

# COMPARATIVE ECOLOGY OF DROUGHT RESPONSE IN HARDWOOD TREES: *ACER SACCHARUM* VERSUS *FRAXINUS AMERICANA*

MARTIN J. LECHOWICZ and NADINE E. IVES

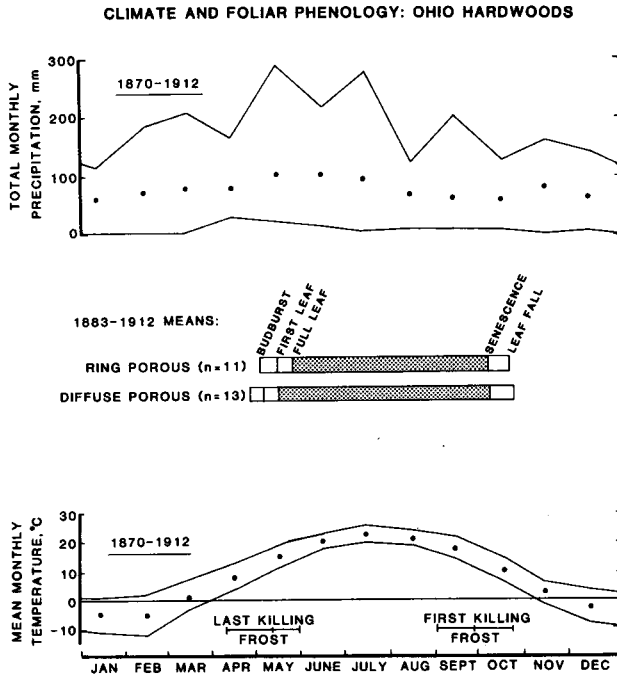
*Department of Biology, McGill University, 1205 Avenue Dr. Penfield, Montreal,  
Quebec, Canada H3A 1B1*

## Abstract

We compared the gas exchange of 2 year old *Acer saccharum* and *Fraxinus americana* established from seed and growing with and without irrigation in an experimental nursery on a well-drained sandy site. *Fraxinus* had consistently higher photosynthesis (A) and stomatal conductance (g) than *Acer* regardless of water regime, but the internal CO<sub>2</sub> concentration (c<sub>i</sub>) and the water use efficiency (A/E) of the two species were comparable when averaged over the growing season. The greater potential productivity of the ring-porous *Fraxinus* is consistent with its shorter canopy duration, greater water conducting capacity, and greater rooting depth. At times, such as after a rain, when edaphic and atmospheric conditions favored photosynthesis throughout the experimental nursery, seedlings of both species in the unirrigated plots exploited this opportunity by attaining temporarily higher rates of photosynthesis compared to those in the irrigated plots. This compensatory response to temporal variation in water availability was associated with a tendency for *Acer* to stabilize c<sub>i</sub> by varying g and, in contrast, for *Fraxinus* to maintain more stable g despite concomitant changes in c<sub>i</sub>. The net result of this compensatory regulation of gas exchange was to minimize intraspecific variation in the mean rates of photosynthesis over the growing season between the irrigated and unirrigated experimental plots. Both species thus tolerated mild drought stress but avoided desiccation and achieved their net seasonal production through different adaptations to variation in water availability.

## Phenology and production ecology in north temperate forests

In forests of north temperate regions, trees must be adapted to two inescapable elements of the seasonal progression of climatic events: a. the occurrence of a lengthy winter period when liquid water is essentially unavailable and b. the unpredictability of water supply during the frost-free season when ambient temperatures do allow significant metabolic activity. Deciduous trees survive the winter period in leafless dormancy, and their net annual production occurs during the warm season when they are in leaf (Hicks and Chabot 1985). In a given region, deciduous trees are generally in leaf during the period between the last and first hard frosts, but there is substantial interspecific variation in the timing of canopy development and canopy duration. Even co-occurring tree species neither break bud at the same time in the spring nor senesce at the same time in the fall (Lechowicz 1984). During 30 years of phenological observations at a site in midcontinental North America where the mean period between hard frosts was 137 days, the mean canopy duration for species of co-occurring deciduous, broad-leaf trees ranged from 130 to 164 days (Smith 1915; Fig. 1). Similar interspecific variation in the timing of bud break and senescence is recorded in other temperate zone forests of North America (Ahlgren 1957; Bell and Johnson 1975), Europe (Höhm 1915, 1916, 1917, 1918; Chalupa 1969; Lausi and Pignatti 1973;



*Fig. 1.* Mean patterns of climate and foliar phenology at a site just west of the shores of Lake Erie in central North America ( $41^{\circ}31' N$ ,  $84^{\circ}9' W$ ). The contrast in the phenology of ring- versus diffuse-porous species, the relationship of canopy duration to the mean frost-free period, and the possibility of drought at any time during the warm season are illustrated. The closed circles in the temperature and precipitation graphs are monthly means, and the upper and lower lines connect monthly maxima and minima. The range and mean of killing frost dates are indicated on the temperature graph. The data are from daily observations made by Thomas Mikesell (Smith 1915).

Comps *et al.* 1987), and Japan (Kikuzawa 1983, 1984; Hirabuki 1984). These interspecific differences in the annual period of canopy duration set an ultimate limit on net annual production for each co-occurring species. All other things being equal, we would expect species that are in leaf for a greater part of each year to have a greater net annual production.

There is, however, evidence suggesting that interspecific differences in canopy duration reflect underlying differences in other aspects of production ecology. The timing of bud break in the spring is correlated with different patterns of shoot extension and with aspects of wood anatomy determining maximum rates of water conduction (Lechowicz 1984; Fig. 1). The earliest leafing species at a site are invariably diffuse-porous and have indeterminate shoot growth, while most later leafing species are ring-porous and have only a single synchronized flush of shoot growth each season. The wide diameter xylem vessels of ring-porous trees cavitate during the winter (Zimmermann 1983) necessitating production of new vessels before the transpirational demand of new leaves can be met; this prerequisite for cambial activity bars the ring-porous species from exploiting the earliest part of the spring used by diffuse-porous species with indeterminate shoot growth (Lechowicz 1984). We

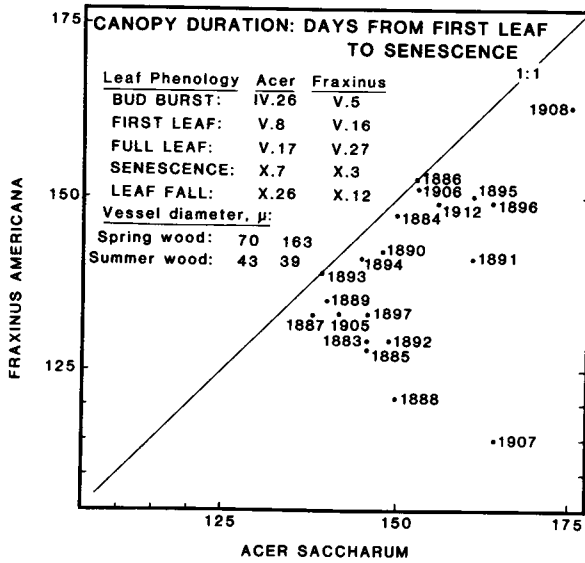


Fig. 2. Graph of the annual values of canopy duration in co-occurring *Fraxinus americana* and *Acer saccharum* with an inset showing other phenological events and wood anatomy for the two species. The phenology data are from Thomas Mikesell (Smith 1915) and the anatomical data from French (1923).

hypothesized that ring-porous species would compensate for this constraint on early season production by maintaining higher rates of gas exchange than co-occurring diffuse-porous species during the other parts of the growing season, including periods of mild drought stress. This would be concordant with the greater potential rates of conduction in the wide vessels of ring- versus diffuse-porous species.

We chose to test this hypothesis by comparing the gas exchange characteristics of two species that are frequently codominant in the forests of eastern North America, the diffuse-porous *Acer saccharum* and the ring-porous *Fraxinus americana*. In a forest where they co-occurred, the mean canopy duration of *Acer* was 11% longer than that of *Fraxinus* (Fig. 2). Although both species have about 20% of their cross-sectional stem area invested in vessels, the maximum vessel diameter of *Acer* is only 43% that of *Fraxinus* (French 1923; Fig. 2). By Poiseuille's Law (Zimmermann 1983) the maximum rate of water conduction in *Fraxinus* will be on the order of 30 times greater than in *Acer*. Considering this and the reported deeper rooting depth of *Fraxinus* (Stout 1956; Watson and Himelick 1982), we expected *Fraxinus* to sustain gas exchange over a broader range of conditions and at an higher mean rate over the growing season than *Acer*. This higher average rate of gas exchange in *Fraxinus* could compensate for its shorter period of canopy duration compared to *Acer*.

## Materials and methods

### *Experimental tree nursery*

In fall 1984 we planted seed from four eastern North American provenances of *Fraxinus americana* and four of *Acer saccharum* in an experimental tree nursery at the Mont St. Hilaire Research Center of McGill University (45°32' N, 73°8' W; 140 m). Seed from each of the species/provenance combinations was sown in a pair of plots; the plots were 1 m<sup>2</sup> raised beds containing 10 cm of commercial topsoil established atop a levelled and cleared area in a deep, natural deposit of sand and gravel laid down during the Lake Champlain phase of the last deglaciation (MacPherson 1967). In 1985 the seedlings in all plots were irrigated and fertilized (11-41-8 in spring, 20-8-20 in early summer, 8-20-30 in late summer: Plant Products, Bramalea, Ontario) from the time of their emergence to assure good establishment. In 1986, however, only one plot in each pair was irrigated while the other was exposed to natural cycles of wetting and drying. All plots continued to be fertilized with granulated, slow-release fertilizer (18-4-6: CIL, Montreal, Quebec) as well as periodically watered with tree seedling (20-8-20 in spring, 8-20-30 later: Plant Products) and trace element (Chelated form: Plant Products) fertilizers. In 1986 plentiful rainfall minimized the contrast between the irrigated and unirrigated plots, but the unirrigated plots had an average of 20% less water in the soil over the growing season based on repeated neutron soil moisture probe measurements (Vose 1980) with a CPN Model 503DR Hydroprobe (Pacheco, CA). Despite this difference in bulk soil water content, the 15 cm depth of the rooting zone in the dry plots did not fall below -0.02 MPa based on twice daily readings with Model 2725 Jet-fill tensiometers (Santa Barbara, CA). The 1986 experiments described below thus contrast the responses of these seedling trees to intermittent mild shortages versus ample supplies of soil water.

### *Experimental protocols*

We assayed the gas exchange of seedlings in the paired plots on 17 occasions between July 9 and September 22, 1986 – the part of the growing season when the water regime of the irrigated and unirrigated nursery plots differed most. The assays were carried out in series that averaged 2.5 hrs duration at different times between 0800 and 1800 hours solar time on days without precipitation. Table 1 summarizes the environmental conditions prevailing during the series of assays.

In each assay series the gas exchange of a random leaf on each of three random seedlings in an experimental plot was measured with a LiCor 6000 portable photosynthesis system (Lincoln, NE). Photosynthetic rates and internal CO<sub>2</sub> concentrations are the mean of 10 consecutive estimates at 2 second intervals; leaf conductance and the transpiration rate used to calculate water use efficiency were estimated using the temporal trend in water vapor concentration extrapolated to time zero when the logging of the reading was begun. The logging cycle was begun when a steady drawdown of CO<sub>2</sub> was evident in the cuvette, usually less than 30 seconds after it was clamped on the leaf. The species/provenance pairs were assayed in a rerandomized order in

Table 1. Environmental conditions during the series of gas exchange assays in the experimental nursery.

	<i>Acer saccharum</i> plots		<i>Fraxinus americana</i> plots	
	Irrigated	Unirrigated	Irrigated	Unirrigated
Photon flux density, $\mu\text{mol m}^{-2}\text{s}^{-1}$	619 $\pm$ 55	670 $\pm$ 53	574 $\pm$ 45	563 $\pm$ 48.3
Vapor pressure deficit, kPa	1.49 $\pm$ 1.00	1.54 $\pm$ 1.00	1.21 $\pm$ 0.70	1.25 $\pm$ 0.71
Leaf temperature, $^{\circ}\text{C}$	23.9 $\pm$ 0.80	24.2 $\pm$ 0.80	23.1 $\pm$ 0.69	23.3 $\pm$ 0.70

each series, and the order of assay of plots in each pair was also randomized. With the exception of a few seedlings that became damaged during the course of the season, the same seedlings were used in all 17 assay series. The assay of the six seedlings in a plot pair generally took about 12 minutes. These data essentially provide 68 'slice-in-time', paired comparisons of the effect of modest differences in water availability on seedling gas exchange over the growing season for each species.

### Statistical methods

We used a simple least squares regression of the paired responses in irrigated versus unirrigated plots to statistically summarize and compare the gas exchange of seedlings under the conditions in the experimental nursery through the season (Proc. REG, SAS Version 5.16, SAS Institute 1985). If the treatment differences in soil water regime had no effect on gas exchange, the slope of the regression of response in the irrigated plot on response in the unirrigated plot for any parameter would not differ significantly from one. The interspecific differences in gas exchange responses to the experimental treatment can be tested by analysis of covariance in the SAS procedure GLM (Freund and Littell 1981, pp. 202-205). By providing a concise summary of paired responses to experimental treatments, this statistical approach takes advantage of the capabilities of the LiCor instrument to rapidly assay gas exchange in the field. Because of the paired experimental design and our sampling throughout the growing season, the regression approach to the data analysis allows rigorous comparisons of gas exchange responses despite the inability to control environmental conditions in the field. Data on four parameters were analyzed: 1. net photosynthetic rate,  $A$ , 2. stomatal conductance,  $g$ , 3. instantaneous water use efficiency,  $A/E$ , and 4. internal  $\text{CO}_2$  concentration,  $c_i$ .

### Results

The photosynthetic rates of *Fraxinus* exceed those of *Acer* across a broad range of edaphic and atmospheric environments (Fig. 3A). The photosynthetic responses of the two species in the irrigated versus dry plots vary significantly in magnitude but not qualitatively (ANCOVA: species effect,  $p=0.0089$ ; slope effect,  $p=0.286$ ). Under conditions favoring higher photosynthetic rates, both species have higher rates of photosynthesis in the dry compared to the irrigated plots (e.g. regression slopes less than one), but this response to dryer conditions is less strong in *Fraxinus* (95%

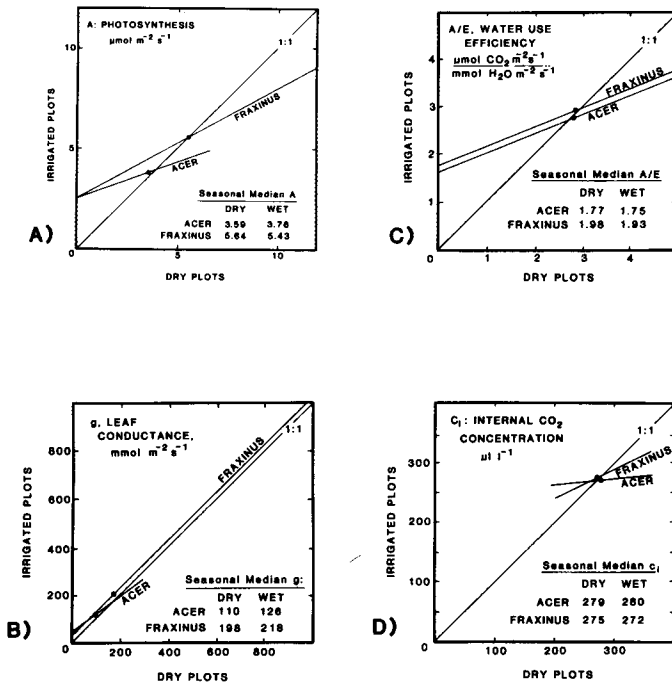


Fig. 3. Gas exchange characteristics of *Fraxinus americana* and *Acer saccharum* in irrigated versus unirrigated plots. The lines for each species represent the regressions of response in the irrigated versus unirrigated plots based on 68 paired assays over the latter half of the 1986 growing season. With one exception (*Acer*  $c_i$ ) all the regression lines are highly significant ( $0.0001 < p < 0.0073$ ) and are drawn only over the range of the actual data. The inset shows the median responses over the growing season; the mean responses are graphed as a closed circle on each graph.

confidence intervals: *Acer*,  $b = 0.35 \pm 0.21$ ; *Fraxinus*,  $b = 0.54 \pm 0.20$ ). The maximal rates of photosynthesis in *Fraxinus* are almost twofold greater than in *Acer*. On average over the latter, more drought prone half of the growing season, the photosynthetic rates of *Fraxinus* exceed those of *Acer* by about 50% regardless of edaphic conditions (Fig. 3A).

The patterns of leaf conductance (Fig. 3B) and internal leaf  $\text{CO}_2$  concentrations (Fig. 3D) provide some insight into the functional basis for the observed differences in photosynthetic responses. Neither response, however, differs significantly between species (ANCOVA: Species effect  $g$ ,  $p = 0.590$ ;  $c_i$ ,  $p = 0.649$ . Slope effect  $g$ ,  $p = 0.542$ ;  $c_i$ ,  $p = 0.092$ ). In accordance with the higher photosynthetic rates of *Fraxinus*, its maximal and mean seasonal leaf conductances exceed those of *Acer* (Fig. 3B). The leaf conductance of *Fraxinus*, however, is less affected by edaphic than atmospheric factors compared to *Acer* – the regression of conductances in the irrigated versus dry plots has a slope of one in *Fraxinus* (95% confidence interval:  $1.00 \pm 0.22$ ), but is lower than one for *Acer* (95% confidence interval:  $0.86 \pm 0.20$ ). When ample water is available, *Acer* maintains an essentially constant internal  $\text{CO}_2$

concentration (*e.g.* regression slope does not differ from zero;  $H_0: b = 0, p = 0.215$ ) while *Fraxinus* does not ( $H_0: b = 0, p = 0.007$ ). The mean and range of internal  $CO_2$  concentrations of both species over the season are comparable (Fig. 3D), but *Acer* appears to stabilize internal  $CO_2$  concentrations through changes in photosynthesis and conductance to a greater degree than *Fraxinus*.

Despite these interspecific differences in photosynthesis, conductance and internal  $CO_2$  concentration, *Fraxinus* and *Acer* achieve markedly similar patterns of water use efficiency (A/E) over the season (Fig. 3C). The two species do not differ significantly in the relation between WUE in the irrigated and unirrigated plots (ANCOVA: species effect,  $p = 0.708$ ; slope effect,  $p = 0.830$ ). On average, the A/E of *Fraxinus* is slightly but not significantly greater, and the range and pattern of A/E in irrigated versus dry plots for both species is virtually identical. Water use efficiency of both species is more stable in the irrigated plots compared to in the unirrigated plots (*e.g.* regression slopes less than one; *Acer* 95% confidence interval:  $b = 0.42 \pm 0.24$ , *Fraxinus* 95% confidence interval:  $b = 0.37 \pm 0.22$ ).

## Discussion

### *Interspecific differences in gas exchange*

In agreement with our original hypothesis and with other results in the literature, *Fraxinus americana* does have higher rates of gas exchange than *Acer saccharum* across a broad range of edaphic and atmospheric conditions. This is consistent with its shorter period of canopy duration (Lechowicz 1984), its greater rooting depth (Stout 1956; Watson and Hemelick 1982), and its greater maximum rates of water conduction (French 1923; Zimmermann 1983). Kozlowski and his associates have compared the responses of *Fraxinus americana* and *Acer saccharum* to drought in a series of short term experiments with potted seedlings (Davies and Kozlowski 1974; Kozlowski *et al.* 1974; Davies and Kozlowski 1977; Pereira and Kozlowski 1977). They showed that, compared to *Fraxinus*, *Acer* had more and smaller stomates that responded more quickly to changes in light and vapor pressure deficit and maintained lower leaf conductance over a broad range of light, temperature, and tissue water potentials. The conductance of *Acer* was greater than that of *Fraxinus* only at plant water potentials above about  $-0.3$  MPa. The recovery of full photosynthetic capacity after a drought period was also longer in *Acer*. These interspecific differences in response to short term drought treatments together with our longer term results for the two species growing under a natural, intermittent drought regime indicate that while *Acer* and *Fraxinus* both tolerate mild drought, they avoid desiccation by different means. *Acer* avoids desiccation by limiting photosynthetic activity to periods when atmospheric conditions do not lead to rapid water loss. *Fraxinus* is less sensitive to atmospheric conditions and relies instead on greater acquisition of soil water and more effective hydraulic transport to meet the evaporative demands in leaf tissues.

The generality of these results for other temperate tree species differing in canopy duration remains to be investigated. Comparison of available data (Davies and Kozlowski 1974; Hinckley *et al.* 1978; Bahari *et al.* 1985; Chambers *et al.* 1985; Ives and Lechowicz, unpublished data) does suggest that the trend holds for various ring-

porous species of *Quercus* compared to *Acer saccharum* – these *Quercus* species, all with shorter canopy durations than *Acer*, also have higher leaf conductances and photosynthetic rates over a broad range of environmental conditions. On the other hand, *Betula papyrifera*, a diffuse-porous species that has longer canopy duration than co-occurring *Acer saccharum* (Lechowicz 1984), also appears to have higher rates of leaf conductance (Pereira and Kozłowski 1978). Considering the diversity of traits that alone and in combination can confer adaptation to intermittent water shortages (Hinckley *et al.* 1981; Kozłowski 1982; Pallardy *et al.* 1983), we should not expect a single uniform relationship between canopy duration and gas exchange parameters. The adaptive interrelationships of these two parameters with others such as rooting depth, rates of fine root turnover, the capacity for osmotic adjustment, the rate of peak stem flow per unit leaf area, the timing of leaf senescence, and similar traits need to be determined with reference to a broader-based interspecific comparison.

*Compensatory adjustment in gas exchange responses to contrasting edaphic water regimes*

Our results indicate that despite their differences in overall rates of gas exchange, both *Fraxinus* and *Acer* may regulate their losses of water and gains of carbon on a whole plant basis over the growing season. Seedlings of either species have higher rates of photosynthesis in the unirrigated plots when conditions are favorable for photosynthesis – the regression slopes are less than one (Fig. 3). In other words, there is more temporal variance in the gas exchange of seedlings in the dry versus the irrigated plots. Seedlings in the dry plots appear to reserve peak photosynthetic activity for periods when conditions favor more rapid carbon gains. Over the season, this compensatory exploitation of favorable conditions acts to equalize the *mean* seasonal rates of photosynthesis across the contrasting soil water regimes.

The basis of this compensatory response in the two species reflects possible differences in their balance of gas exchange responses to atmospheric versus soil drought events. Schulze (1986) has reviewed the two major control loops that govern the exchange of carbon dioxide and water vapor: 1. a feedback response dependent on leaf water status and 2. a feedforward response dependent on the water vapor gradient between leaf and air. The balance of these two control mechanisms in a given species can affect the pattern of stomatal conductance and internal CO<sub>2</sub> in contrasting soil water regimes. If the feedback loop dominates, we would expect stomatal conductance to be less responsive to atmospheric drought events and consequently to observe greater fluctuations in internal CO<sub>2</sub> concentrations. Conversely, in a predominantly feedforward system, any adverse effects of reduced mesophyll water potentials on photosynthesis and respiration that induce variation in  $c_i$  should be minimized because stomatal conductances respond rapidly to atmospheric conditions. The feedforward system should be more sensitive to atmospheric drought, the feedback system more sensitive to soil drought.

In our experimental nursery, the  $c_i$  of *Acer* was relatively stable through variations in  $g$ . This is consistent with the greater stomatal sensitivity of *Acer* demonstrated by Davies and Kozłowski (1974, 1977) and suggests the dominance of the feedforward control system in its mechanisms for avoiding desiccation. In contrast, the feedback

control system appears to predominate in *Fraxinus*. This is again consistent with Davies and Kozlowski's data on short term stomatal responses: *Fraxinus* maintains a relatively invariant stomatal conductance across a broad range of plant water potentials (Davies and Kozlowski 1977). The generality and limits of these variant desiccation avoidance mechanisms and associated compensatory regulation of gas exchange in response to seasonal variations in soil water availability and atmospheric drought merit investigation.

### Acknowledgements

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