

## Comparison of Adjustments to Drought Stress Among Seedlings of Several Oak Species

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In order to compare the adjustment of 6 oak species to water stress, the components of water status, tissue elastic modulus, free proline content of leaves and morphological characteristics were determined in pot culture. *Quercus dentata* and *Q. mongolica* responded effectively to drought with high root : shoot (R/S) ratio or maintenance of high turgor pressure by large and fast osmotic adjustment and *Q. variabilis* with maintenance of high turgor pressure by low elastic modulus under drought. Meanwhile, *Q. aliena* and *Q. serrata* responded effectively with low osmotic potential ( $\psi_o$ ) at full saturation and *Q. acutissima* with long root in spite of rigid cell wall and high osmotic potential ( $\psi_o$ ) at full saturation. Proline content in leaves of *Q. dentata*, *Q. mongolica* and *Q. aliena* increased early and rapidly at high leaf water potential ( $\psi_{leaf}$ ). The results indicate that 6 oak species have adjustment different from each other to water stress.

**Keywords :** drought resistance, oak, water status, elastic modulus, morphological adaptation

Drought resistance of plants is the capacity to withstand periods of drought (Larcher, 1980). Plants resist the possible damaging effects of drought by either avoiding or tolerating the stress but a mixture of both strategies is more often represented (Levitt, 1972). In periods or sites of drought, the strategies of plants to limited water supply are as follows; (1) minimizing water loss by the morphological adaptations such as low stomatal density, high leaf hair density and small absorption of irradiance in leaves, and controlling transpiration by stomatal closing, (2) increasing water absorption from soil and (3) increasing drought resistance by osmotic and elastic adjustment which allows the leaves to maintain turgor pressure at low water potential (Levitt, 1972; Han and Kim, 1980; Jones, 1983; Kozłowski *et al.*, 1991).

The objective of this paper is to compare some ecophysiological adjustments to drought stress in terms of water status and morphological adaptations in 6 oak species using the data obtained from pot culture.

### METHODS

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### Plants and cultivation

The seedlings of 6 oak species including *Quercus aliena*, *Q. acutissima*, *Q. serrata*, *Q. dentata*, *Q. mongolica* and *Q. variabilis* were tested in this study.

One seed was sown in a polystyrene pot filled with about 150 mL of soil (clay : humus = 5 : 1 by vol.) and germinated in a greenhouse. Seedlings with stems about 5 cm long were transplanted into plastic pots (18 cm d., 13 cm h.) filled with 3 kg of soil (clay : humus = 4 : 1 by vol.). Plants were irrigated with tap water 3 times per week and half-strength Hoagland's solution once a month.

### Drought treatment and measurement of water status

Eighty days after transplant, watering was stopped. The duration of the water stress cycle was 15 d to 25 d. Each stress treatment consisted of 4 replicates. The severity of the water stress was monitored by measuring the water status (Wilson *et al.*, 1980; Suh and Kim, 1981; Kim and Lee-Stadelmann, 1984; Ihm, 1989): leaf water potential ( $\psi_{leaf}$ ) was measured with dew-point microvoltmeter (HR-33T, Wescor)

and leaf chambers (C-52, Wescor) operating in the dew point mode, osmotic potential ( $\psi_o$ ) was determined by measuring  $\psi_{leaf}$  of frozen and thawed leaf discs with the water potential measuring equipment, relative water content (RWC) and water saturation deficit (WSD) were recorded and the bulk volumetric modulus ( $\epsilon$ ) was calculated as described by Kim (1990).

Water status was determined with fully expanded leaves at dawn before 08:00. All leaves sampled for water status measurements were wiped with moist paper towels prior to use. Proline content of leaves was determined by the method of Bates *et al.* (1973) and Kim (1990).

To examine morphological characteristics of plants, plants were harvested at the end of experiment, and then length of main root, root:shoot ratio (R/S) and leaf area ratio (LAR) were determined by the methods of Evans (1972).

## RESULTS

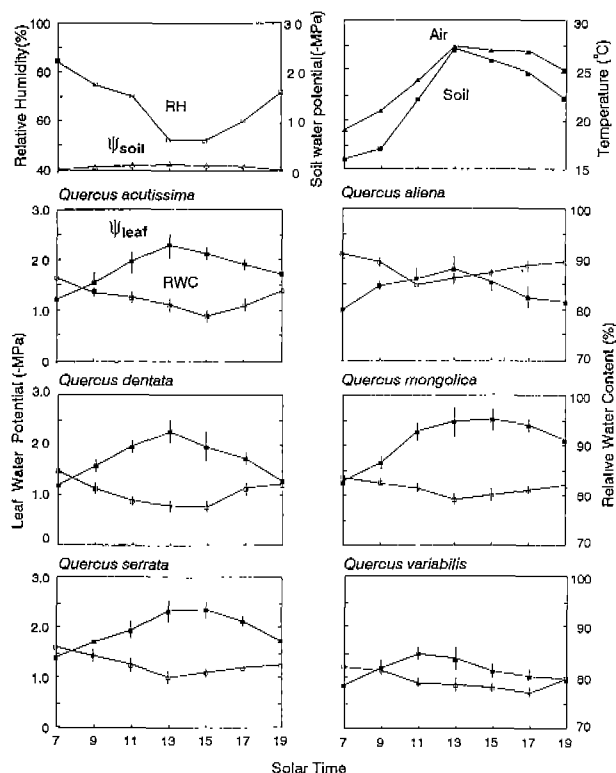
### Diurnal courses of water status

The  $\psi_{leaf}$  of 6 oak seedlings under watering were as high as  $-0.85$  MPa to  $-1.35$  MPa in the morning (7:00) and as low as  $-1.47$  MPa to  $-2.51$  MPa at midday (13:00) and then increased to  $-1.0$  MPa to  $-2.10$  MPa in the evening (19:00) (Fig. 1 and Table 1). The diurnal trends in the RWC of leaves in all seedlings were also similar to those in the  $\psi_{leaf}$  with time elapsed.

### Development of water deficit

WSD under watering was kept constant with 8.2% to 15.3%. However, under withdrawal of water it was kept constant for the first 9 d and thereafter increased rapidly above 50% in all species. Under watering mean WSD were 11.3, 8.2, 12.2, 10.2, 11.2 and 15.3% in *Q. acutissima*, *Q. aliena*, *Q. dentata*, *Q. mongolica*, *Q. serrata* and *Q. variabilis*, respectively (Fig. 2). The high WSD and  $\psi_{leaf}$  of *Q. variabilis* indicate that this species has been adapted to water stress in dry habitat with an avoidance mechanism related to several morphological characteristics.

Under watering the  $\psi_{leaf}$  at dawn in 6 species was kept almost constant during the experiment period. However, under withdrawal of water it was kept co-



**Fig. 1.** Diurnal courses of relative humidity (RH), soil water potential ( $\psi_{soil}$ ), air and soil temperature, leaf water potential ( $\psi_{leaf}$ ) and relative water content (RWC) of 6 oak species under watering from June 3 to June 10, 1989. Soil water potential was measured from 3 replicates per pot. Bars represent  $\pm$  SD.

**Table 1.** Changes in leaf water potential ( $\psi_{leaf}$ ) and relative water content (RWC) between 7:00 and 13:00 from June 3 to June 10, 1989

Species	$\psi_{leaf}$		RWC	
	7:00 (-MPa)	13:00 (-MPa)	7:00 (%)	13:00 (%)
<i>Quercus acutissima</i>	1.23	2.40	86.5	79.0
<i>Q. aliena</i>	1.01	1.81	91.0	86.1
<i>Q. dentata</i>	1.21	2.28	85.0	76.9
<i>Q. mongolica</i>	1.28	2.51	83.6	79.1
<i>Q. serrata</i>	1.35	2.42	85.9	80.2
<i>Q. variabilis</i>	0.85	1.47	82.3	78.8

stant for the early 7 d and decreased gradually with a rate of 0.11 to 0.17 MPa/d until the 17th d except that  $\psi_{leaf}$  of *Q. variabilis* decreased slowly with a rate of 0.02 MPa/d. After 17 d, it decreased rapidly below  $-6.0$  MPa in all species (Fig. 2).

### Adjustment to water deficit

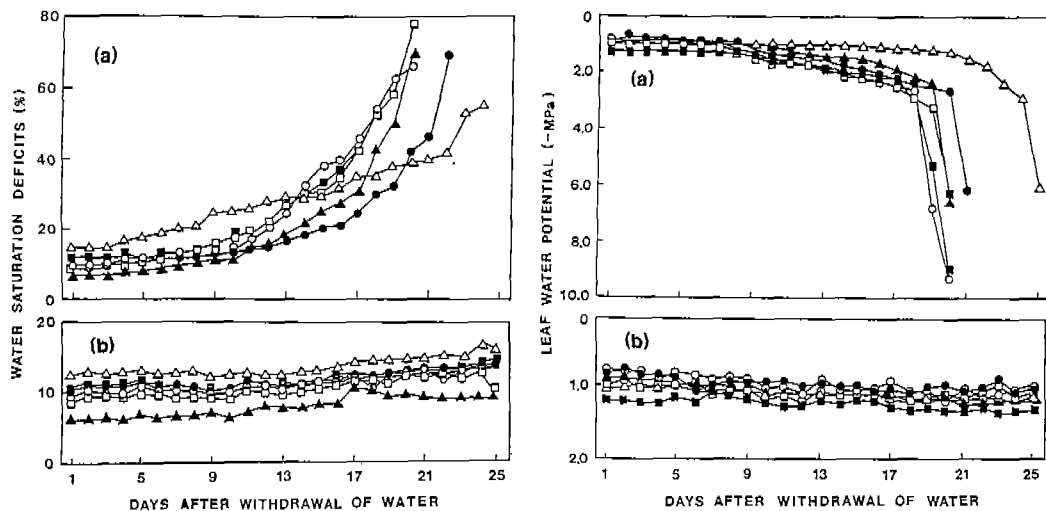


Fig. 2. Changes in water saturation deficit and leaf water potential under withdrawal of water (a) and under watering (b). *Q. acutissima*, ●-●; *Q. aliena*, ▲-▲; *Q. dentata*, ■-■; *Q. mongolica*, □-□; *Q. serrata*, ○-○; *Q. variabilis*, △-△.

Table 2. Comparisons of osmotic potential at full turgor ( $\psi_{o(100)}$ ), linear regression coefficients between osmotic potential ( $\psi_o$ ) and WSD or  $\psi_{leaf}$ , and elastic moduli ( $\epsilon$ ) for 6 oak species

Species	$\psi_{o(100)}$ (-MPa)	Slope of WSD- $\psi_o$	Slope of $\psi_{leaf}$ - $\psi_o$	$\epsilon$ (MPa)
<i>Quercus acutissima</i>	1.3	0.110	0.845	10.8
<i>Q. aliena</i>	2.0	0.081	0.623	4.3
<i>Q. dentata</i>	1.7	0.263	1.748	8.3
<i>Q. mongolica</i>	1.3	0.068	1.104	4.9
<i>Q. serrata</i>	2.1	0.077	0.726	8.6
<i>Q. variabilis</i>	1.8	0.049	0.857	3.8

The  $\psi_o$  at full saturation ( $\psi_{o(100)}$ ) of *Q. mongolica* and *Q. acutissima* were higher than those of the other species. Linear regression coefficients between WSD and  $\psi_o$  of *Q. acutissima* and *Q. dentata* were larger and those between  $\psi_{leaf}$  and  $\psi_o$  of *Q. dentata* and *Q. mongolica* were larger than those of the other species. Volumetric moduli of elasticity ( $\epsilon$ ) of leaves of *Q. acutissima* were the highest among all the species (Table 2).

**Changes in free proline content**

Proline content of leaves under water stress increased rapidly at above -2 MPa of  $\psi_{leaf}$  in *Q. mongolica*, *Q. dentata*, *Q. aliena* and *Q. serrata* but at below -2 MPa in *Q. variabilis* and *Q. acutissima* (Fig. 3). In relationship between proline content and RWC, proline increased rapidly at below 35% of the

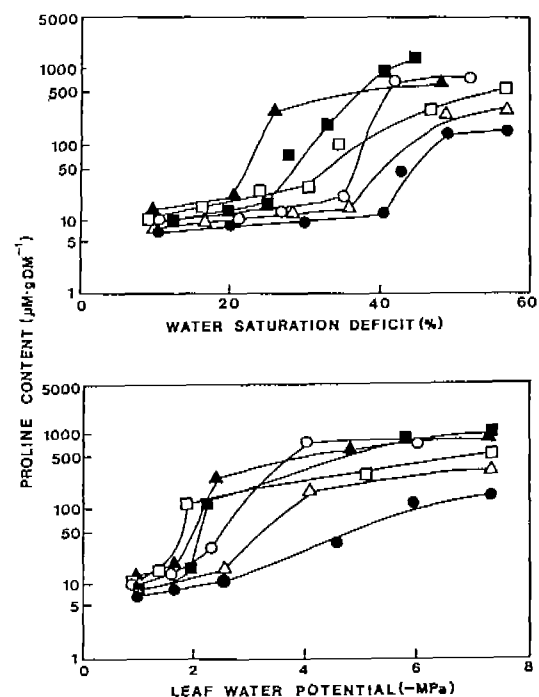


Fig. 3. Relationships between free proline content and water saturation deficit (above) or leaf water potential (below) of oak leaves. *Q. acutissima*, ●-●; *Q. aliena*, ▲-▲; *Q. dentata*, ■-■; *Q. mongolica*, □-□; *Q. serrata*, ○-○; *Q. variabilis*, △-△.

WSD in *Q. aliena*, *Q. dentata* and *Q. mongolica* but at above 35% of the WSD in *Q. serrata*, *Q. variabilis* and *Q. acutissima* (Fig. 3).

**Morphological characteristics of plants**

**Table 3.** Comparison of root:shoot (R/S) ratio, leaf area ratio (LAR) and length of main root in 6 oak species grown in greenhouse. Values represent mean  $\pm$  SD

Species	R/S ratio (g/g)	LAR (cm <sup>2</sup> /g)	Length of main root (cm)
<i>Quercus acutissima</i>	1.5 $\pm$ 0.4	35 $\pm$ 7	52 $\pm$ 16
<i>Q. aliena</i>	1.8 $\pm$ 0.7	38 $\pm$ 3	27 $\pm$ 9
<i>Q. dentata</i>	2.3 $\pm$ 1.0	28 $\pm$ 4	17 $\pm$ 6
<i>Q. mongolica</i>	1.1 $\pm$ 0.3	42 $\pm$ 3	22 $\pm$ 5
<i>Q. serrata</i>	1.9 $\pm$ 0.2	35 $\pm$ 4	40 $\pm$ 16
<i>Q. variabilis</i>	0.9 $\pm$ 0.2	51 $\pm$ 5	23 $\pm$ 10

R/S ratio was the highest (2.3) in *Q. dentata* but the lowest (0.9) in *Q. variabilis*, and the main root length was the longest (52 cm) in *Q. acutissima* among the 6 oak species studied (Table 3).

The leaf area ratio (LAR) was the highest (51 cm<sup>2</sup>/g) in *Q. variabilis* but the lowest (28 cm<sup>2</sup>/g) in *Q. dentata* among the 6 oak species studied.

## DISCUSSION

The data obtained in this study show the changes of  $\psi_{\text{leaf}}$  and RWC of the 6 oak species along diurnal cycles. This cycle is due to the increase of the water uptake and the decrease of the water loss (Dawson and Bliss, 1989). The small variation in  $\psi_{\text{leaf}}$  of *Q. variabilis* throughout the diurnal course suggests that it depends on avoidance mechanisms to water stress with the characteristics such as decreasing water loss, effective stomatal control, low stomatal density and small guard cell size (Kim and Kim, 1994). The  $\epsilon$  of *Q. variabilis*, *Q. aliena* and *Q. mongolica* were lower than those of the other species. As a result, they have a large capacity for maintaining high turgor pressure as water content of tissue decreases.

The increase in proline under drought is related to osmotic regulation (Morgan, 1984; Ibarra-Caballero *et al.*, 1988). The rapid accumulation of proline in *Q. dentata* and *Q. mongolica* indicates a correlation with resistance of drought stress.

The  $\psi_{\alpha(100)}$  of leaves of *Q. mongolica* and *Q. acutissima* are higher than those of the other species. Their high  $\psi_{\alpha(100)}$  is compensated for by low  $\epsilon$  or a rapid decrease in  $\psi_{\alpha}$  in response to drought stress. *Quercus dentata* has rigid cell wall but it is compensated for by a rapid decrease of the  $\psi_{\alpha}$ . The leaves of *Q. aliena* and *Q. serrata* have very low  $\psi_{\alpha(100)}$  and may be fur-

ther reduced by a moderately passive drop of the  $\psi_{\alpha}$ . *Q. acutissima* has the highest  $\psi_{\alpha(100)}$  of  $-1.3$  MPa and the rigidest cell wall among the 6 oak species studied.

*Quercus mongolica* and *Q. variabilis* have low R/S ratio, but *Q. dentata* has high R/S ratio. This suggests that the latter depends on the effective water uptake from soil. *Q. acutissima*, *Q. aliena* and *Q. serrata* have moderate R/S ratio and longer main root length than the other species. Such characteristics may be related with the adaptation to absorb water effectively from deep soil in response to drought. LAR of *Q. dentata* was the lowest among all the species, those of *Q. acutissima*, *Q. aliena* and *Q. serrata* were moderate and those of *Q. mongolica* and *Q. variabilis* were higher than those of the other species. Such morphological characteristics in relation to drought resistance are compensated for each other. Especially, *Q. dentata* has a leaf morphology very effective in drought resistance.

In conclusion, under drought stress *Q. dentata* and *Q. mongolica* responded effectively by means of high R/S ratio or turgor maintenance by larger and faster osmotic adjustment, and *Q. variabilis* by means of turgor maintenance by low  $\epsilon$ . These adaptations, especially at the individual level, suggest that in dry habitats and during dry periods they may grow well and survive better than the other species. However, *Q. aliena* and *Q. serrata* resist to drought stress by means of low  $\psi_{\alpha(100)}$  and high R/S ratio, and *Q. acutissima* by means of long root.

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## 참나무屬 幼植物의 乾燥스트레스에 대한 調整能의 比較

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### 적 요

한국의 대표적인 참나무속 식물인 상수리나무(*Quercus acutissima*), 갈참나무(*Q. aliena*), 떡갈나무(*Q. dentata*), 신갈나무(*Q. mongolica*), 졸참나무(*Q. serrata*) 및 굴참나무(*Q. variabilis*)의 수분 스트레스에 대한 조정능과 형태적 적응을 알아보기 위하여, 화분 재배한 유식물을 재료로 토양 수분포텐셜( $\psi_{\text{soil}}$ )의 감소에 따른 잎의 수분상태, 세포벽 탄력도, 유리 proline 함량 및 식물의 R/S(root/shoot) 비를 측정하고 각 특성 사이의 상호 관계를 검토하였다. 떡갈나무와 신갈나무는 높은 R/S 비로 인한 효과적인 수분흡수나 삼투조정을 하고, 굴참나무는 낮은 세포벽 탄력도에 의한 팽압유지로 건조에 적응하였다. 심하지 않은 수분스트레스하에서 신갈나무, 떡갈나무 및 갈참나무 잎의 proline 함량은 많이 증가하였다. 이것은 참나무속 유식물이 이러한 적응에 의해 건조기나 건조한 생육지에서 잘 성장하고 생존할 수 있음을 시사한다. 한편, 갈참나무와 졸참나무는 낮은 포화삼투포텐셜과 높은 R/S 비를 갖고, 상수리나무는 높은 포화삼투포텐셜 및 딱딱한 세포벽과 같은 불리한 특성을 가지지만 긴 주근으로 깊은 곳에서 수분흡수를 할 수 있는 특성을 가졌다. 이상의 결과는 6종의 참나무속 식물이 건조에 대해 생리생태학적으로 서로 다른 조정능을 가지고 있음을 시사한다.

주요어: 건조저항성, 참나무속, 수분상태, 세포벽 탄력도, 형태적 적응

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