STOMATAL CONDUCTANCE OF SEEDLINGS OF THREE OAK SPECIES SUBJECTED TO NITROGEN FERTILIZATION AND DROUGHT TREATMENTS

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Abstract: Both nitrogen-fertilized and unfertilized white oak, bur oak, and red oak seedlings were subjected to progressive drought in a greenhouse study. Stomatal conductance was measured before and during drought treatment. When water was not limiting to seedling growth and function, N-fertilized white oak showed greater maximum stomatal conductance (200 mmol m^{-2} s^{-1}) compared to N-deficient white oak (74 mmol m^{-2} s^{-1}). Neither bur oak nor red oak showed any discernible differences in stomatal conductance between fertilization treatments before imposition of drought. During drought, N-limited red oak maintained greater stomatal conductance at a lower soil relative water content compared to N-fertilized red oak. N-fertilized bur oak decreased stomatal conductance partially during moderate drought and ceased conductance completely during extreme drought, whereas N-deficient bur oak maintained high levels of conductance during moderate drought and halted conductance precipitously during severe drought. No discernible difference between N-fertilization treatments was found for white oak stomatal conductance during drought. Red oak and white oak seedlings exhibited lower stomatal conductance values less readily and under drier soil conditions than did bur oak, suggesting superior drought adaptability of bur oak.

INTRODUCTION

Stomatal conductance represents a compromise between carbon assimilation and excessive water loss by transpiration (Ludlow 1980). Mineral nutrient status may directly affect rates of photosynthesis by altering the content and function of key metabolites and enzymes and may also have indirect effects by altering stomatal respones. Nutrient deficiency may increase or decrease stomatal sensitivity to soil moisture availability (Radin *et al.* 1982; Lahiri 1980; Wang *et al.* 1988). Thus, the stomatal and photosynthetic response to drought for a given species may be altered by nutrient status.

White oak (*Quercus alba* L.), red oak (*Q. rubra* L.), and bur oak (*Q. macrocarpa* Michx.) are oaks of the central hardwood region. Bur oak traditionally has been characterized as drought-tolerant and the most xeric of the three species, though it is bimodal in distribution

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occuring on both mesic and xeric sites (Abrams 1986), while white and especially red oak are regarded as more exclusively mesic (Fowells 1965).

We examined the effects of two nitrogen regimes on stomatal conductance of bur, red, and white oak seedlings during the progressive soil drying of an artificially imposed drought.

METHODS

Fifty 2-0 bare-root dormant seedlings of each of red oak, white oak, and bur oak were planted in a steam-sterilized 1:1:1 loamy soil:vermiculite:peat moss mix in 60 cm tall by 10 cm wide cylindrical pots. Half of the plants of each species were given 200 ml of N-free 1/4 strength modified Hoagland's solution weekly and the other half were given the same plus 5 ppm N as NH_4NO_3. Plants were watered daily. After sixteen weeks in the greenhouse (26° day, 18° night, photoperiod extended to 16 h by sodium vapor lamps) drought was imposed by withholding water.

The results of a preliminary study indicated that the plants reached their daily maximum level of stomatal conductance between 1000 and 1100 local standard time; therefore all stomatal conductance measurements were made between those hours. Plants were sampled randomly. Stomatal conductance was measured on the abaxial leaf surface with a steady state diffusion porometer (LI-1600 Li-Cor, Lincoln, NE); relative humidity varied between 15 and 30% on the days when measurements were taken. Predawn leaf water potential was measured on a subsample of fully-expanded leaves with a pressure chamber (# 3000 Soil Moisture Corp., Santa Barbara, CA) at 0300-0400 the morning following stomatal conductance measurements. This allowed us to determine the relationship between soil relative water content and soil water potential estimated as predawn leaf water potential (Nobel 1983). Soil relative water content was determined by weighing the pots during the afternoon of each measurement day and comparing the soil mass of each pot with the saturated (12 h after final watering) soil mass and the dry (constant weight at 70°) soil mass. The formula used to calculate relative water content (RWC) was:

$$RWC = (\text{fresh mass} - \text{dry mass}) / (\text{saturated mass} - \text{dry mass}).$$

Leaf relative water content was determined but it was not found to differ by species or treatment.

RESULTS AND DISCUSSION

Stomatal response was interpreted by boundary line analysis (Webb 1972) where a line is drawn at the boundary of the maximum stomatal conductance values and all points below are assumed to be limited by some factor other than that of the independent variable (Hinckley et al. 1978). This technique is useful owing to the fact that stomata respond to the complex interaction of a number of environmental and endogenous factors that could not be controlled during this experiment (e.g. daily variation in solar radiation). Conductance measurements >10 mmol $m^{-2}s^{-1}$ were considered to signify at least partially opened stomates based on our measurements of leaves with completely closed stomates indicating that cuticular conductance for all species was about 3-8 mmol $m^{-2}s^{-1}$.

Stomatal Response with High Soil Moisture

White oak increased its maximum rate of stomatal conductance from 74 to 200 mmol $m^{-2}s^{-1}$ when supplied with N fertilizer and water was not limiting (Figures 1*a,b*). This is consistent with the results of Minshall (1975) who found that urea or nitrate stimulated transpiration of tomato, Mingeau and Robelin (1972) who found that N-deficiency decreased transpiration of sunflower, and Nagarajah (1981) who found that N-deficiency of tea caused a decrease in stomatal conductance and transpiration. A general correlation between foliar N and net photosynthesis and stomatal conductance has been reported in an extensive survey of native C_3 plants (Field and Mooney 1986). Neither red oak (Figures 1*c,d*) nor bur oak (Figures 1*e,f*) showed any response to N fertilization treatment when soil moisture levels were high.

Stomatal Response during Drought

White oak +N and -N showed similar responses during drought (Figures 1*a,b*): both N-fertilized and N-deficient plants decreased stomatal conductance suddenly at 22% RWC (-1.8 MPa soil water potential). Red oak stomatal conductance ceased at about 22% RWC (-1.8 MPa) when supplied with N (Figure 1*c*), but continued until 19% RWC (-2.5 MPa) during N-deficiency (Figure 1*d*). This resembles the response of N-deficient beans as described by Shimshi (1970). The response of bur oak is the most distinctive. N-fertilized bur oak accomplished a partial decrease of stomatal conductance at about 33% RWC (-0.5 MPa) and maintained moderately low stomatal conductance to below 20% RWC (-2.1 MPa) (Figure 1*e*). The response of N-deficient bur oak differs; its stomates halted conductance suddenly at about 23% RWC (-1.5 MPa) (Figure 1*f*).

These data suggest a drought adaptation of bur oak seedlings. Under conditions of soil nitrogen availability, bur oak seems to employ a drought avoidance tactic (Jones 1980); the seedlings avoid excessive plant water loss and rapid depletion of limited soil water reserves by closing stomates partially as soil water potential decreases below -0.5 MPa, allowing only a limited level of gas exchange and water loss. These results are similar to those obtained with bur oak under drought conditions in Kansas forests (Abrams and Knapp 1986). This apparent anticipation of extreme drought reflects the ecological performance of bur oak which occurs on droughty sites and soils as well as on more mesic sites which support red and white oak (Fowells 1965).

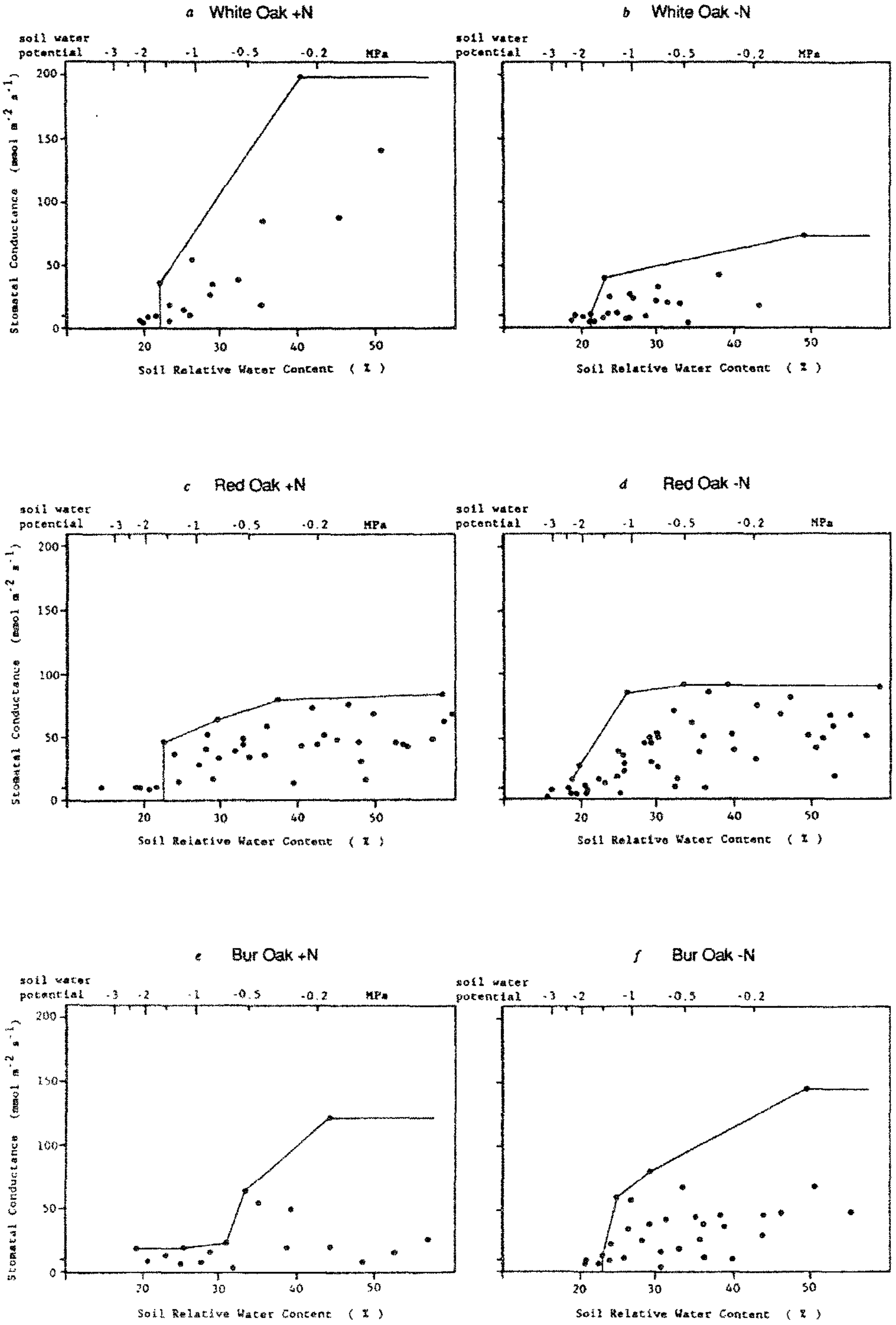

Figure 1. Stomatal conductance of N-fertilized and unfertilized white oak (*a*,*b*), red oak (*c*,*d*), and bur oak (*e*,*f*) seedlings during a progressive drought.

The stomatal conductance data may reflect the fact that white and red oak thrive naturally on more mesic sites than bur oak; on mesic sites stomatal sensitivity to increasing drought is less critical for survival. Bur oak on a mesic site would incur all the disadvantages of an anticipatory response to moderate drought (less capability for photosynthetic gas exchange, slower growth) in exchange for only marginal benefits (water conservation during relatively rare extreme droughts). The tendency of N-deficient red oak to maintain stomatal conductance during extreme drought conditions may indicate that red oak requires N to conserve water. The absence of the drought-adaptive stomatal response in N-deficient bur oak may reflect a nitrogen requirement for the expression of the drought-adaptive response. This suggests a mechanism to explain the seemingly anomolous findings of Abrams (1985) that the growth rate of bur oak trees in Kansas stands was greatest when available soil NH_4 and NO_3 were lowest. Perhaps anticipatory stomatal closing of bur oak with the onset of drought was sufficiently enhanced on soils of greater N fertility in Kansas' dry climate to reduce net photosynthesis and growth of the trees.

LITERATURE CITED

Abrams, M.D. 1985. Age-diameter relationships of *Quercus* species in relation to edaphic factors in gallery forests in northeast Kansas. For. Ecol. Manage. 13:181-193.

Abrams, M.D. 1986. Historical development of gallery forests in northeast Kansas. Vegetatio 65: 29-37.

Abrams, M. D. and A. K. Knapp 1986. Seasonal water relations of three gallery forest hardwood species in northeast Kansas. Forest Sci. 32:687-696.

Bahari, Z.A., Pallardy, S.G. and W.C. Parker. 1985. Photosynthesis, water relations, and drought adaptation in six woody species of oak-hickory forests in central Missouri. Forest Sci. 31:557-569.

Barrs, H.D. 1971. Cyclic variations in stomatal aperture, transpiration, and leaf water potential under constant environmental conditions. Ann. Rev. Plant Physiol. 22: 223-236.

Field, C. and H. A. Mooney. 1986. The photosynthesis-nitrogen relationship in wild plants. In On the Economy of Plant Form and Function (T. J. Givnish, ed.). Cambridge University Press, London. 717 pp.

Fowells, H.A. 1965. Silvics of Forest Trees of the United States. U.S.D.A. Agric. Handbook no. 271. 762 pp.

Hinckley, T.M., Aslin, R.G., Aubuchon, R.R., Metcalf, C.L. and J.E. Roberts. 1978. Leaf conductance and photosynthesis in four species of the oak-hickory forest type. For. Sci. 24:73-84.

Jones, H.G. 1980. Interaction and integration of adaptive responses to water stress: the implications of an unpredictable environment. In Adaptation of Plants to Water and High Temperature Stress (Turner, N.C. and P.J. Kramer, eds.) Wiley & Sons., New York. 482 pp.

Lahiri, A.N. 1980. Interaction of water stress and mineral nutrition on growth and yield. In Adaptation of Plants to Water and High Temperature Stress (Turner, N.C. and P.J. Kramer, eds.) Wiley & Sons, New York. 482 pp.

Ludlow, M.M. 1980. Adaptive significance of stomatal responses to water stress. In Adaptations of Plants to Water and High Temperature Stress (Turner, N.C. and P.J. Kramer, eds.) Wiley & Sons, New York. 482 pp.

Mingeau, M. and M. Robelin. 1972. Le transfert de l'eau dans la plante: action particulière de la nutrition azotée. Ann. Agron. 23:419-427.

Minshall, W.H. 1975. Stimulation of transpiration by nitrogenous materials. Can. J. Bot. 53:1259-1265.

Nagarajah, S. 1981. The effect of nitrogen on plant water relations in tea (Camellia sinensis). Physiol. Plant. 51:304-308.

Nobel, P.S. 1983. Biophysical Plant Physiology and Ecology. W.H. Freeman, San Francisco. 608 pp.

Radin, J.W., Parker, L.L. and G. Guinn. 1982. Water relations of cotton plants under nitrogen deficiency. V. Environmental control of abscisic acid and stomatal sensitivity to abscisic acid. Plant Physiol. 70:1066-1070.

Shimshi, D. 1970. The effect of nitrogen supply on some indices of plant-water relationships of beans (*Phaseolus vulgaris* L.). New Phytol. 69:413-424.

Wang, D., Bachelard, E.P. and J.C.G. Banks. 1988. Growth and water relations of seedlings of two subspecies of *Eucalyptus globulus*. Tree Physiol. 4:129-138.

Webb, R.A. 1972. Use of the boundary line in the analysis of biological data. J. Hort. Sci. 47:309-319.