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Genotypes from Contrasting Sites in Central Pennsylvania**



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Functional Ecology, Vol. 4, No. 6 (1990), 727-733.

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Photosynthesis and water relations during drought in *Acer rubrum* L. genotypes from contrasting sites in central Pennsylvania

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Abstract. Variation in gas exchange and water relations during drought, and in leaf morphology were studied in 1-year-old greenhouse-grown *Acer rubrum* L. seedlings originating from four contrasting sites in central Pennsylvania: bog (hydric), valley (mesic), ridge and barrens (xeric). During the middle and later stages of drought, bog plants had lower net photosynthesis and leaf conductance than did the three upland sources. Bog plants also had higher (less negative) shoot water potential at the incipient wilting point. Day-to-day instantaneous measurements of leaf water potential were unobtainable due to foam from the phloem which obscured initial xylem sap exudation. Bog plants had higher pre-drought osmotic potentials than the barrens plants and were the only source to osmotically adjust between pre- and peak drought. During peak drought there were no differences in osmotic potentials, relative water content at zero turgor or tissue elasticity among any of the sources. Barrens plants had leaves with relatively high stomatal density and small guard cells, whereas leaves of bog plants had high specific mass and stomatal density and intermediate guard cell length. Most differences observed in this study were between the bog vs upland sources, and not among the latter. The lack of differences among the upland sources may be due to gene flow between sites or the relatively recent invasion of *A. rubrum* to the sites.

Key-words: Bog, gas exchange, osmotic adjustment, tissue elasticity, uplands

Introduction

Many species with large geographic ranges exhibit an impressive array of genetic adaptation for local conditions, including variation in gas exchange, plant–water relations and gross morphology (Mooney & Billings, 1961; Donselman & Flint,

1982; Parker & Pallardy, 1985; Bongarten & Teskey, 1986; Abrams, 1988a; Abrams, Kubiske & Steiner, 1990a). However, ecophysiological studies of genotypes within a restricted geographic area are much less common (Shavers, Chapin & Billings, 1979) and have generally focused on altitudinal variation to changes in temperature and light (Fryer & Ledig, 1972; Anderson & McNaughton, 1973; Slatyer & Ferrar, 1977). Thus, there is a very limited pool of data concerning drought responses and adaptations in genotypes from nearby sites of differing moisture relations (Gurevitch *et al.*, 1986; Farris, 1987), particularly with woody plants (Abrams, 1988a). It is poorly understood whether genotypic variation in drought resistance routinely contributes to the success of species on diverse neighbouring sites, or whether this success is due to physiological and morphological plasticity (Abrams, 1986; Schlichting, 1986).

Acer rubrum L. occurs on sites of widely contrasting soil moisture conditions in eastern North America, ranging from very wet to very dry (Fowells, 1965). *A. rubrum* also exists on virtually all topographic positions within the ridge and valley province of central Pennsylvania (G.J. Nowacki & M.D. Abrams, unpublished observations). Thus, this species is ideally suited for the study of localized genotypic variation from contrasting sites. Moreover, physiological mechanisms that may explain the success of *A. rubrum* on diverse sites are lacking (Townsend & Roberts, 1973). The purpose of this study was to investigate genotypic variation in ecophysiological responses during drought, and in leaf morphology in four sources of *A. rubrum* to test the hypothesis that plant drought resistance increases with the dryness of the site.

Materials and methods

Study site description

A. rubrum seeds were collected on 2 June 1989 from natural populations on four sites near State College, Pennsylvania, USA (40° 47' 36" N, 77° 51' 37" W), representing a moisture gradient from

hydric (bog) to mesic (valley) to xeric (ridge top and barrens). The valley, ridge and barrens are collectively referred to as upland sources. *A. rubrum* is a cross-pollinated, dioecious species, in which seeds on one tree represent one female parent and one or more male parents. The bog population was located 9 km south-east of State College at the Bear Meadows National Landmark and situated on a saturated or submerged organic soil with underlying sandstone interbedded with shale (Braker, 1981). The valley population was located 2 km north-west of State College on a nearly level, deep, well-drained cherty limestone soil, with moderate permeability and high available water capacity. The ridge population was found 10 km north-west of State College on a steep, moderately deep, well-drained sandstone soil, with moderately rapid permeability and low available water capacity. The barrens population was located 3 km west of State College on a deep, well-drained sandstone soil, with rapid permeability and very low available water capacity (Braker, 1981). Average monthly precipitation in the study area varies from 6.5 to 9.7 cm and total annual precipitation averages 93.4 cm. Average monthly minimum winter temperatures (December–March) range from -5 to -7°C and average maximum summer temperatures (June–August) range from 26 to 28°C .

Seedling establishment

Seeds of all sources were planted immediately after collection in seed trays. Seedlings were transplanted to individual pots (8363 cm^3) 18 days later (20 June 1989). The potting mix used in this study was peat, loam, vermiculite and perlite (3:1:1:1). Seedlings were grown in a naturally lighted greenhouse, supplemented with sodium vapour lamps with a daily photoperiod of 16 h. Seedlings were randomly arranged on a greenhouse bench, kept well watered and periodically rotated to minimize possible positional effects associated with environmental gradients in the greenhouse.

Photosynthesis and plant–water relations

Six to eight seedlings of similar size and vigour from each source were selected for study and arranged in a completely randomized design. On 29 January 1990, the seedlings were watered to soil capacity, after which time water was withheld for the duration of the 31-day study. Thereafter, at 1–4-day intervals at midday (11.00–13.00h),

measurements of net photosynthesis (A) and leaf conductance to water vapour diffusion (g_{wv}) were made on a fully expanded leaf at the mid- to upper-canopy of the six to eight seedlings from each source in a random order. Gas exchange measurements were made during relatively cloud-free conditions with a portable photosynthesis unit (LCA-2, ADC Ltd, Herts, UK) that uses the mass balance technique for estimating leaf CO_2 exchange. The ADC system was also used to estimate leaf temperature (T_{leaf}) and measure photosynthetic photon flux density (PPFD) for each leaf used in gas exchange measurements. When midday A for an individual plant fell below $0.4\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ (hereafter called incipient wilting) the terminal 5 cm of the shoot was cut, stripped of bark and measured for water potential (final shoot ψ) with a pressure chamber (Model 600, PMS Instruments Co., Corvallis, Oregon). Day-to-day instantaneous measurements of leaf–water potentials were unobtainable in this study due to foaming phloem exudate obscuring the initial xylem sap exudation at the cut petiole (cf. Bahari Pallardy & Parker, 1985). At midday in the greenhouse during the study period, mean (\pm SE) PPFD was $491 \pm 33\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ and relative humidity was $39 \pm 4\%$; T_{leaf} averaged $26.8 \pm 1.8^{\circ}\text{C}$ and did not differ significantly among the populations or sample dates.

Tissue–water relations

During pre-drought conditions, phloem foam obscuring xylem sap was not a significant problem in most pressure–volume (P–V) samples because both were exuded at a similarly high water potential (e.g. -0.05 to -0.20 MPa). During the period of maximum drought, leaf samples were also suitable for P–V analysis because phloem foam was only apparent during the initial stages of sampling, after which P–V relationships of xylem sap exhibited typical form (see Results section). On the first day after cessation of watering (pre-drought), four leaves from each population were collected before dawn from the greenhouse and subjected to P–V analysis, without further artificial rehydration. Otherwise, methods employed for constructing the P–V curves ($1/\psi$ vs relative water content, RWC) were similar to those of Robichaux (1984), in which the weight and ψ of leaves were periodically measured as they dried by free transpiration under ambient conditions on the laboratory bench. Samples were not rehydrated to avoid potential shifts in P–V relationships (Parker & Pallardy, 1987; Kubiske & Abrams, 1990). At the

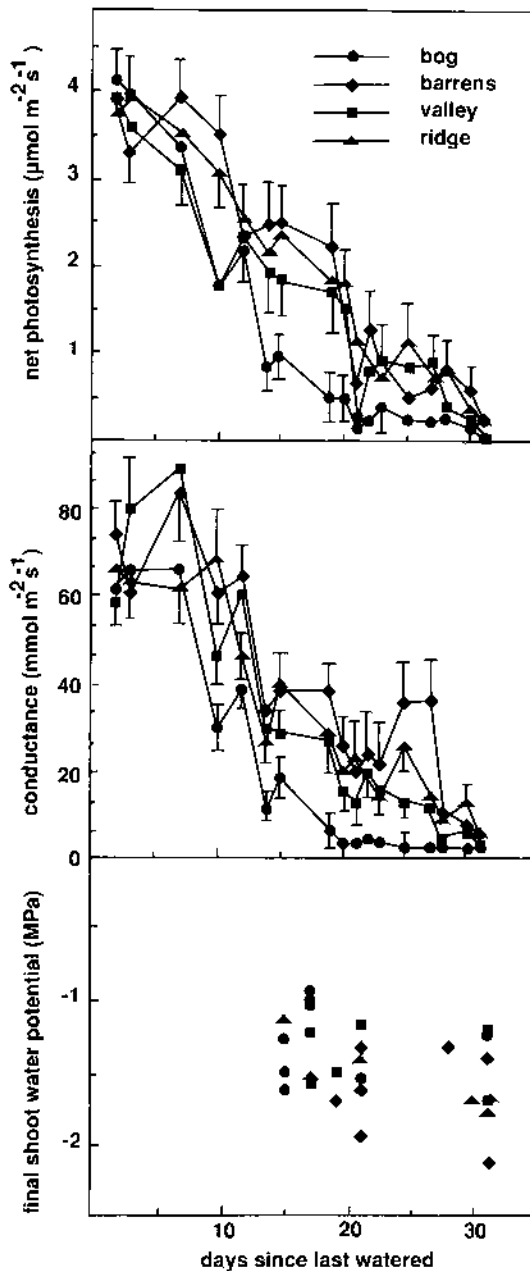


Fig. 1. Changes in net photosynthesis, leaf conductance to water vapour diffusion and final shoot water potential during a 31-day drought in four genotypes of *Acer rubrum*. Vertical bars represent the standard error of the mean.

later stages of drought (after day 15) when a plant reached incipient wilting (peak drought), it was watered to soil capacity and allowed to naturally rehydrate for 3 h. Immediately afterwards a leaf was harvested and used in P–V analysis. Thus, timing of P–V analysis at the later stages of drought varied (days 15–31) until five plants from each source were evaluated. A short period of natural rehydration during the peak drought period was

necessary to obtain sufficient P–V data iterations before the turgor loss point (cf. Kubiske & Abrams, 1990). In addition, parallel leaf samples were collected on the respective dates for all pre- and peak drought specimens and rehydrated for 12 h in darkness in sealed beakers solely to determine the level of ψ for fully hydrated tissue.

Tissue weights were estimated at saturated ψ via regression of P–V data above and including the turgor loss point for each sample (cf. Ladiges, 1975; Kubiske & Abrams, 1990). The initial region of phloem foam exudate in a few of the pre-drought samples and nearly all peak drought samples were excluded from the regression analysis. Estimated saturated sample weights were then used to calculate RWC and standard P–V parameters: the osmotic potential at full turgor (ψ_{π}^{100}) and zero turgor (ψ_{π}^0), relative water content at zero turgor (RWC_0) and the bulk modulus of elasticity (ϵ , calculated according to Robichaux & Canfield, 1985).

Leaf morphology

Prior to the drought study, specific leaf mass, leaf thickness, and stomatal density and guard cell length were measured at the mid-canopy on 10 seedlings from each population. Three measurements of stomatal density and guard cell length were made on each leaf with cellulose acetate impressions of the lower leaf surface (Payne, 1970). Free-hand transverse sections of leaves taken at an approximate mid-point between major veins were measured under a light microscope for leaf thickness. Specific leaf mass was determined by weighing oven-dried (80°C, 48 h) sections of fresh material of known area.

Plant- and tissue-water relations, photosynthesis and leaf morphology data were analysed using one-way analysis of variance for a completely randomized design, Pearson product-moment correlation and Tukey's multiple-range test at $P < 0.05$.

Results

Photosynthesis and plant–water relations

All four *A. rubrum* sources exhibited a significant decrease in A and g_{wv} during the 31-day drought (Fig. 1). During the early stages of drought there were no significant differences among the sources in A or g_{wv} . However, between days 14 and 31, A was significantly lower in the bog vs the three upland sources. Similarly, g_{wv} was significantly lower in the bog than upland sources between days

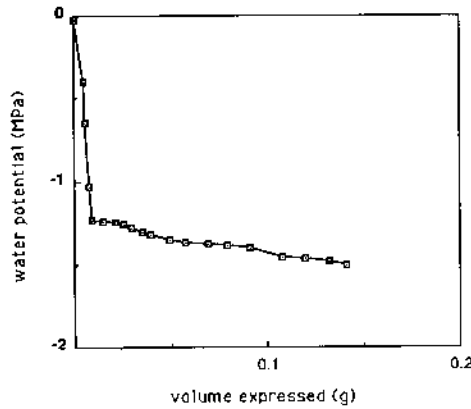


Fig. 2. Moisture release curve of a ridge plant of *Acer rubrum* during the peak drought period.

10 and 31 of drought. In general, there was no significant difference in A or g_{wv} between the upland sources. Mean final shoot ψ (\pm SE) at incipient wilting was -1.28 ± 0.08 , -1.40 ± 0.08 , -1.53 ± 0.08 and -1.65 ± 0.11 MPa for the bog, valley, ridge and barrens sources, respectively. These values were significantly ($P < 0.05$) higher in the bog source than the ridge and barrens sources. The bog source also exhibited the three highest final shoot ψ (-0.98 to -1.07 MPa) among all study plants, whereas the barrens source exhibited the two lowest values (-1.95 and -2.15 MPa) (Fig. 1). Final shoot ψ was not significantly different among the three upland sources, but was correlated ($P < 0.05$) with days since last watered ($r = -0.41$) for all sources combined.

Tissue-water relations

The unsuitability of *A. rubrum* leaves for instantaneous day-to-day measurement of plant ψ in this study is illustrated in a moisture release curve of a

leaf from a non-rehydrated ridge plant during peak drought (Fig. 2). The shoot ψ for this plant on that day was -1.15 MPa, yet leaf phloem exudate was first observed at -0.05 MPa. The phloem foam obscured the point at which xylem sap first appeared at the cut petiole. However, this point was clearly revealed in moisture release and P-V curves, which exhibited an initial rapid drop in ψ with extremely little volume loss, which was interpreted as foaming phloem exudate, followed by a relatively slow decrease in ψ with much greater volume loss. The break in the curve closely matched the final shoot ψ in the study plant and was considered the start of xylem exudation. Because the leaf illustrated in Fig. 2 was very near the wilting point, a short period of natural rehydration was needed to obtain several iterations of P-V data (excluding the initial region of phloem exudation) above the turgor loss point to derive tissue weight at full turgor. Otherwise, P-V analysis of leaves of the study plants provided interpretable results.

At the pre-drought sample date, ψ_{π}^{100} and ψ_{π}^0 were significantly higher (less negative) in the bog plants than in the barrens plants (Table 1). At that time, bog plants had higher RWC_0 ($P < 0.05$) than did valley plants. A limited amount of adjustment in P-V parameters in response to drought occurred in the study plants. Only the bog source exhibited significant osmotic adjustment between the pre- and peak drought periods. This resulted in no significant difference among the sources in ψ_{π}^{100} or ψ_{π}^0 during peak drought. The standard error of the mean for ψ_{π}^{100} and ψ_{π}^0 were three to eight times higher in upland vs bog plants during both pre- and peak drought. Valley plants had higher RWC_0 at peak vs pre-drought. No significant difference in ϵ was detected among the sources at any time

Table 1. Summary of tissue-water relation variables ($\bar{x} \pm$ SE) derived from pressure-volume analysis of the four *Acer rubrum* sources.

Drought status and seed source	ψ_{π}^{100} (MPa)	ψ_{π}^0 (MPa)	RWC_0 (%)	ϵ (MPa)
<i>Pre-drought</i>				
Bog	-0.93 ± 0.02^a	-1.19 ± 0.02^a	91.2 ± 1.0^a	3.25 ± 0.31^a
Valley	-1.21 ± 0.13^{ab}	-1.46 ± 0.08^{ab}	83.9 ± 2.4^b	5.18 ± 1.67^a
Ridge	-1.28 ± 0.11^{ab}	-1.52 ± 0.08^{ab}	88.1 ± 1.2^{ab}	6.05 ± 1.62^a
Barrens	-1.43 ± 0.16^b	-1.61 ± 0.12^b	86.0 ± 1.6^{ab}	5.09 ± 1.82^a
<i>Peak drought</i>				
Bog	-1.08 ± 0.03^b	-1.41 ± 0.03^b	88.9 ± 1.3^a	3.87 ± 0.18^{ab}
Valley	-1.14 ± 0.12^{ab}	-1.54 ± 0.11^{ab}	90.2 ± 1.2^a	3.82 ± 0.78^{ab}
Ridge	-1.13 ± 0.14^{ab}	-1.61 ± 0.10^{ab}	89.1 ± 0.9^a	2.17 ± 0.18^b
Barrens	-1.13 ± 0.09^{ab}	-1.46 ± 0.13^{ab}	90.5 ± 1.4^a	4.29 ± 0.56^{ab}

Means in a column followed by the same letter are not significantly different. ψ_{π}^{100} = osmotic potential at full turgor; ψ_{π}^0 = osmotic potential at zero turgor; RWC_0 = relative water content at zero turgor; ϵ = bulk modulus of elasticity.

Table 2. Leaf structural characteristics of the four *Acer rubrum* sources.

Source	Leaf thickness (μm)	Specific leaf mass (mg cm^{-2})	Stomatal density (mm^{-2})	Guard cell length (μm)
Bog	134.5 \pm 5.1 ^a	4.12 \pm 0.12 ^b	460.4 \pm 18.9 ^a	28.3 \pm 0.5 ^b
Valley	120.1 \pm 4.6 ^a	3.19 \pm 0.18 ^a	350.2 \pm 14.3 ^b	30.6 \pm 0.5 ^c
Ridge	124.2 \pm 5.2 ^a	3.34 \pm 0.16 ^a	349.8 \pm 5.5 ^b	27.5 \pm 0.5 ^{ab}
Barrens	131.6 \pm 7.6 ^a	3.38 \pm 0.23 ^a	471.2 \pm 5.5 ^a	26.3 \pm 0.6 ^a

Means (\pm SE) in a column followed by the same letter are not significantly different.

during the study, although ridge plants exhibited significantly lower ϵ (more elastic tissue) at peak drought.

Leaf morphology

No differences in leaf thickness were found among the four sources, although specific leaf mass was highest ($P < 0.05$) in the bog plants (Table 2). Bog and barrens plants had greater stomatal density than did ridge and valley plants. Guard cell length was low in ridge and barrens, intermediate in bog and high in valley plants.

Discussion

Based on topographic position and soil features it seems reasonable to rank the *A. rubrum* sources used in this study as hydric, mesic and xeric for the bog, valley, and ridge and barrens populations, respectively. The results of this study suggest considerable genotypic variation in physiological responses to drought between the bog and three upland sources, but very little difference among the upland sources. Most importantly, bog plants had lower gas exchange with increasing drought and higher shoot water potential at incipient wilting than the upland plants. Previous studies of tree genotypes also reported higher A or g_{wv} in xeric vs mesic populations during drought (McGee, Schmierbach & Bazzaz, 1981; Abrams, 1988a; Abrams *et al.*, 1990a). In contrast, transpiration was reported to be higher in *A. rubrum* genotypes from swamp vs dry sites in eastern USA during both high and low ψ (Townsend & Roberts, 1973). However, *A. rubrum* populations used in that study were widely distant, ranging from Virginia and New Jersey for wet sites and West Virginia and Georgia for dry sites. Thus, the transpiration results may more greatly reflect regional than local genotypic variation. Nonetheless, wilting of *A. rubrum* leaves in that study started at higher stem ψ in wet site (-0.85 to

-1.22 MPa) than dry site (-1.65 to -1.96 MPa), similar to the results of this study.

Adjustment in osmotic potentials and elasticity during drought may promote turgor and limit desiccation (Turner & Jones, 1980; Tyree & Jarvis, 1982; Abrams, 1988b). In this study, limited adjustments in P-V parameters occurred in the upland *A. rubrum*, and during peak drought there were no observed genotypic differences in ψ_{π} , RWC_0 or ϵ . The lowest variability in osmotic potentials was exhibited in bog plants, suggesting less genotypic variation in this characteristic than in upland plants. Bog plants were the only source to display significant osmotic adjustment from pre- to peak drought. Despite the hydric conditions, plants in a bog may experience periodic water stress due to low root/shoot ratio, low permeability and water conductivity of roots, and high vapour pressure deficit (Kozlowski & Pallardy, 1984; Settler *et al.*, 1987). Differences in ψ_{π} between the bog (higher ψ_{π}) and barrens sources were evident during pre-drought, but not peak drought, conditions (cf. Parker & Pallardy, 1988).

Previous field studies of tissue-water relations in upland *A. rubrum* reported no change in ψ_{π} during a moist growing season in Wisconsin (Abrams, 1988c) and lowered ψ_{π} during a drought in North Carolina (Roberts, Strain & Knoerr, 1980). The ψ_{π} developed by *A. rubrum* in both of those studies was considerably lower than that exhibited by any source in this greenhouse study. There is increasing evidence that less osmotic adjustment during drought may occur in greenhouse vs field studies and in tree species or genotypes from the north-east vs the more arid regions of the USA (Parker & Pallardy, 1985; Abrams, 1988b; Abrams *et al.*, 1990a; Abrams, Schultz & Kleiner, 1990b; Seiler & Cazell, 1990). Previous studies of genotypic variation in P-V parameters during drought are inconsistent in that ψ_{π} was lower in xeric vs mesic plants in some studies (Abrams, 1988a; Nguyen & Lamant, 1989; Abrams *et al.*, 1990a), but not in other (Ladiges,

1975; Parker & Pallardy, 1985; Bongarten & Teskey, 1986).

Plants from xeric sites often have thicker leaves, with higher specific mass, stomatal density and lower guard cell length than plants on mesic sites (Jackson, 1967; Carpenter & Smith, 1975, 1981; Abrams & Kubiske, 1990). Many of these differences were also reported in xeric vs mesic genotypes of tree species (Donselman & Flint, 1982; Abrams, 1988a; Abrams *et al.*, 1990a). In this study, only a few genotype differences in leaf morphology were consistent with source location. For example, barrens plants had high stomatal density and low guard cell length relative to the other sources. Ridge plants also had lower guard cell length than the valley plants. Theoretically, smaller guard cells should result in higher water-use efficiency (CO₂ uptake/water loss) than larger guard cells (Bidwell, 1974). On the other hand, bog plants had higher specific leaf mass than the other sources, higher stomatal density than valley and ridge plants, and intermediate guard cell length.

In conclusion, differences in *A. rubrum* genotypes were most apparent when comparing gas exchange and final shoot water potential during the peak drought period in the bog vs upland sources. However, osmotic adjustment to drought and some xerophytic leaf features in bog plants may be a response or adaptation to periodic water stress in that habitat. Some morphological, but few physiological, differences were observed among the upland sources in this study. This lack of difference may be due to gene flow between the upland sites which would restrict population differentiation (Endler, 1977), or to the recent invasion of *A. rubrum* to the sites. The upland sites were dominated by older *Quercus* species, and were probably invaded by *A. rubrum* from more protected areas within the last 60–80 years as a result of fire exclusion (Lorimer, 1984; Nowacki, Abrams & Lorimer, 1990; G.J. Nowacki & M.D. Abrams, unpublished observations). The survival of species on greatly contrasting sites may be due to a combination of genetic differentiation and physiological and morphological plasticity (Shavers, Chapin & Billings, 1979; Abrams, 1986; Abrams, 1988a). It seems likely that the success of *A. rubrum* on the range of sites studied in central Pennsylvania is due only in part to genotypic variation, suggesting the importance of plasticity in this species.

Acknowledgments

Jim Zaczek aided in seed collection and seedling establishment and maintenance.

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Received 29 March 1990; revised 11 June 1990; accepted 19 June 1990