

Stomatal Control and Strategy Segregation to Drought Stress in Young Trees of Several Oak Species

Kim, Jong-Wook and Joon-Ho Kim

Department of Biology, Seoul National University

수종 참나무속 유식물의 건조스트레스에 대한 기공저항의 조절과 전략의 분화

김종욱 · 김준호

서울대학교 생물학과

ABSTRACT

Leaf diffusive resistance (LDR), stomatal density, length of guard cell and hair density of leaves of 6 oak species were determined under withdrawal of water, and their strategies of drought stress were analyzed by principal component analysis. LDR of *Quercus acutissima*, *Q. aliena* and *Q. serrata* increased earlier than those of the other species at high leaf water potential (ψ_{leaf}) or low water saturation deficit (WSD), which was an avoidance mechanism reducing damage by water stress. *Q. variabilis* with low stomatal density, small stomatal size and high hair density had avoidance mechanisms increasing LDR at high ψ_{leaf} . However, *Q. mongolica* and *Q. dentata* increased LDR at low ψ_{leaf} as xeric species do. Results from principal component analysis on the 15 variables related to strategies of drought stress indicated that the 6 oak species were divided into 2 groups: (1) *Q. acutissima*, *Q. aliena* and *Q. serrata* as mesic habitat species and (2) *Q. variabilis*, *Q. mongolica* and *Q. dentata* as xeric habitat species. Among three xeric species *Q. acutissima* differed from the other two species in the drought strategies such as high hair density, low stomatal density, high leaf area ratio, stomatal closing at low ψ_{leaf} and small cell wall elasticity. The results could reasonably explain their drought strategies in natural habitat.

Key words: Drought stress, Leaf diffusive resistance, Oak, Stomata

INTRODUCTION

In periods or sites of drought, the strategies of plants to regulate limited water supply are (1) minimizing water loss by morphological adaptations and controlling transpiration,

(2) increasing water absorption from soil, and (3) increasing drought resistance by osmotic and elastic adjustment (Levitt 1972, Jones 1983). Kim and Kim (1994) reported that the 6 oak species had different osmotic and elastic adjustment and avoidance mechanisms including morphological adaptations.

Low stomatal density decreases transpiration per unit leaf area and increases drought resistance (Heichel 1971, Miskin *et al.* 1972). Plants from dry sites closed their stomata at less relative water contents in leaves than those from wet sites (Sanchez-Diaz and Kramer 1971, Tobiessen and Kana 1974, Davies and Kozlowski 1977).

The distribution of plant species was frequently explained by environmental factors such as topography and soil moisture gradients but rarely by adjustment to drought stress (Jayasuriya and Pemadasa 1983, Meiners *et al.* 1984, McCarthy *et al.* 1987). Combining with the results of the study by Kim and Kim (1994) on drought resistance in relation to water status and morphological adaptation, the strategy segregation to drought was determined by principal component analysis.

The objectives of this paper are to describe the relationships between leaf diffusive resistance and water status of leaf, and the mechanisms of stomatal adjustment to water stress in 6 oak species, and to investigate the strategy segregation to drought.

MATERIALS AND METHODS

Plants and cultivation

The seedlings of 6 *Quercus* species including *Quercus acutissima*, *Q. aliena*, *Q. dentata*, *Q. mongolica*, *Q. serrata* and *Q. variabilis* were grown in a controlled growth chamber (YGC-250, Yanaco) equipped with white fluorescence lamps at $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ quantum flux density, $27^\circ\text{C}/20^\circ\text{C}$ in temperature, 50% constant in relative humidity and 15h/9h in photoperiod. The conditions for germination and growth of the plants were described in Kim and Kim (1994).

Drought treatment and measurement of water status

After 80 d of transplanting, watering was stopped with the duration of the water stress cycle of 15 d to 25 d. Each stress treatment consisted of 4 replicates. The measurement of soil water potential (ψ_{soil}), ψ_{leaf} and water saturation deficit (WSD) of leaves were described in Kim (1990) and Kim and Kim (1994). The relationship between moisture content and water potential of soil used during the experiment period was shown in Fig. 1.

Measurement of leaf diffusive resistance

Measurements of leaf diffusive resistance were made on the abaxial surfaces of fully expanded leaves using a diffusion porometer (Lambda, LI-65) with a sensor cup as described by Kanemasu *et al.* (1969).

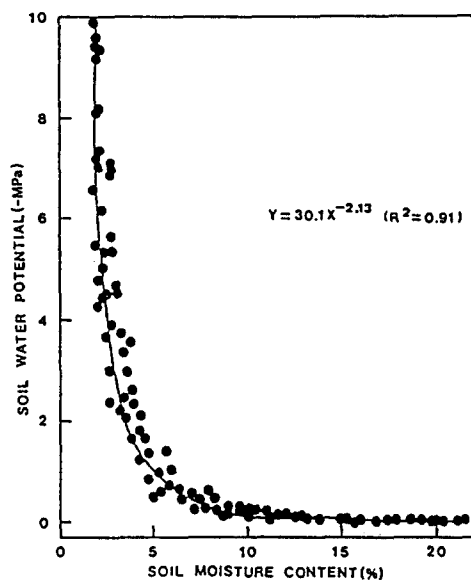


Fig. 1. Relationship between moisture content and water potential of soil in the pots. The line was fitted by the equation of power function.

time, ψ_{leaf} , ψ_{soil} , WSD and soil moisture content (SMC) at stomatal closing obtained from this study, and the changing rate of turgor potential (ψ_t) with ψ_{leaf} , of ψ_o with WSD and ψ_{leaf} , elastic modulus, leaf area ratio (LAR), root:shoot (R/S) ratio and root length obtained from the study of Kim (1990) and Kim and Kim (1994) on drought resistance by oak species in relation to water status and morphological adaptation. This yielded 2 principal components with eigen values greater than 1.0.

RESULTS

Changes in leaf diffusive resistance with water status of plant and soil

The points in which the stomata were closed and the transpiration rate were dependent on the vapor conductance of the epidermis occurred on 13th, 8th, 13th, 11th, 8th and 18th day in *Q. acutissima*, *Q. aliena*, *Q. dentata*, *Q. mongolica*, *Q. serrata* and *Q. variabilis*, respectively (Fig. 2).

Under withdrawal of water, LDR of leaf abaxial surface reached completely to stomatal closing point at 20, 12, 36, 20, 17 and 39% of WSD and at -1.3 , -1.2 , -2.2 , -1.7 , -1.3 and -1.3 MPa of ψ_{leaf} in *Q. acutissima*, *Q. aliena*, *Q. dentata*, *Q. mongolica*, *Q. serrata* and *Q. variabilis*, respectively (Figs. 3 and 4).

Stomatal density, size of guard cell and hair density

The stomatal density on leaf abaxial surface was 741, 681, 974, 930, 668 and 574 per mm^2

Stomatal density, size of guard cell and hair density

Density of stomata and hair (No./ mm^2) and length (μm) of guard cells were obtained from leaf-epidermis replica on the abaxial surface with manicure (Slavik 1974, Ha 1989). Three microscope fields ($\times 400$) from 3 leaves per 10 individuals in each species were used for counting of the density and size. The significance of difference among species were determined by Duncan's multiple range test (SAS, 1987).

Principal component analysis (PCA)

Principal component analysis (PCA) in the SAS package (1987) was carried out on the 15 variables; stomatal density, length of guard cell, hair density, initial

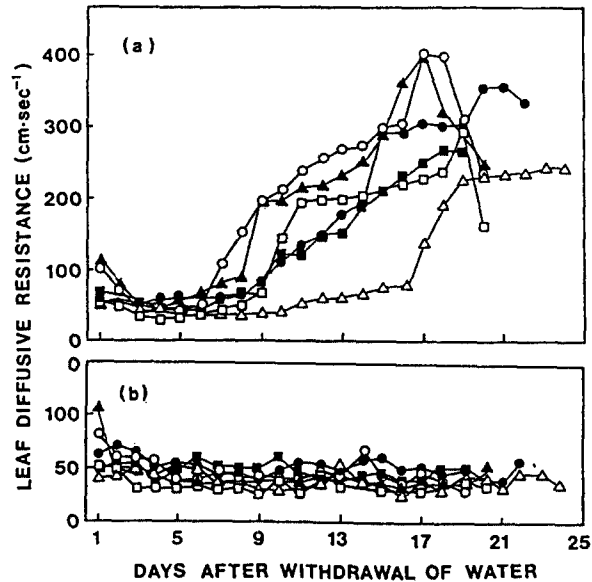


Fig. 2. Changes in diffusive resistance of abaxial surface of oak leaves under withdrawal of water (a) and under watering (b) in the growth chamber after withdrawal of water. *Q. acutissima* ●—●, *Q. aliena* ▲—▲, *Q. dentata* ■—■, *Q. mongolica* □—□, *Q. serrata* ○—○, *Q. variabilis* △—△.

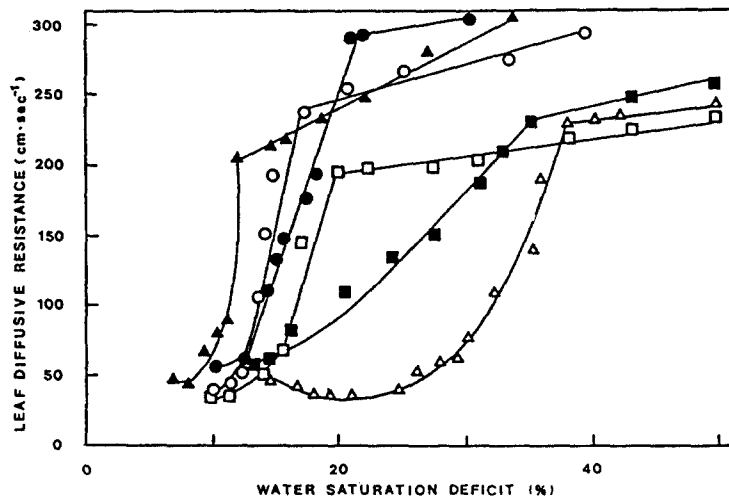


Fig. 3. Relationships between water saturation deficit and diffusive resistance of abaxial surface of oak leaves in the growth chamber after withdrawal of water. *Q. acutissima* ●—●, *Q. aliena* ▲—▲, *Q. dentata* ■—■, *Q. mongolica* □—□, *Q. serrata* ○—○, *Q. variabilis* △—△.

(76 : 70 : 100 : 95 : 69 : 59), the length of guard cell was 12.1, 15.7, 13.2, 14.1, 13.9 and 10.3 μm (77 : 100 : 84 : 90 : 89 : 66) and the hair density was 59, —, 4, 22, 44 and 151 per mm^2 (39 : — : 3 : 15 : 29 : 100) in *Q. acutissima*, *Q. aliena*, *Q. dentata*, *Q. mongolica*, *Q. serrata* and *Q.*

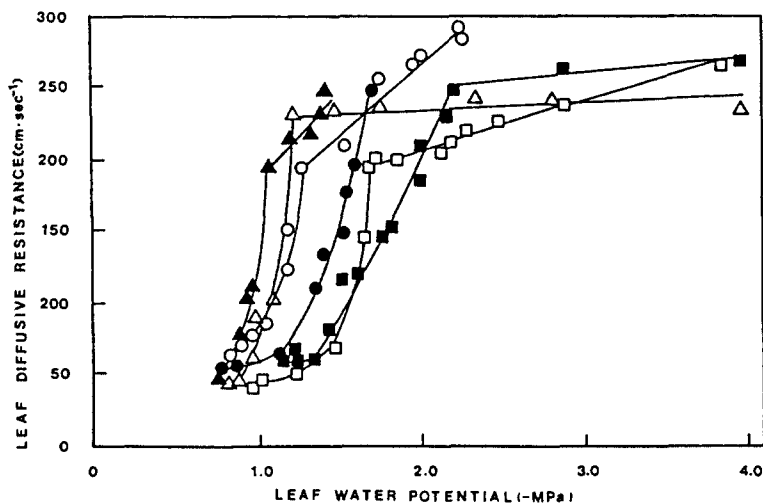


Fig. 4. Relationships between water potential and diffusive resistance of abaxial surface of oak leaves in the growth chamber after withdrawal of water. *Q. acutissima* ●-●, *Q. aliena* ▲-▲, *Q. dentata* ■-■, *Q. mongolica* □-□, *Q. serrata* ○-○, *Q. variabilis* △-△.

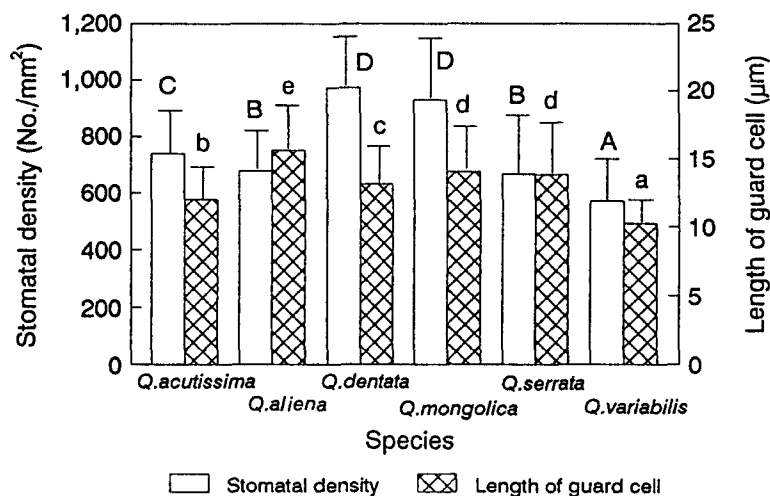


Fig. 5. Stomatal density (\pm SD) and length of guard cell (\pm SD) on the abaxial surfaces of the leaves of 6 oak species. The same scripts were not significantly different among species ($P < 0.05$).

variabilis, respectively (Figs. 5 and 6). Hair density of *Q. aliena* was not measured. Simple hairs were observed on leaf abaxial surfaces of *Q. acutissima*, *Q. mongolica* and *Q. serrata*, and stellate hairs on those of *Q. dentata* and *Q. variabilis*.

Principal component analysis

Principal component analysis (PCA) was carried out on 15 variables. The 6 oak species

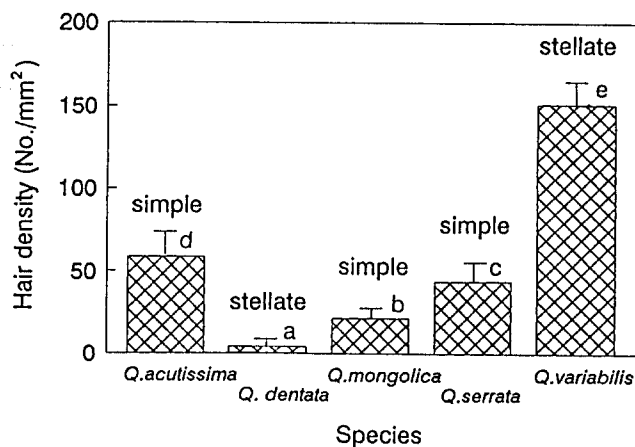


Fig. 6. Hair density (\pm SD) and hair type on the abaxial surfaces of the leaves of 5 oak species. The same scripts were not significantly different among species ($P < 0.05$). That of *Q. aliena* was not measured.

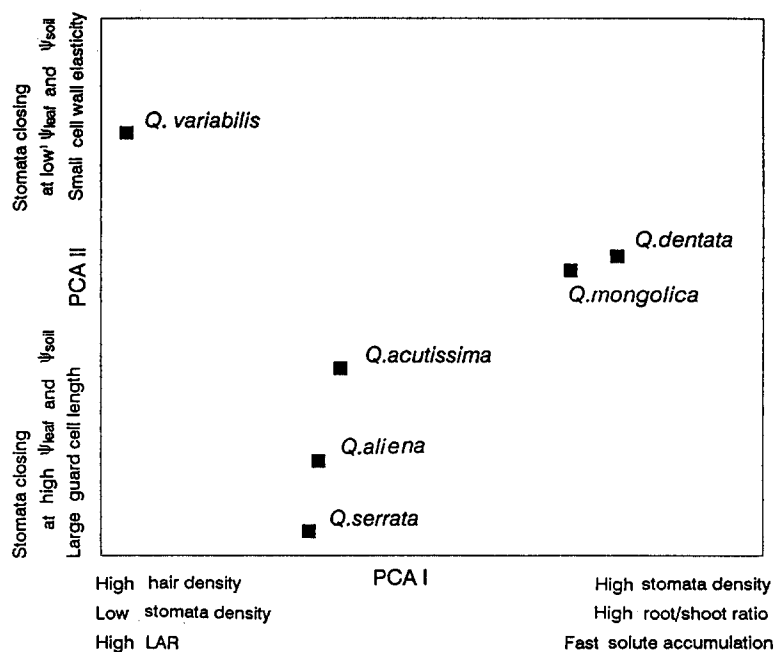


Fig. 7. Principal component analysis of 15 variables related with adjustment to drought stress of 6 oak species. Axis I (80% of the variance) is hair and stomata density-solute accumulation gradient. Axis II (19% of the variance) is stomatal control-elasticity gradient.

were plotted in the space defined by the first two PCA axes (Fig. 7). The correlation matrix between eigen values and 15 variables related with strategies of drought stress was shown in Table 1. Total variances accounted for by the Axes I and II were 80% and

Table 1. Principal component analysis of the correlation matrix of 15 variables related with adjustment to water stress of 6 oak species. Two factors had eigen values greater than one

Variables	Factor	
	I	II
Stomatal density	0.986	0.016
Length of guard cell	0.438	-0.697
Hair density	-0.831	0.504
Leaf area ratio	-0.668	0.487
Initial time at stomatal closing	-0.505	0.861
ψ_{leaf} at stomatal closing	0.028	0.731
WSD at stomatal closing	-0.341	0.753
ψ_{soil} at stomatal closing	0.135	0.909
SMC at stomatal closing	0.221	-0.871
Root /shoot ratio	0.469	-0.519
Length of main root	-0.301	-0.545
Changing rate of ψ_t with ψ_{leaf}	-0.344	0.483
Changing rate of ψ_o with WSD	0.590	-0.025
Changing rate of ψ_o with ψ_{leaf}	0.749	0.310
Elastic modulus	0.293	-0.774
Variance	80.4	18.6

19%, respectively.

DISCUSSION

Foregoing data first show adjustments to drought stress by minimizing water loss through the control of transpiration such as stomatal closings and through morphological adaptations in the leaves of 6 oak species. After withdrawal of water, LDR of *Q. acutissima*, *Q. aliena* and *Q. serrata* increased earlier than those of the other species at lower ψ_{leaf} or higher WSD, which suggests an avoidance mechanism reducing damage by water stress and preventing irreversible responses to the stress such as cell death (Tobiessen and Kana 1974).

The other adaptations to drought are the morphological characteristics such as low stomatal density and high leaf hair density decreasing transpiration. The stomatal density of *Q. dentata* and *Q. mongolica* were higher than those of the other species, while that of *Q. variabilis* was the lowest among the 6 oak species studied. Guard cells of *Q. variabilis* and *Q. acutissima* were smaller than those of the other species, especially those of *Q. aliena* were the largest. This indicates that the characteristics of leaves in relation to stomatal morphology are compensated for each other. The hair density of *Q. variabilis* was 3 to 50 times higher than those of the other species, which may effectively reduce its transpiration.

Principal component analysis (PCA) was carried out to investigate the strategies concerned with adjustment to drought stress. Axis I was designated as a gradient for hair

and stomatal density, LAR, R/S ratio and solute accumulation, and Axis II as a gradient for stomatal closing, guard cell length and cell elasticity. Fig. 7 showed that on Axis I the 6 oak species were divided into 3 groups; (1) *Q. variabilis* characterized by high hair density, high LAR and low stomatal density, (2) *Q. mongolica* and *Q. dentata* by high stomatal density, high R/S ratio and fast solute accumulation and (3) *Q. acutissima*, *Q. aliena* and *Q. serrata* by moderate characters; on Axis II the oak species were divided into 2 groups; (1) *Q. variabilis*, *Q. mongolica* and *Q. dentata*, which were distributed in xeric habitat of high altitude or steep slope, were characterized by late stomatal closing under heavy drought and small cell wall elasticity, and (2) *Q. acutissima*, *Q. aliena* and *Q. serrata*, which were generally distributed through mesic habitat of low altitude, were characterized by earlier stomatal closing under light drought and large guard cell. Many workers have described xeric and mesic habitat of oak species in Korea (Cheong and Lee 1965, Kim *et al.* 1981, Kim *et al.* 1982, Kim *et al.* 1988, Forest Research Institute 1988, Lee 1989). A striking contrast was focused in that *Q. variabilis* had high hair density, low stomatal density and showed earlier stomatal closing at high ψ_{leaf} while *Q. mongolica* and *Q. dentata* had high stomatal density and high R/S ratio, and showed fast solute accumulation. These 6 oak species may be segregated from each other by their drought strategies along the moisture gradient.

적 요

참나무속 식물 6종류의 잎의 확산저항, 기공밀도, 공변세포의 길이 및 털의 밀도를 측정하여 건조스트레스에 대한 이 식물들의 전략을 주성분분석법으로 분석하였다. 상수리나무, 갈참나무 및 졸참나무의 잎의 확산저항은 다른 3종보다 높은 ψ_{leaf} 또는 낮은 WSD에서 빠르게 상승함으로써 수분스트레스를 회피하였다. 굴참나무는 높은 ψ_{leaf} , 낮은 기공밀도, 작은 기공 크기 및 높은 털밀도로 수분스트레스를 회피하였다. 그러나, 신갈나무와 떡갈나무는 낮은 ψ_{leaf} 에서 기공 확산저항의 상승을 보였다. 건조스트레스에 대한 조정능과 관련된 15변수의 주성분분석에서 참나무속 식물은 2그룹, 즉 건성생육지종인 굴참나무, 신갈나무 및 떡갈나무와 중성생육지종인 상수리나무, 갈참나무 및 졸참나무로 구별되었고, 건성생육지종인 굴참나무는 높은 털밀도, 낮은 기공밀도 및 높은 LAR에서 신갈나무 및 떡갈나무와 다시 구별되었다. 이 결과는 자연생육지에서 참나무속 식물의 건조에 대한 전략을 잘 설명하고 있다.

LITERATURE CITED

- Cheong, T.H. and W.C. Lee. 1965. A study of the Korean woody plant zone favorable region for the growth and proper species. J. Fac. Sungkumwan Univ. 10:329-434.
- Davies, W.J. and T.T. Kozlowski. 1977. Variation among woody plants in stomata conductance and photosynthesis during and after drought. Plant and Soil 46:435-444.
- Forest Research Institute. 1988. Studies on the development and utilization of Korean oak resources. Forest Research Institute, Seoul. 226p.

- Ha, S.H. 1989. Performance and photosynthesis of seedlings of several *Quercus* plants grown under the different light intensities. Seoul National Univ. M.S. Thesis, Seoul, 67p.
- Heichel, G.H. 1971. Stomatal movements, frequencies, and resistances in two maize varieties differing in photosynthetic capacity. *J. Exp. Bot.* 22:644-649.
- Jayasuriya, A.H.M. and M.A. Pemadasa. 1983. Factors affecting the distribution of tree species in a dry zone montane forest in Sri Lanka. *J. Ecol.* 71:571-583.
- Jones, H.G. 1983. *Plants and microclimate*. Cambridge Univ. Press, Cambridge. 323p.
- Kanemasu, E.T., G.W. Thurtell and C.B. Tanner. 1969. Design, calibration and field use of stomatal diffusion porometer. *Plant Physiol.* 44:881-885.
- Kim, Y.S., S.C. Kim and B.U. Oh. 1981. Distribution atlas of plants of Korea (V): atlas of Fagaceae in Korea. *J. Fac. Sci. Eng. College. Korea Univ.* pp. 93-133.
- Kim, J.H., Y.D. Rim, D.S. Cho, S.D. Koh and B.M. Min. 1982. Studies on the community structure, phytomass and primary productivity of the climax forest of Piagol Valley in Mt. Chiri. The report of the KACN, No. 21:53-73.
- Kim, J.W. 1990. Comparisons of adjustment to water stress of several oak seedlings in Korea. Seoul National Univ. M.S. Thesis, Seoul. 62p.
- Kim, J.W. and J.H. Kim. 1994. Comparison of adjustment to drought stress among seedlings of several oak species. *J. Plant Biol.* 37 : 343-347.
- Kim, J.U., Y.J. Yim and B.S. Kil. 1988. Classification and pattern analysis of the forest vegetation in Daedunsan Provincial Park, Korea. *Korean J. Ecol.* 11:109-122.
- Lee, C.S. 1989. A study on the succession of pine forests damaged by pine gall midge. Seoul National Univ. Ph. D. Thesis, Seoul. 105p.
- Levitt, T. 1972. Responses of plants to environmental stresses. Vol. II. Academic Press, New York, 657p.
- McCarthy, B.C., C.A. Hammer, G.L. Kauffman and P.D. Cantino. 1987. Vegetation patterns and structure of an old-growth forest in southeastern Ohio. *Bull. Torrey Bot. Club* 114:33-45.
- Meiners, T.M., D.W. Smith, T.L. Sharik and D.E. Beck. 1984. Soil and plant water stress in an Appalachian oak forest in relation to topography and stand age. *Plant and Soil* 80:171-179.
- Miskin, K.E., D.C. Rasmusson and D.N. Moss. 1972. Inheritance and physiological effects of stomatal frequency in barley. *Crop Sci.* 12:780-783.
- Sanchez-Diaz, M.F. and P.J. Kramer. 1971. Behavior of corn and sorghum under water stress and during recovery. *Plant Physiol.* 48:613-616.
- SAS. 1987. *SAS /STAT guide for personal computers*. SAS Institute Inc., Cary. 378p.
- Slavik, B. 1974. *Methods of studying plant water relations*. Springer-Verlag, New York. 818p.
- Tobiessen, P. and T.M. Kana. 1974. Drought-stress avoidance in three pioneer tree species. *Ecology* 55:667-670.