *Abies holophylla*. The some leaves such as *Ginkgo*, *Fraxinus*, *Populus*, *Salix*, and *Acer* normally retained more than 80% of osmotic water at incipient plasmolysis, show a superior osmoregulation or conservation by means of their cell wall properties as compared with other leaves such as *Betula* and

*Cornus* (Cheung *et al.*, 1975). The values of RWC\* were between 82 to 87% in *Pinus koraiensis* and 83 to 92% in *Abies holophylla* in Table 1. These values were higher than 77.9% in *Cryptomeria japonica* shoot (Yahata, 1979).

Consequently, as the comparative values of  $\pi$ ,  $\pi_p$ ,  $V_p/V_o$ ,  $E_{max}$ , Ns/DW, and RWC\* above discussed, it might be suggested that *Abies holophylla* shoot could have more or less a greater ability of drought tolerance as compared with *Pinus koraiensis* shoot.

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