

Effects of Light, Temperature, and Water Stress on the Photosynthesis and Respiration Rates of Leaves in Four Oak Species^{1*}

Sang Sup Han² and Ha Sun Kim²

4種의 참나무葉의 光合成速度와 呼吸速度에 미치는 光, 溫度, 水分의 影響^{1*}

韓相燮² · 金河善²

ABSTRACT

The present study has been designed to define the effects of photosynthetically active radiation, leaf temperature, and water stress on photosynthesis and respiration of leaves of four oak species (*Quercus mongolica*, *Quercus aliena*, *Quercus variabilis*, and *Quercus serrata*).

The results obtained are as follows :

1. The estimated light compensation points at which Pn approached zero were 38, 24, 20, and 18 $\mu\text{Em}^{-2}\text{s}^{-1}$ for *Q. aliena*, *Q. variabilis*, *Q. mongolica*, and *Q. serrata*, respectively. The light saturation points occurred at 500 $\mu\text{Em}^{-2}\text{s}^{-1}$ in three oak species except *Q. aliena*.
2. The maximum rates of Pn were 19.7, 15.2, 11.2, and 11.0 mg CO₂ dm⁻²h⁻¹ for *Q. variabilis*, *Q. serrata*, *Q. mongolica*, and *Q. aliena* leaves, respectively.
3. The transpiration rates of *Q. variabilis* and *Q. serrata* leaves were slightly higher than those of *Q. mongolica* and *Q. aliena* leaves at various photosynthetically active radiations(PAR), but cuticular transpiration rates at dark were similar in four oak species.
4. The optimum photosynthesis occurred at 25°C in *Q. aliena*, *Q. variabilis*, and *Q. serrata* leaves, but 20°C in *Q. mongolica* leaves. In four oak species, the net photosynthesis approached zero at about 40°C.
5. The dark respiration rates of leaves exhibited the following ranking of species : *Q. variabilis* > *Q. mongolica* > *Q. aliena* > *Q. serrata*.
6. The maximum productive efficiency(Pg/Rd) of leaves occurred highest in *Q. serrata* at 20°C, then in *Q. mongolica* at 20°C, then in *Q. aliena* at 25°C, and finally in *Q. variabilis* at 15°C.
7. The decrease of net photosynthesis in *Q. serrata* began at about -1.2 MPa, and then approached zero at -2.9 MPa of leaf water potential. The decrease of net photosynthesis began at 3% of water loss, and then approached zero at 17.5% of water loss.
8. As indicated by tissue-water relations parameters, it may be suggested that *Q. aliena* and *Q. variabilis* are more tolerant and favored on xeric forest soils than *Q. mongolica* and *Q. serrata*.

Key words : photosynthesis ; respiration ; four oak species

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² 江原大學校 林科大學 College of Forestry, Kangweon National University, Chuncheon 200-701, Korea.

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要 約

우리나라 溫帶林에 分布하는 落葉性 참나무類의 生理·生態的 習性を 밝히기 위하여 이번 연구에서는 신갈나무, 갈참나무, 굴참나무, 졸참나무 葉의 光合成速度와 呼吸速度에 미치는 光, 溫度, 水分의 影響을 調査 하였다. 그 結果를 要約하면 다음과 같다.

1. 졸참나무, 신갈나무, 굴참나무, 갈참나무 葉의 光補償點은 각각 $18, 20, 24, 38 \mu\text{Em}^{-2}\text{S}^{-1}$ 였으며, 光飽和點은 갈참나무 葉을 제외한 3樹種에서 약 $500 \mu\text{Em}^{-2} \cdot \text{s}^{-1}$ 였다.

2. 갈참나무, 신갈나무, 졸참나무, 굴참나무 葉의 最大 純光合成速度는 각각 11.0, 11.2, 15.2, 19.7 $\text{mg CO}_2 \text{dm}^{-2}\text{h}^{-1}$ 였다.

3. 굴참나무와 졸참나무葉의 氣孔蒸散速度는 신갈나무와 갈참나무葉 보다 높았으며 角皮蒸散速度는 4 樹種 모두 비슷 하였다.

4. 最適光合成 溫度는 신갈나무葉에서는 약 20°C , 갈참나무, 굴참나무, 졸참나무葉에서는 약 25°C 였으며, 4樹種 모두 약 40°C 에서 純光合成速度가 0에 달했다.

5. 葉의 暗呼吸速度의 크기는 굴참나무>신갈나무>갈참나무>졸참나무 순이었다.

6. 葉의 最大 生産效率(Pg/Rd)은 졸참나무와 신갈나무는 20°C , 갈참나무는 25°C , 굴참나무는 15°C 에서 일어났으며 그 크기는 졸참나무>신갈나무>갈참나무>굴참나무 순이었다.

7. 졸참나무葉의 純光合成速度는 -1.2Mpa 에서 初期減少가 시작되어 -2.9Mpa 에서 0에 달했다. 또 葉이 3%의 水分損失을 받으면 純光合成速度의 初期減少가 시작되어 17.5%의 水分損失에서 0에 달했다.

8. p-v曲線에 의해 얻은 水分特性因子로 判斷할때 갈참나무와 굴참나무가 신갈나무와 졸참나무 보다 耐乾性이 더 強함을 알 수 있었다.

INTRODUCTION

The oak species is dominantly distributed throught the Korean Peninsular and its stock volume occupy the 27% of the total stock volume to forest ecosystem in Korea (Forest Research Institute, 1988). In Korea, *Quercus mongolica*, *Q. aliena*, *Q. variabilis*, *Q. serrata*, *Q. acutissima*, and *Q. dentata* are the main tall deciduous trees of oak species in cool temperate zone. These species generally dominates on xeric, shallow forest soil (Maruyama & Toyama, 1987), but they are occasionally observed in slightly different environmental conditions. For instance, *Q. mongolica* is often favored on mesic north- and east-facing aspects, higher and middle slopes having moderately deep soils. Especially *Q. mongolica* is an edaphic climax species of broad-leaved deciduous forests in the cool temperate zone, whereas the *Q. serrata* is a substitutional vegetation species of broad-leaved evergreen forests in the warm temperate zone (Maruyama &

Toyama, 1987; Miyawaki, 1977; Numata, 1974). In cool temperate zone, *Q. dentata* and *Q. acutissima* are favored on xeric south-and west-facing aspects, upper and sunny slopes and ridges (Chung, 1972).

The oak species used in this study (*Q. mongolica*, *Q. aliena*, *Q. variabilis*, and *Q. serrata*) characteristically represent slightly different habitat segregation in cool temperate zone in Korea. To clarify the cause of such ecophysiological habitats, the measurement of photosynthesis and respiration is potentially important because the rates of photosynthesis and respiration of leaves sensitively respond to changes in environmental factors such as light, temperature, and water stress. Recently many ecophysiological studies have been reported concerning the effects of photosynthetically active radiation, temperature, and water deficit on leaf photosynthesis and leaf conductance of foreign oak species (Chambers, 1976; Endo & Oikawa, 1985; Hinckley et al., 1978; Maruyama & Toyama, 1987; Parker et al., 1982). However, few comprehensive studies

have been reported concerning the photosynthesis and respiration rates associated with environmental factors on oak species in Korea.

The purpose of this study was to investigate the effects of photosynthetically active radiation, temperature, and water stress on photosynthesis rate, and the temperature response of dark respiration rate of leaves in four deciduous oak species distributed in cool temperate zone in Korea.

MATERIALS AND METHODS

The measurements of net photosynthesis (Pn) and dark respiration were conducted on the attached leaves of 2-year-old *Quercus mongolica*, *Quercus aliena*, *Quercus variabilis*, and *Quercus serrata* seedlings which are raised in the pot in the nursery of Kangweon National University. The changes of CO₂ concentration in the acrylic assimilation chamber (12cm x 13cm x 10cm), in which the attached leaves were enclosed, were measured under controlled conditions in the laboratory using an infrared CO₂ gas analyzer (ADC-225MK₃) in an open system. The leaf temperature in the chamber was controlled using a water cooled heat exchanger (Yamato, CTE-22 W). The leaf surface temperature in the chamber was measured with a thermocouple clipped to the underside of the leaf and recorded by an automatic recorder (TOA, EPR-221A). The rate of ambient air supplied into the chamber was 2 ℓ/min. The air in the chamber was mixed by a small fan with a velocity of 1 m/sec. The light was supplied from an incandescent spotlight (1000 W) which was passed in acrylic water bath. The photosynthetic active radiation (PAR) was measured by a Quantum Radio-Photometer (Crump, Cat. No. 550).

The leaf water potential during the photosynthesis measurement was measured as stem dried. The measurements of photosynthesis and leaf water potential were always finished within 24 hours after stem cut. The transpiration rates at various light intensities were measured by decreas-

ing rate of leaf weight. The leaf water potential and tissue-water relations parameters in P-V curves were measured with a pressure chamber (DIK-PC-40, Japan). The samples used in the experiments of P-V curves were collected from 20 to 25 year-old trees growing in campus of Kangweon National University. The samples were selected from upper crown positions of the southern aspect to avoid possible spatial variations in the parameters arising from difference in illumination or height that have been reported in other studies (Hellkvist et al., 1974; Parker et al., 1982; Tyree et al., 1978). The collection time was usually in the evening after 7 p.m. and the measurements of samples in P-V curves were always finished within 48 hours from collection time. An excised branch about 50 cm long was immersed in a water bottle and immediately transported to the laboratory where their branch was recut under water bath. This sample was then allowed to resaturate overnight in the dark at room temperature (about 25°C). Since oak leaves have very short petioles, a single leaf attached to a twig about 5 cm long was used in experiments of P-V curves for each species. The details for measurement and analysis of water relations parameters in P-V curves were similar to those described by Cheung et al. (1975), Han & Choi (1983, 1986), Maruyama & Morikawa (1983, 1984), Tyree Hammel (1972), Tyree et al. (1978), and Yahata (1979).

RESULTS AND DISCUSSION

1. Changes in photosynthesis and transpiration with light intensity

The net photosynthesis of four oak species leaves in August was shown in Fig. 1. The estimated light compensation points at which Pn approached zero were 38, 24, 20, and 18 $\mu\text{Em}^{-2}\text{s}^{-1}$ for *Q. aliena*, *Q. variabilis*, *Q. mongolica*, and *Q. serrata*, respectively. This exhibited the following ranking of species from most to least efficient at low light intensities: *Q. serrata* > *Q. mongolica* > *Q. variabilis* > *Q. aliena*. According to

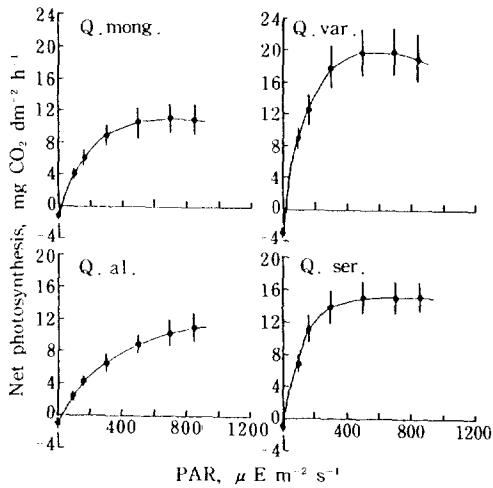


Fig. 1. The effect of photosynthetically active radiation on net photosynthesis in *Q. mongolica*, *Q. aliena*, *Q. variabilis*, and *Q. serrata* leaves. Each plot is mean of three measurements. Vertical bars indicate the standard deviation for three to five measurements.

Hinckley et al. (1978), the light compensation points were 30, 32, and $28 \mu E m^{-2} s^{-1}$ for black, white, and northern red oak, respectively. The maximum rates of Pn were 19.7, 15.2, 11.2, and $11.0 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ for *Q. variabilis*, *Q. serrata*, *Q. mongolica*, and *Q. aliena*, respectively. The $19.7 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ in *Q. variabilis* is relatively high value as compared with other three oak species. The maximum rates of Pn were about $12 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ in white oak; about $10 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ in black and northern red oak (Hinckley et al., 1978); $12.7 \pm 4.9 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ in *Q. mongolica* var. *grosseserrata*; $16.2 \pm 1.8 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ in *Q. serrata* (Maruyama & Toyama, 1987). The light saturation occurred at $500 \mu E m^{-2} s^{-1}$ in three oak species except *Q. aliena* (Fig. 1). Hinckley et al. (1978) noted that the light saturation points were 400 to $500 \mu E m^{-2} s^{-1}$ in white, black, and northern red oak leaves.

The transpiration rates of *Q. aliena*, *Q. variabilis*, *Q. serrata* leaves under favorable water condition increased with increasing of photosynthetically active radiation, PAR except *Q. mongolica* (Fig. 2). *Q. mongolica* leaves approximately

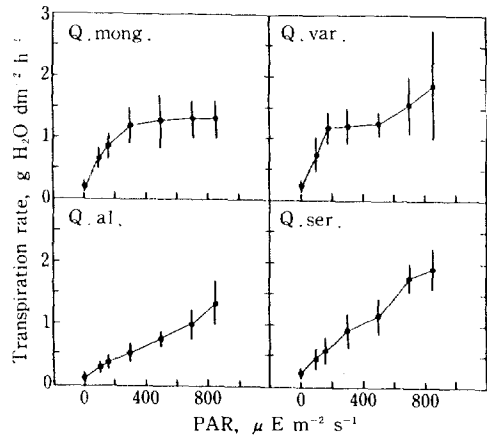


Fig. 2. Effect of photosynthetically active radiation on transpiration rate in *Q. mongolica*, *Q. aliena*, *Q. variabilis*, and *Q. serrata* leaves under full water condition. Each plot is mean of ten measurements. Vertical bars indicate the standard deviation for ten measurements.

saturated at about $500 \mu E m^{-2} s^{-1}$. The transpiration rates of *Q. variabilis* and *Q. serrata* were slightly higher than those of *Q. mongolica* and *Q. aliena* at various PAR, but cuticular transpiration rates at dark were similar in four oak species (Fig. 2). The maximum transpiration rates at photosynthetic light saturation (over $500 \mu E m^{-2} s^{-1}$) in four oak species were relatively lower compared with other oak species such as $2.9 \pm 0.6 \text{ g H}_2\text{O dm}^{-2} \text{ h}^{-2}$ in *Q. mongolica* var. *grosseserrata* and 3.0 ± 0.5 in *Q. serrata* (Maruyama & Toyama, 1987).

2. Changes in photosynthesis and respiration with leaf temperature changes

The relationships between relative photosynthesis and leaf temperature are shown in Fig. 3. The optimum temperature for photosynthesis were 25°C in *Q. aliena*, *Q. variabilis*, and *Q. serrata* leaves, but 20°C in *Q. mongolica* leaves. After reaching a species specific optimum, relative photosynthesis decreased with increasing leaf temperature. In general, leaf temperature can influence the photosynthesis both through its effects on leaf conductance and its influence on

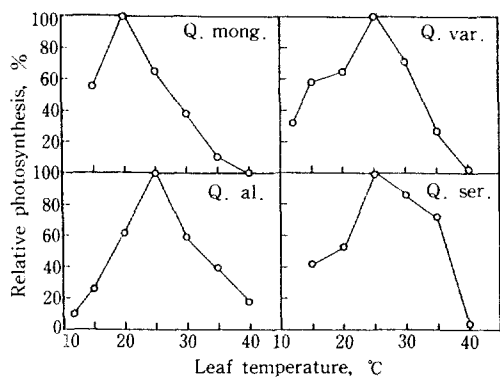


Fig. 3. Relative photosynthesis at various temperatures in *Q. mongolica*, *Q. aliena*, *Q. variabilis*, and *Q. serrata* leaves in August. Each plot is mean of three measurements.

enzymatic activity (Black, 1973; Hinckley et al., 1978). In addition, the optimum temperature for photosynthesis can at least partially explain the most favorable temperature regime in plants. *Q. variabilis* and *Q. serrata* have a rather broad plateau of high photosynthesis rates than *Q. mongolica* and *Q. aliena* (Fig. 3). Especially *Q. mongolica* and *Q. variabilis* were high photosynthesis at low temperature regime while *Q. serrata* was high photosynthesis at high temperature regime. This may partly explain that *Q. serrata* is a substitutional vegetation species of broad-leaved evergreen forest in warm temperate zone (Maruyama & Toyama, 1987) and *Q. mongolica* and *Q. variabilis* are more favored on upper slopes at highland in cool temperate zone (Chung, 1972). In all the species, the relative photosynthesis approached zero at about 40°C (Fig. 3). Hinckley et al. (1978) estimated that net photosynthesis would reach zero as leaf temperature approached 44°C in white, black, and northern red oak leaves. Lassoic and chambers (1976) observed that the net carbon exchange rate approached zero at 37.5°C in northern red oak sapling.

On the other hand, the changes in dark respiration rates of leaves with increasing leaf temperature for four oak species were shown in Fig. 4. The Arrhenius plots for dark respiration

rates were represented as a convex curve at 15°C in *Q. mongolica*, 20°C in *Q. variabilis* and *Q. serrata*, and 23°C in *Q. aliena*. The dark respiration rates usually increased rapidly until about 20°C, and then gradually increased over 20°C (Fig. 4). Especially the dark respiration rate in *Q. variabilis* leaves was higher than those of other three oak species in all temperature ranges. The measured dark respiration rates herein exhibited the following ranking of species: *Q. variabilis* > *Q. mongolica* > *Q. aliena* > *Q. serrata*.

The values of productive efficiency (Pg/Rd, gross photosynthesis to dark respiration) at various temperatures for *Q. mongolica*, *Q. aliena*, *Q. variabilis*, and *Q. serrata* leaves were shown in Table 1. The maximum productive efficiency occurs highest in *Q. serrata* at 20°C, then in *Q. mongolica* at 20°C, then in *Q. aliena* at 25°C, and finally in *Q. variabilis* at 15°C. In general, it may explain that the species containing high productive efficiency grows well on their given environmental conditions. In all species, the productive efficiencies were relatively high at low temperature regime, and decreased rapidly over 30°C. This pattern is similar to other reports (Hagihara, 1973; Han & Yi, 1985). Although

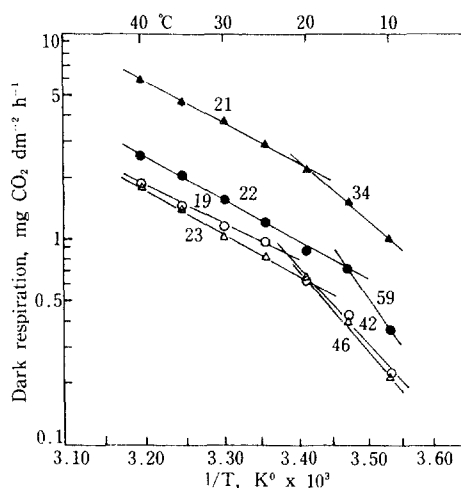


Fig. 4. Arrhenius plots for dark respiration of *Q. mongolica* (●), *Q. aliena* (○), *Q. variabilis* (▲), and *Q. serrata* (△) leaves in August. Each plot is mean of three measurements.

Table 1. The values of productive efficiency (Pg/Rd) in various temperatures for *Q. mongolica*, *Q. aliena*, *Q. variabilis*, and *Q. serrata* leaves. Each value is the mean of three measurements.

Temperature °C	Productive efficiency, Pg/Rd			
	<i>Q. mong.</i>	<i>Q. al.</i>	<i>Q. var.</i>	<i>Q. ser.</i>
15	9.55	7.64	8.86	15.76
20	13.57	11.60	6.89	20.76
25	6.96	12.36	7.93	18.91
30	3.79	6.62	4.84	11.91
35	1.61	3.89	3.22	8.44
40	0.81	2.14	1.14	1.53

Q. variabilis was the highest in net photosynthesis among four oak species, its productive efficiency was the lowest in all measured temperature ranges because dark respiration rate was exceptionally high as shown in Fig. 4. In addition, *Q. serrata* has a rather broad temperature range of high productive efficiency from 15°C to 30°C. Also this may be partially explained that *Q. serrata* is broadly distributed from warm temperate zone to cool temperate zone in Korea.

3. Ecophysiological interpretations on water relations parameters

The relative photosynthesis for water potential and water loss in *Q. serrata* leaves in August was shown in Fig. 5. The relative photosynthesis in *Q. serrata* began at about -1.2 MPa, then approached zero at -2.9 MPa of leaf water potential. Maruyama & Toyama(1987) reported that the initial decrease of net photosynthesis in August began at about -0.7 MPa in *Fagus crenata*, -0.8 MPa in *Q. mongolica* var. *grosseserrata*, and -1.0 to -1.2 MPa in *Q. serrata*. In general, it has been observed that the net photosynthesis begins to decline at different leaf water potential among species and seasons (Larcher, 1975; Maruyama & Toyama, 1987). In conifer, the initial decrease occurred at -1.2 MPa in Douglas-fir, -1.4 MPa in white spruce and western hemlock, -0.8 MPa in lodgepole pine(Brix, 1979), and -1.0 MPa in June and -1.3 MPa in July for *Picea ghehnii*(Takahashi, 1981).

On the other hand, the water potential at which

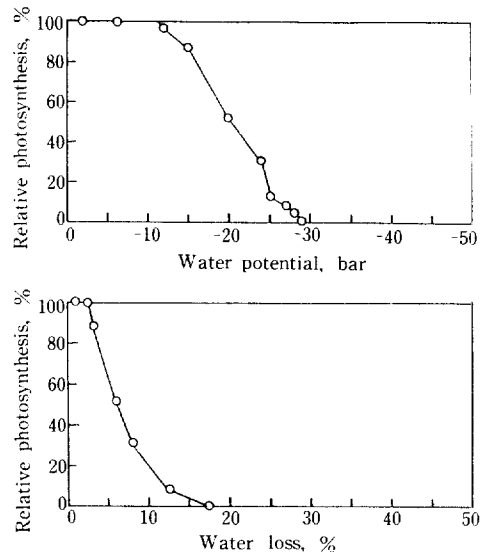


Fig. 5. Relative photosynthesis for water potential and water loss in *Q. serrata* leaves in August. Each plot is mean of three measurements.

net photosynthesis approached zero may be taken to be the critical water potential for CO₂ balance in plant(Larcher, 1975). This critical water potential is determined by marked or complete closing of the stomata as well as by the direct effect of water shortage on the protoplasm. Once this state has been reached, a renewed water supply does not lead to an immediate recovery of photosynthesis, and the original photosynthetic capacity may never be achieved again(Larcher, 1975). The critical water potential at which net photosynthesis approached zero was -2.9 MPa in *Q. serrata*(Fig. 5). However, unlike this result, Maruyama & Toyama(1987) noted that the net photosynthesis rates of *Q. serrata* had relatively high values(30 to 50% of as saturated water condition) even at -3.0 MPa of xylem pressure potential. In conifer, the critical water potentials occurred at below -4.0 MPa in Douglas-fir, -3.5 MPa in western hemlock, -2.5 MPa in white spruce, and -2.0 MPa in lodgepole pine(Brix, 1979).

The decrease of net photosynthesis based on water loss began at 3% of water loss in leaf tissues, then progressed rapidly with increasing

Table 2. Water relations parameters of leaves in August. π_o is the original osmotic pressure. π_p is the osmotic pressure at incipient plasmolysis. $RWC_{(t|p)}$ is the relative water content at turgor loss point. E_{max} is the bulk elastic modulus of the cell wall at full turgor pressure. Each value is mean of three measurements.

Species	π_o -MPa	π_p -MPa	$RWC_{(t p)}$ %	E_{max} MPa
<i>Q. mongolica</i>	2.08	2.30	88.7	14.7
<i>Q. aliena</i>	2.28	2.48	90.1	23.6
<i>Q. variabilis</i>	2.23	2.37	88.8	17.0
<i>Q. serrata</i>	2.05	2.41	85.7	11.7

water loss, finally approached zero at 17.5% of water loss(Fig. 5). Larcher(1975) described that net photosynthesis approached zero at about 12 to 17% of water loss in *Fagus silvatica*, 20% in *Olea europaea*, 34% in *Stipa capillata*, and 37% in *Gossypium herbaceum*.

The tissue-water relations parameters of four oak species leaves in August obtained from P-V curves were shown in Table 2. The values of original osmotic pressure, π_o at full saturation in *Q. mongolica* and *Q. serrata* were 0.15 to 0.20 MPa lower than those of *Q. aliena* and *Q. variabilis*. These π_o values in four oak species were lower than the seasonal mean values of π_p -1.19 MPa in white oak and -1.76 MPa in northern red oak(Parker et al., 1982). The value of osmotic pressure at incipient plasmolysis, π_p in *Q. mongolica* was the highest among four oak species. The π_p values of four oak species were 0.14 to 0.36 MPa lower than the values of π_p (Table 2). These π_p values were similar to other results in *Q. mongolica* var. *grosseserrata* and *Q. acutissima* leaves(Han & Choi, 1986), but higher than the seasonal mean π_p values, -2.64 MPa in white oak and -2.62 MPa in northern red oak (Parker et al., 1982).

The relative water contents at incipient plasmolysis($RWC_{(t|p)}=V_p/V_o$) retained more than 80% in four oak species(Table 2). As indicated by $RWC_{(t|p)}$, *Ginkgo biloba*, *Fraxinus pennsylvanica*, *Populus sargentii*, *Salix lasiandra*, and *Acer saccharinum* leaves retained more than 80%, but

Betula occidentalis and *Cornus stolonifera* leaves retained 60 to 64%(Cheung et al., 1975). Also the $RWC_{(t|p)}$ in white oak, northern red oak, and mockernut hickory leaves retained 67% to 75% (Parker et al., 1982). The leaves normally retained more than 80% show a superior osmoregulation(or water conservation) by means of their cell wall properties compared with other leaves in which $RWC_{(t|p)}$ is between 60 to 64% such as *Betula occidentalis* and *Cornus stolonifera* (Cheung et al., 1975). The values of E_{max} in *Q. aliena* and *Q. variabilis* leaves were slightly higher than those of *Q. mongolica* and *Q. serrata* leaves(Table 2).

Parker et al.(1975) noted that low values of π_o and π_p , and high values of E_{max} and $RWC_{(t|p)}$ exhibited by white oak indicated a superior capacity to sustain stomatal opening and water uptake from dry soil and to maintain relatively high values of relative water content as leaf water potential declined. The evident drought-avoiding responses of mockernut hickory indicated by high values of π_p and low values of E_{max} and $RWC_{(t|p)}$ suggest a low competitive ability on xeric sites(Parker et al., 1982). Consequently, as indicated by tissue-water relations parameters (Table 2), it may be suggested that *Q. aliena* and *Q. variabilis* are more tolerant and favored on xeric forest soils than *Q. mongolica* and *Q. serrata*. However, the measurements in P-V curves were made only during a limited season of the year, mainly in August, so in this paper the discussion for water relations parameters is restricted to this period.

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