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Functional ecology of hardwood trees under chronic drought

Nadine E. Ives

Department of Biology, McGill University,
1205 avenue Docteur Penfield, Montréal,
Québec, H3A 1B1 Canada

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A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

I compared the interrelationships among traits affecting interspecific variation in the growth of seedlings of 22 hardwood tree species subjected to chronic intermittent drought. Leaf traits were the most responsive to contrasting water regimes; canopy architecture, hydraulic conductivity and leaf phenology were less affected. Relative growth rate (RGR) under drought, however, was most closely related to variation in canopy duration: species in leaf longer had greater RGR. Secondarily, maintaining higher stomatal conductance (g) under drought further enhanced RGR. Higher g is associated with a higher photosynthetic rate (A), but the relationship between A and g varied with internal CO_2 concentration (c_i), foliar nitrogen and specific leaf mass. Species with weaker homeostatic control over c_i had higher water use efficiency. While photosynthetic characteristics were related primarily to species' shade tolerance, water use efficiency was most closely related to habitat moisture preference.

RÉSUMÉ

Les relations entre les traits affectant la variation interspécifique durant la croissance de jeunes plantes de 22 espèces d'arbres feuillés exposés chroniquement à des périodes de sécheresse ont été comparées. Les traits relatifs aux feuilles étaient les plus influencés par les régimes d'arrosage tandis que l'architecture du feuillage, la conductivité hydraulique et la phénologie foliare furent moins affectées. Le taux de croissance relatif (RGR) lors de périodes de sécheresse était relié plus étroitement à la variation de la durée du feuillage: *i.e.* les espèces avec un feuillage durant plus longtemps démontrèrent un plus grand RGR. De plus, le maintien de la conductance stomatale (g) lors de sécheresse fit augmenter la valeur du RGR. Une plus grande g est associée avec un taux de photosynthèse (A) plus élevé. Cependant la relation entre A et g varie avec la concentration interne de CO_2 (c_i), l'azote foliaire et la masse spécifique des feuilles. Les espèces ayant un contrôle homéostatique plus faible par rapport à c_i ont démontré une plus grande efficacité d'utilisation de l'eau. Les caractéristiques photosynthétiques étaient majoritairement reliées à la tolérance de l'espèce à l'ombre alors que l'efficacité de l'utilisation de l'eau était majoritairement reliée à une préférence envers le taux d'humidité de l'habitat.

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I dedicate this thesis to all the women around the world - past, present and future - who are striving to lead balanced, whole lives and are, thus, transforming the world around them. May all women's work be acknowledged and receive the respect it deserves.

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PREFACE

I am required by the Faculty of Graduate Studies to reproduce the following statement:

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This thesis consists of a general introduction followed by three chapters and a statement of general conclusions and original contributions. Chapters 1 and 2 are prepared for submission to scientific journals. They are written in the first person, but will be submitted for publication as manuscripts co-authored with my thesis supervisor, Dr. Martin J. Lechowicz. The results from an initial study undertaken during my preliminary field season, 1986, have been published as a book chapter (Lechowicz & Ives 1989) and are not included in this thesis. The data presented in Wang, Ives & Lechowicz (1992) are also not directly included in this thesis.

The general introduction provides an overview of the comparative approach taken and a brief rationale for the selection of species and traits studied in this thesis and the methodologies used for study. The focus is on the choice of traits and methodology as more detailed discussion of the importance and implications of various traits are given in the introductions to the individual chapters. Appendices provide background information on seed sources, planting dates and descriptions of certain field and laboratory protocols and calculations that are not detailed in the individual chapters. The great increase over the last two decades of studies involving field measurement of leaf gas exchange and the use of carbon isotope ratios has led to some concern regarding the interpretation of these types of data. Therefore, in Appendix V I have addressed the issues of concern relevant to the data presented in this thesis regarding these two types of data. The references for the general introduction, the three chapters and the appendices are included in a single Literature Cited section following the General Conclusions to avoid unnecessary duplication.

GENERAL INTRODUCTION

As the field of functional ecology develops, it has become clear that despite a wealth of information on the growth, physiology, morphology and anatomy of trees, we still are far from understanding the functional integration of different traits and whole plant response to environmental stress (Körner 1991, Ceulemans 1990). Far from being discouraging, the current situation presents exciting challenges because 1) we do have considerable understanding of some of the pieces (*e.g.* leaf physiology), 2) technological and methodological advances over the past two decades have made it possible to measure certain parameters in many plants or species concurrently and with much greater ease than was possible before (*e.g.* portable infrared gas analyzers, the technique for measuring xylem hydraulic conductivity developed by Sperry, Donnelly & Tyree (1988a) and carbon isotope analysis) and 3) various models are being developed that describe or predict responses to particular conditions and, most recently, to attempt to link different aspects of response. Efforts to describe the functional integration of responses are currently receiving considerable attention (Küppers 1989, Kikuzawa 1991, Hilbert, Larigauderie & Reynolds 1991).

Comparative studies are an integral part of functional ecology. As outlined by Keddy (1992), the three basic components of functional ecology are 1) the measurement of carefully chosen traits across species, 2) exploration of the relationships among traits, and 3) determination of the relationships between traits and environments. Ultimately, to fully understand whole plant response to environment, one would have to examine all traits in all species in all environments. Obviously, this is impossible and the task becomes one of choosing appropriate traits, species and environments that will add to our understanding of the traits and species studied and which may also allow testable predictions of the responses of other species or responses to different environments.

The study of these multifactorial and coordinated plant responses is complicated by phenotypic plasticity in individual traits. The phenotypic characteristics of a plant arise jointly from its genotype and the environment in which it develops (Bell & Lechowicz 1994). The exact nature of a trait will vary across different environments; however, not all traits will vary equally across environments, *i.e.* not all traits will be equally plastic (Schlichting 1986, 1989). In general, we expect variability in traits among species to be greater than that attributable to plastic responses.

The focus of this thesis is on the integrated responses of deciduous hardwood trees to soil water shortage. The thesis is an interspecific comparison of the degree and nature of plastic response to water shortage and an examination of the relationships between traits and relative growth rate in a water-limited environment. In this general introduction, I will outline the rationale for my choice of the species, traits and environments studied and the approach and methodology used. I will then briefly outline the contents of the three thesis chapters.

Soil water availability is a major determinant of plant abundance and diversity (Kramer 1983, Currie & Paquin 1987). Even in mesic temperate forests, soil water availability is a major factor determining the growth of trees (Bassett 1964, Zimmermann & Brown 1971, Kozlowski, Kramer & Pallardy 1990, Gholz, Ewel & Teskey 1990). How trees respond to different soil water availability and the traits that determine the range of soil moisture regimes in which a species is found are, thus, of considerable interest. Tree species exhibit a wide range of variation in drought tolerance; therefore, an environment seen as stressful to one species may not be stressful to another and no uniformly stressful environment can be imposed in a cross-species comparison. I chose two test environments (irrigated and non-irrigated treatments) that represent two of the many environments in which the tree species chosen are found growing naturally. Although many studies have focussed on response to extreme drought events, either natural (*e.g.* Hinckley *et al.* 1979, Dougherty & Hinckley 1981, Briggs, Jurik & Gates 1986) or imposed (*e.g.* Davies &

Kozlowski 1977, Ni & Pallardy 1991), I have examined tree seedling performance under conditions of chronic intermittent water shortage. Since the drought treatment was imposed for a five-year period, the responses seen reflect long-term adjustment to chronic drought as well as short-term adjustment to drought events.

I chose to do a broad comparison across a number of deciduous hardwood species of the northeastern deciduous forest of North America. The total number of species chosen was limited for pragmatic reasons. To best compare the functional relationships among traits and across species, one needs a parsimonious set of traits that can be measured using the same techniques across all species. I chose to study eastern decidous hardwoods because these species share a common growth form, deciduous habit and basic leaf structure. I excluded evergreen coniferous species because the conifers differ from hardwoods in wood anatomy, growth pattern, leaf structure and leaf longevity. These differences would compound the difficulty of measuring the various traits of interest and also of interpreting the patterns seen. In chosing the eastern hardwood species, I excluded prairie and aridland species. These were omitted because the habitats in which they occur differ greatly from that of the eastern forest and, thus, they are likely to show adaptations quite different from those of eastern species, again adding further complexity and confounding interpretation of response to the chronic drought regime imposed. I, therefore, chose species growing within a single ecoregion (Braun 1950). An additional, practical, constraint on species choice was that all species chosen had to be able to grow and overwinter outdoors in southern Québec.

The maximum richness of trees species in temperate North America (approximately 180 species) is found in the southeastern United States (Currie & Paquin 1987). In constrast, approximately 75 species are found in the region encompassing southern Ontario and Québec (Currie and Paquin 1987). Of those approximately 75 species, 22 are included in this study (Table 1). The species chosen are a representative sample of eastern trees in terms of their habitat moisture

Table 1. Tree species included in the study.

Acer pensylvanicum	striped maple
A. rubrum	red maple
A. saccharinum	silver maple
A. saccharum	sugar maple
Betula alleghaniensis	yellow birch
B. papyrifera	paper birch
B. populifolia	grey birch
Carya cordiformis	bitternut hickory
C. ovata	shagbark hickory
Castanea dentata	American chestnut
Celtis occidentalis	hackberry
Fraxinus americana	white ash
F. pennsylvanica	green ash
Juglans cinerea	butternut
J. nigra	black walnut
Populus balsamifera	balsam poplar
P. deltoides	eastern cottonwood
P. tremuloides	quaking aspen
Prunus pensylvanica	pin cherry
Quercus rubra	northern red oak
Ulmus americana	American elm

preference and shade tolerance groupings (Table 2). These 22 species share a common growth form and deciduous habit, but exhibit a range of variation in physiology (*e.g.* Bunce, Miller & Chabot 1977, Abrams 1988a, Abrams, Schultz & Kleiner 1990), phenology (Ahlgren 1957, Bell & Johnson 1975, Lechowicz 1984), architecture (Horn 1971, Canham 1988), wood anatomy (Panshin & de Zeeuw 1980, Lechowicz 1984), life history characteristics (Loehle 1988, Burns & Honkala 1990) and habitat moisture preference (Curtis 1959, Maycock & Curtis 1960, Peet & Loucks 1977). They, thus, comprise a good group for comparative study, having enough variation to allow examination of the interrelationships among traits and between traits and environment, but also co-occuring across sites of a range of soil moisture availability.

The 22 species represent 11 genera and 8 families. There is some concern about making comparisons across a group of species, some of which are more closely related phylogenetically than others (Figure 1) (Harvey & Pagel 1991). I argue that, for several reasons, the different phylogenetic relationships among species do not interfere with a comparative study of the nature of the one being considered here. First, the differences in traits (*e.g.* photosynthetic rates, shade tolerance, habitat moisture preference) are often greater among congeneric species than between species of different genera. Second, for plants, it is impossible to remove or even account for phylogenetic bias because the phylogenetic distances between groups are poorly resolved due to the lack of a good fossil record (Chase *et al.* 1993). Third, the focus of this study is on whole plant performance. My primary interest is in the functional ecology of these hardwood trees and present variations in "design" rather than in the evolution of traits.

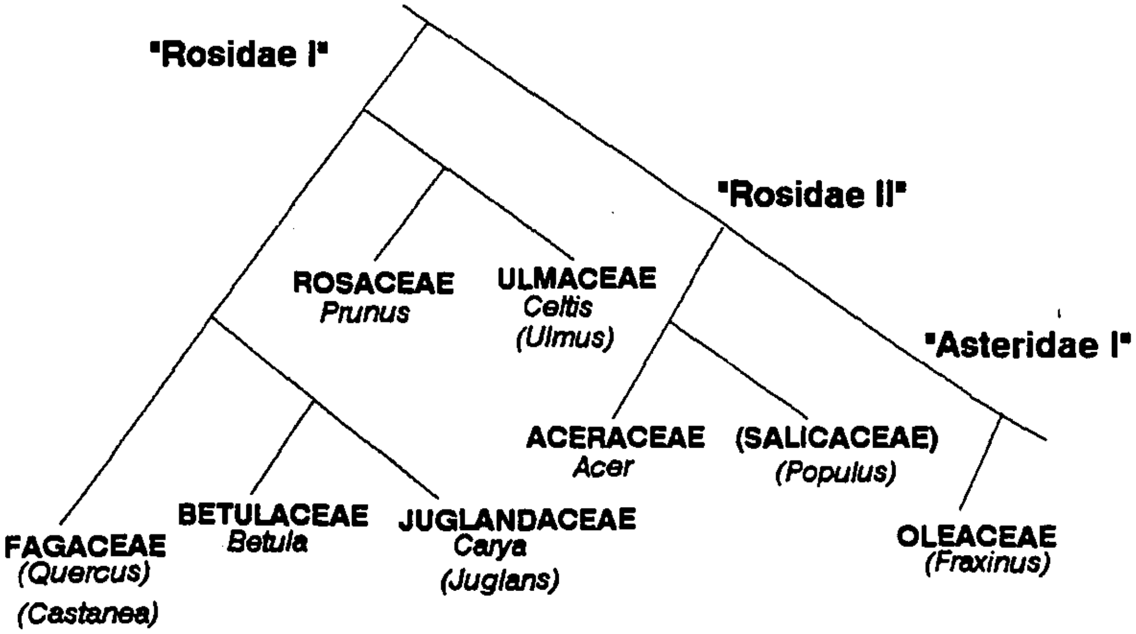
Several species would have been desirable additions to the group of species studied. *Tilia americana* (basswood), *Ostrya virginiana* (ironwood), and *Carpinus caroliniana* (hornbeam) were originally intended to be included in the study, however,

Table 2. Tree species distributions according to habitat moisture preference and shade tolerance. Percentages are based on a comparison of the distributions of 116 tree species of the eastern North American forest (Ives *unpubl.*). Percentages in this study total greater than 100 due to the bimodal classification of several species.

Habitat Moisture Preference

	% All trees / % This study	**Dry**	**Dry-mesic**	**Mesic**	**Wet-mesic**	**Wet**
Shade Tolerance	**Very intolerant**	3%/-	2%/9%	1%/-	1%/5%	6%/14%
	Intolerant	9%/-	2%/5%	5%/5%	11%/14%	13%/-
	Intermediate	5%/5%	3%/9%	-/-	7%/18%	5%/5%
	Tolerant	2%/-	2%/9%	5%/-	3%/9%	5%/5%
	Very tolerant	-/-	-/-	5%/9%	2%/-	2%/-

Figure 1. Contemporary understanding of the phylogenetic relationships among the genera included in this study. The relationships follow Cronquist (1988) and Chase et al (1993). The former is based on classical systematic methods and agrees in all respects with the most recent molecular phylogeny for this part of the angiosperms. Taxa in parentheses were not directly studied in Chase et al (1993) but closely related taxa were. It is important to note that the phylogenetic distances among groups are not known, but the basic lines of descent are properly estimated (Chase et al 1993)



these species have low germination rates (Burns & Honkala 1990) and insufficient numbers of seedlings germinated in the nursery. *Fagus grandifolia* (American beech) was planted but, although the seedlings germinated, they suffered considerable rabbit damage and were unable to tolerate the high insolation level of the nursery; therefore, *F. grandifolia* was also not included. A number of oak species (particularly *Quercus alba, Q. bicolor* and *Q. macrocarpa*) would have been welcome additions, but were not included due to space limitations.

Choice of traits and methodology.

Detailed reviews of the traits studied are given in the introductions of Chapters 1 and 2. Here, I will briefly outline the traits chosen (Table 3) and the methodological approach.

a. Leaf traits. Leaf responses to plant and soil water status have been the primary focus of studies of response to water availability. Much research has focussed on stomatal regulation of water loss, the integration of stomatal conductance and photosynthesis, and water use efficiency as described by the model developed by Farquhar and co-workers (Farquhar, von Caemmerer & Berry 1980, Farquhar & Sharkey 1982). There are numerous cross-species field comparisons of the gas exchange of trees (*e.g.* Bunce, Miller & Chabot 1977, Briggs, Jurik & Gates 1986, Abrams, Schulz & Kleiner 1990) and experimental studies of the effects of different water regimes among species (*e.g.* Ni & Pallardy 1991) and within species (*e.g.* Abrams, Kubiske & Steiner 1990, Parker & Pallardy 1991, Ellsworth & Reich 1992a). However, most of the studies include relatively few measurements over a short period of time and comparisons among studies are often limited due to different sampling or measurement protocols and/or different environmental conditions and tree age. To broaden our understanding of tree performance under more or less natural

Table 3. Traits related to tree carbon and water relations. See text for explanation (* indicates traits included in the study).

Leaf traits:	* photosynthesis (A)
	* stomatal conductance (g)
	* internal CO_2 concentration (c_i)
	* water use efficiency (A/E)
	* carbon isotope ratio ($\delta^{13}C$)
	* leaf nitrogen (N) content
	leaf nutrition apart from N
	leaf biochemistry
	stomatal size and density
	* specific leaf mass (SLM)
	leaf density and thickness
	tissue water relations
	* timing of budbreak and fall senescence
	* canopy duration
	leaf turnover rate (individual leaf life spans)
Hydraulic conductivity:	* maximum conductivity/branch cross-sectional area
	* maximum conductivity/leaf area supplied
	* loss of conductivity by late winter
	loss of conductivity due to drought alone
	vulnerability curves
	measurements of wood anatomy
Root traits:	root growth
	fine root turnover rates
	root hydraulic conductivity
	root-to-shoot ratio
	hydraulic lift
	mycorrhizal associations
Growth and canopy architecture:	* relative growth rate over five years (incorporating growth in height, stem diameter and total branch length)
	* leaf display index (LDI, leaf area/branch length)
	* canopy area/height
	* leaf area/total stem and branch length
	* wood density
	detailed phenology of shoot growth
	whole plant biomass
	proportional allocation to roots, stems, and leaves

conditions, I conducted extensive gas exchange measurements across a broad range of species growing under uniform conditions in an experimental tree nursery.

The approach I chose was to take multiple series of gas exchange assays over the course of the growing season. My main focus is on actual plant performance under close to natural field conditions, rather than on maximum potential performance under optimal conditions (light saturation and ample soil moisture). I examined the primary gas exchange parameters (see Table 3): photosynthesis rate (A), stomatal conductance (g), internal CO_2 concentration (c_i) and instantaneous water use efficiency (the ratio of photosynthesis, A, to transpiration, E: A/E). I also measured carbon isotope ratio ($\delta^{13}C$), a measure of long-term integrated water use efficiency independent of the gas exchange measurements. Repeated gas exchange measurements taken over one summer (Chapter 1) or two summers (Chapters 2 and 3) allowed estimation of seasonal mean performance over the range of conditions encountered (sunny days, cloudy days, days after rainfall, days during dry spells). Maximum values were calculated as the 95th percentile of the total number of values obtained. Other leaf traits measured were leaf nitrogen (N) content and specific leaf mass (SLM), which are related to photosynthetic capacity (Field & Mooney 1986, Gutschick & Wiegel 1988, Reich, Walter & Ellsworth 1992) and which also influence leaf water use efficiency (WUE) (Gutschick & Wiegel 1988, Walters & Reich 1989). A number of other leaf traits were not included. SLM is composed of leaf thickness and leaf density, which may vary independently (Witkowski & Lamont 1991). Leaf nutrition apart from N and leaf biochemical traits, such as chlorophyll a/b ratio and photosynthetic enzyme levels, were not studied. Nor were stomatal density and size. I assumed that interspecific and between-treatment variation in these traits will be reflected in photosynthetic performance. Leaf tissue water relations were also not included. Although species are known to differ in the leaf water potential (Ψ_{leaf}) at which stomata close, the extent of osmotic adjustment as Ψ_{leaf} decreases and cell wall elasticity (Tobiessen & Kana 1974, Abrams 1988b, Ni & Pallardy 1991), these traits have not been related consistently to leaf gas exchange during water shortage or to drought tolerance at the leaf or plant level (Kramer 1988, Abrams 1988b). Again, any adaptive response in these parameters is assumed to be reflected in the traits that were measured. The experimental design of the study limited me to essentially non-destructive sampling, except for the collection of leaf samples toward the end of the growing season and branch harvests at the end of the study.

For northern deciduous trees, the time available for photosynthesis is limited by the cold winters during which the trees are leafless and dormant. However, even within a single forest, tree species break bud in spring and senesce in fall at different times and, thus, utilize different proportions of the season available (Lechowicz 1984). Canopy duration is, therefore, an important aspect of annual carbon relations. I recorded the timing of spring budbreak and fall senescence and calculated canopy duration as a measure of the time available for carbon gain. An important aspect of leaf phenology that was not included is leaf turnover rate. Recent studies have linked the life span of individual leaves to their photosynthetic capacity and a number of other traits (Koike 1987, Kikuzawa 1991, Reich, Walters & Ellsworth 1991b). Leaf longevity has not been studied in North American trees and information on leaf turnover rates of the trees in this study would add a useful dimension to interpretation of whole tree function. However, it was not feasible to obtain such data due to limited time and human resources.

b. Hydraulic architecture and conductivity. Tree species differ in the organization of their water-conducting systems, or hydraulic architecture (Zimmermann 1983). Hardwood trees can be grouped on the basis of their wood anatomy into three basic groups: 1) ring-porous species, which produce large diameter xylem vessels in spring followed by much narrower vessels in summer, 2) diffuse-porous species, which produce only narrow diameter vessels and show a gradual decrease in vessel diameter between spring and summer vessels, and 3) semi-ring-porous species, which have an intermediate pattern of vessel diameter distribution (Panshin & de Zeeuw 1980, Lechowicz 1984). These differences in wood anatomy are related to the conductive capacity of the xylem both in terms of potential rate of water delivery to the leaf canopy (Zimmermann 1983) and also vulnerability to xylem cavitation under conditions of drought and as a result of winter freeze-thaw cycles (Zimmermann 1983, Wang, Ives & Lechowicz 1992). Wood anatomy is also related to the timing of spring budbreak: ring-porous species consistently leaf out later than diffuse-porous species because the former need to develop new xylem vessels to conduct water to the expanding buds, while the latter have functional xylem remaining from the previous season (Zasada & Zahner 1969, Chaney & Kozlowski 1977, Lechowicz 1984).

I measured maximum hydraulic conductivity, in relation to both branch cross-sectional area and leaf area supplied. These parameters give an indication of the tree's hydraulic efficiency. Percent loss of conductivity by late winter due to summer drought and winter freezing was calculated to examine the relationship between loss of conductivity and the timing of spring budbreak. Additional measurements of loss of conductivity in late summer would have allowed separation of the effects of summer drought and winter freezing, but were not feasible. Likewise, calculation of xylem vulnerability curves (plotting percent cavitation against xylem water potential) would have added useful information. Wood anatomical studies would have added direct evidence of phenotypic plasticity in wood formation and allowed greater explanation of the hydraulic conductivity data (*e.g.* low conductivity due to blocked xylem vessels *versus* narrow vessels); however, proper preparation and analysis of wood samples of a large number of species was beyond the scope of this study.

c. *Root traits.* Measurement of below-ground traits was not possible due to the experimental design of the study (there were several young trees in each m^2 plot, precluding the possibility of identifying which roots belonged to a given tree) and the lack of sufficient material for destructive harvests during the study. However, in an ideal situation a number of root traits would have been included (Table 3). These include root growth rates, fine root turnover rates, root-to-shoot ratio, and mycorrhizal associations. The phenomenon of hydraulic lift (the uptake of water by deep roots and its release into shallower zones of the soil) has been reported for *Acer saccharum* as well as aridland species (Dawson 1993); the prevalence of this phenomenon among mesic trees is unknown, but could be of considerable importance in plant and community water relations.

The lack of data on root traits necessitates the assumption that above-ground growth reflects the ability of the root system to support stem, branches and leaves (*i.e.* that above- and below-ground growth is balanced), as has been shown in other studies (Hilbert, Larigauderie & Reynolds 1991). The ability of the root system to transport water will be reflected in the stem hydraulic conductivity.

d. Growth and canopy architecture. Early seedling height growth is critical for tree seedlings in order to establish above-ground dominance in a competitive environment (Pacala *et al.* 1994, Kobe *et al.* 1994). Therefore, rather than the more traditional mass-based calculation of RGR, the relevant measure for tree seedlings is an RGR based on height growth. Hence, I calculated a composite index of RGR over five years that incorporated growth in plant height, stem basal diameter and total branch length (to take into account the variation in branch architecture, *i.e.* allocation to lateral growth *versus* height growth, among the species). As an indication of canopy architecture, I measured leaf area/branch length (leaf display index, LDI), which describes how leaves are displayed along a branch. For a whole tree measure of leaf display, I calculated canopy area/height and, for the 22 species data set (Chapter 3), canopy area/total stem and branch length. Wood density was measured as an estimate of investment in tensile strength (Niklas 1994) and resistance to pathogens (Loehle 1988) and windthrow (King 1986). It was not possible to measure whole plant biomass or proportional allocation to roots, stem and leaves because it was not possible to do complete plant harvests at the end of the five-year study. It was also not possible to study in detail the phenology of shoot growth, although observations were made of the time of terminal bud formation.

In summary, I have chosen a group of species broadly representative of the deciduous hardwoods of the northeastern North American forest. The traits I have included represent major aspects of the functional ecology of hardwood trees, including leaf physiology, foliar phenology, canopy architecture and hydraulic architecture. My focus is on the interactions among traits as they relate to whole tree response to water shortage and to relative growth rate under conditions of chronic intermittent drought. Below I briefly outline the contents of the three thesis chapters.

Outline of the three chapters

Chapter 1

Chapter 1 involves a comparison of four species: *Acer saccharum, Betula papyrifera, Fraxinus americana* and *Quercus rubra*. Each species is an important component of the eastern deciduous forest: *A. saccharum* is a mesic, shade tolerant dominant species, *B. papyrifera* is a shade intolerant, early successional species most common on dry-mesic sites, *F. americana* is a wet-mesic species of intermediate shade tolerance, and *Q. rubra* is a species of intermediate shade tolerance most commonly found on dry-mesic sites (Burns & Honkala 1990). *Acer saccharum* and *B. papyrifera* have diffuse-porous wood anatomy; *F. americana* and *Q. rubra* are ring-porous (Panshin & de Zeeuw 1980). The seedlings were grown under two contrasting water regimes: irrigated seedlings received ample water, while non-irrigated seedlings were subject to a regime of chronic intermittent water shortage. Traits measured included all those marked with * in Table 3 (except canopy area/total stem and branch length). The same individuals were used for all measurements. Responses of individual traits to water availability were examined along with the interrelationships among traits. Responses that were uniform across species were found in addition to species-specific responses. Leaf level traits showed the greatest plasticity in response to contrasting soil water availability.

Chapter 2

Chapter 2 examines in greater detail the interrelationships among the leaf traits that were found in Chapter 1 to show the greatest response to soil water availability. Chapter 2 consists of a detailed study of the gas exchange and other leaf traits of 22 species growing under conditions of chronic intermittent drought. Gas exchange was measured repeatedly over two growing seasons. This broad comparison across species growing under the same environmental conditions allows determination of the gas exchange patterns that exist in temperate deciduous hardwood trees and allows predictions to be made for species not included in the study. Some relationships among traits that have been reported in the literature were supported and previously uninvestigated relationships were found.

Chapter 3

Chapter 3 summarizes and combines the findings of the first two chapters by examining a whole suite of traits (marked with * in Table 3) as they relate to RGR (as in Chapter 1) in the 22 species that were the focus of Chapter 2. There are as yet no general expectations for whole tree response to water shortage; in this chapter, interspecific variation in RGR under conditions of chronic intermittent drought was found to be most closely related to canopy duration, but also to water use over the growing season.

Chapter 1

Functional ecology of tree growth under chronic drought

Abstract

Four species of deciduous hardwood trees (*Acer saccharum, Betula papyrifera, Fraxinus americana* and *Quercus rubra*) grown in an experimental nursery over a five-year period showed interspecific variation in response to chronic intermittent water shortage. *Betula papyrifera* had the highest RGR under irrigated conditions; this was related to a large canopy area relative to height, high gas exchange rates and a long canopy duration. Under non-irrigated conditions, *B. papyrifera* maintained a much higher RGR than the other species, despite a 42% reduction in growth. It had the greatest phenotypic plasticity of the four species, showing reduced allocation to leaves in response to water shortage and producing leaves of higher specific mass (SLM) that were able to maintain seasonal mean photosynthesis rate (A) at the same level as under irrigated conditions despite a significant reduction in seasonal mean stomatal conductance (g). Leaves of non-irrigated seedlings also senesced later, resulting in a longer canopy duration than under irrigated conditions. These responses indicate that *B. papyrifera* is geared toward maximizing carbon gain under both well-watered conditions and conditions of chronic intermittent drought. Rapid growth is necessary for this early successional short-lived species that colonizes disturbed sites, but generally persists for only one generation and, thus, must reach maturity and reproduce before being replaced by more shade tolerant species.

Acer saccharum, Fraxinus americana and *Quercus rubra* persist in late successional forests and under irrigated conditions attained similar moderate growth rates in the fairly high light environment of the experimental nursery. *Acer saccharum*, however, differed from the other two species in having low photosynthetic capacity (A_{max}) and lower seasonal mean gas exchange rates maintained

over a longer canopy duration. Under non-irrigated conditions, *A. saccharum* had reduced seasonal mean g, but maintained seasonal mean A at a rate similar to that under irrigated conditions. It, thus, had the least reduction in RGR (20%) under non-irrigated conditions. Its conservative physiology is well-suited for persistence over long periods in the low light environment of the forest understory.

In contrast to *A. saccharum*, *F. americana* and *Q. rubra* had gas exchange rates similar to those of *B. papyrifera* under irrigated conditions, but showed significant reductions in seasonal mean A under conditions of water shortage. In these ring-porous species, great reductions in g to reduce the risk of xylem cavitation, without the concomitant increase in photosynthetic capacity shown by *B. papyrifera*, resulted in reductions in RGR of 44% and 29% in *F. americana* and *Q. rubra*, respectively. *Fraxinus americana*, a species of wet-mesic habitats, was the most severely affected by water shortage.

In all species, leaf traits showed the greatest phenotypic plasticity between irrigated and non-irrigated seedlings. Leaf phenology, hydraulic conductivity and canopy architecture were less plastic. Although hydraulic conductivity did not respond to differences in soil water availability, it was correlated with maximum gas exchange rates indicating coordination between the physiological activity and transpirational demands of the canopy and the ability to supply the canopy with water to meet those demands. All species suffered >50% loss of conductive capacity by late winter due to xylem embolism (both irrigation treatments combined). However, percent loss of conductivity due to embolism was not related to maximum hydraulic conductivity nor to timing of spring budbreak. Thus, although wood anatomy is related to timing of spring budbreak in an evolutionary sense, proximate cues predominate in control of the actual date of budbreak under the conditions of chronic intermittent drought imposed in this study.

In addition to the species-specific gas exchange responses mentioned above, there were responses that were uniform across all species. All species had reduced seasonal mean g under non-irrigated *versus* irrigated conditions. This resulted in higher water use efficiency (WUE), both in the short-term (A/E) and also over the long-term ($\delta^{13}C$). Seasonal mean internal CO_2 concentration (c_i) was lower under non-irrigated conditions, but also more variable over the season. Variability in c_i (estimated as the standard deviation of c_i values from repeated measurements over the season) was highly correlated with WUE, suggesting that deviating from their c_i setpoint is an integral part of the response leading to increased WUE in these tree species. Thus, not only were leaf physiological traits more plastic than other traits, but the four species shared similar mechanisms of response at the leaf level, despite differences in other traits.

Introduction

Most trees in the temperate forests of North America encounter periods of water shortage during the growing season, commonly on an annual basis (Zahner 1968, Parker 1969, Hinckley *et al.* 1981, Kramer 1983). Tree growth is affected by even relatively mild soil water deficit (Fraser 1962, Zahner 1968, Sands & Mulligan 1990) and the availability of water is generally recognized as the major factor limiting the growth and distribution of trees (Parker 1969, Zimmermann & Brown 1971, Kozlowski, Kramer & Pallardy 1990). Tree species differ in their ability to withstand water shortage and this has long been associated with species distributions along a moisture gradient (Transeau 1905, Curtis 1959, Peet & Loucks 1977). There have been many studies of the responses of trees to water shortage. These responses are reflected in all aspects of tree structure and function, including growth (Bassett 1964, Zahner 1968, Hinckley *et al.* 1979) and architecture (Zimmermann & Brown 1971), hydraulic architecture (Kramer 1964, Bissing 1982, Woodcock 1989, Aloni 1991, Shumway, Steiner & Kolb 1993) and hydraulic conductivity (Tyree & Dixon 1986, Cochard & Tyree 1990, Khalil & Grace 1992), leaf phenology (Hinckley *et al.* 1979, Parker & Pallardy 1985, Kozlowski 1991), leaf structure (Abrams, Kubiske & Steiner 1990, Sands & Mulligan 1990) and gas exchange (*e.g.* Davies & Kozlowski 1977, Weber & Gates 1990, Abrams, Schultz & Kleiner 1990, Ni & Pallardy 1991, Ellsworth & Reich 1992a). These responses are dynamic and are expressed in both short-term responses to drought events and long-term adjustment to chronic water shortage (Sands & Mulligan 1990). The phenotypic plasticity of a population or species will be expressed in the extent to which individuals of that population or species are able to adjust to contrasting environmental conditions (Kuiper & Kuiper 1988), in this case, soil moisture regime. Not only may species differ in their ability to adjust to contrasting soil moisture regimes, *i.e.* differ in phenotypic plasticity (Bradshaw 1965, Schlichting 1986), but some of the traits involved in the overall response may show considerable plasticity, while other traits may be less plastic

(Schlichting 1989). The traits that are stable or less plastic may possibly constrain the responses of other traits (Bradshaw 1965, Watson & Casper 1984, Schlichting 1986, 1989). Such differential and presumably coordinated plasticity in traits is not well studied (Schlichting 1986, 1989). Thus, although leaf physiological responses to natural or imposed drought have been documented in numerous species (*e.g.* Briggs, Jurik & Gates 1986, Bunce, Miller & Chabot 1977, Kelliher & Tauer 1980, Parker & Pallardy 1985, DeLucia & Heckathorn 1989, Lechowicz & Ives 1989, Ellsworth & Reich 1992a), we know little about the effects of interactions with other traits on these responses. The extent of leaf-level response and its effect on growth will likely depend on other traits involved in plant carbon and water relations and the plasticity in those traits because a plant's response to water shortage is integrated at the organismal level (Dickson & Isebrands 1991).

The approach I chose to examine response to water shortage at the whole tree level was to compare the effects of chronic intermittent drought on leaf physiology, leaf phenology, hydraulic conductivity and aspects of above-ground growth across four co-occurring hardwood species: *Acer saccharum* Marsh., *Betula papyrifera* Marsh., *Fraxinus americana* L. and *Quercus rubra* L. These species differ in physiology, phenology, morphology and hydraulic architecture yet naturally co-occur as saplings on successional sites (Braun 1950, Lambert & Maycock 1968), including the area surrounding my study site (Maycock 1961, *personal observation*). I grew the species from seed in a common experimental nursery with and without chronic intermittent water shortage. I examined the phenotypic plasticity of individual traits and also investigated the interactions among these traits and their effects on plant growth. The broad purpose of the present paper is to examine coordinated responses to water shortage at the sapling level in these four tree species. Specifically, I 1) determine which traits respond to chronic intermittent water shortage (*i.e.* which traits are plastic), 2) examine interspecific variation in responses to water shortage (interspecific variation in plasticity), 3) examine the correlations among these traits, and 4) examine how these responses and correlations are related to growth over a five-year period.

The traits I have chosen to investigate are related to tree carbon and water relations and have been shown to respond to water availability and/or may constrain the responses of other traits. These traits are discussed below starting with traits deemed least phenotypically plastic and proceeding to more plastic traits. The expected responses of individual traits are summarized in Table 1, which should be referred to while reading the following literature review.

The inherent ability of a tree to deliver water to its leaf canopy depends in large part on its hydraulic architecture, the size and frequency of the water-conducting conduits (Zimmermann 1983). Although wood anatomy may vary somewhat among individuals within a species (Metcalfe & Chalk 1983) and also depending on the location sampled within the tree (Zimmermann 1978, Creber & Chaloner 1984), I regard wood anatomy as a relatively fixed and non-plastic trait for the following reasons. First, wood can often be identified to the generic, if not specific, level based on anatomical traits (*e.g.* Greguss 1945, Core, Côté & Day 1979, Panshin & de Zeeuw 1980). Second, wood anatomy is relatively conservative in evolutionary terms, basic anatomical traits often being retained at the generic or even higher taxonomic levels (Metcalfe & Chalk 1983). From another perspective, wood anatomy is not plastic in the sense that once xylem vessels have formed, they are unchangeable, unlike leaf nitrogen content or stomatal conductance, for example.

The major short-term effect of water shortage on hydraulic architecture is the cavitation of xylem conduits, which may occur when transpirational demand exceeds the ability of the xylem to deliver water to the canopy (Zimmermann 1983). A break in the transpirational stream in a xylem vessel is quickly filled with air, causing an embolism which prevents further water transport through that vessel. Although embolisms may dissolve, cavitation generally is thought to permanently block the

Table 1. Expected responses of mesic hardwood trees to soil water shortage. Time indicates the approximate duration of water shortage that will induce the response.

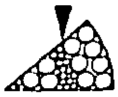
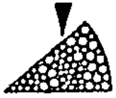
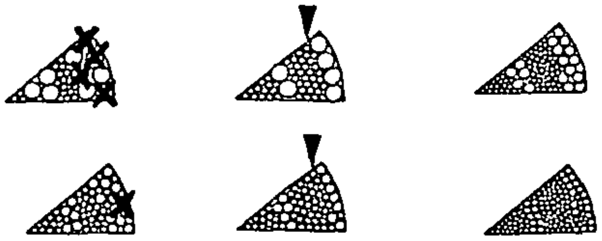
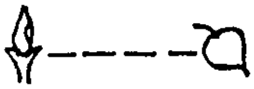
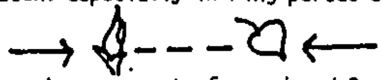
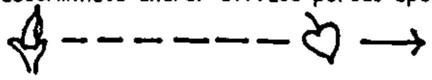
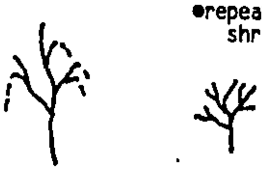
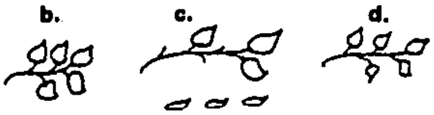
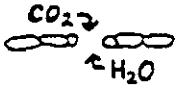
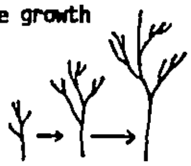
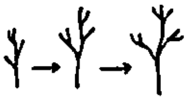
Trait	short-term --------> Response --------> long-term
time:	●hrs ●days ●weeks ●months ●years
Xylem vessels ring-porous  diffuse-porous 	● a. loss of conductivity due to embolism[1] - less in diffuse-porous species?[1,2] ● b. early transition to latewood[3,4] ● c. smaller diameter vessels?[3,5] a. cavitation b. less earlywood c. smaller vessels 
Spring budbreak 	●delayed? ●unaffected[6]
Fall senescence 	●premature [7,8] - especially in ring-porous species? ●delayed, especially in indeterminate species?
Canopy duration 	●shorter due to early senescence? and, possibly, delayed budbeak? especially in ring-porous species?  ●longer, to compensate for reduced C gain, especially in indeterminate and/or diffuse-porous species? 
Apical growth and canopy architecture 	●branch abscission[9] ●repeated dieback, shrubby appearance[10] 
Leaf development and leaf display index 	●leaf expansion ceases, leaves smaller[3,11] ● smaller leaves[11,12] ● a. decrease in LDI due to leaf abscission? ● b. LDI increases? - due decrease in extension growth[3] ● c. LDI decreases due to continued early leaf abscission? ● d. LDI unchanged? - decreased shoot extension, but smaller leaves[3]  

Table 1 (continued)

Trait	short-term --------> Response --------> long-term				
time:	●hrs	●days	●weeks	●months	●years
Stomatal conductance and photosynthesis  	●decreased[13,14] ●unchanged[15]			●low ●high[16,17]	
Water use efficiency 	●increased[18] ●unchanged ●decreased[19]			●high[20] ●low[21]	
Leaf nitrogen concentration 		●a. increased if C gain reduced more than nutrient uptake[22] ●b. decreased if N uptake more restricted than C gain[23] a. 		b. 	
Specific leaf mass 			●increased in indeterminate species that produce new leaves 	●increased in all species[10,12] 	
Tree growth 				●reduced[9,11] 	

References:

1. Zimmermann 1983.
2. Wang et al. 1992.
3. Zahner 1968.
4. Creber & Chaloner 1984.
5. Aloni 1987.
6. Hinckley et al. 1979.
7. Parker 1969.
8. Parker & Pallardy 1985.
9. Sands & Mulligan 1990.
10. Zimmermann & Brown 1971.
11. Kozlowski 1991.
12. Witkowski & Lamont 1991.
13. Davies & Kozlowski 1997.
14. Parker & Pallardy 1991.
15. Tobiessen & Kana 1974.
16. Abrams, Kubiske & Steiner 1990.
17. Ni & Pallardy 1991.
18. Reich, Walters & Tabone 1989.
19. Abrams, Schultz & Kleiner 1990.
20. Field, Merino & Mooney 1983.
21. Bunce, Miller & Chabot 1977.
22. van den Driessche 1974.
23. Chapin 1991.

vessel (Milburn 1991), reducing water transport to the canopy. Within a species, larger vessels are more susceptible to cavitation than vessels of smaller diameter (Tyree & Dixon 1986). This generalization may not hold across species because other anatomical features, especially the size of the vessel pit membrane pore, also influence susceptibility to cavitation (Tyree & Sperry 1989). However, among dicotyledonous trees, ring-porous species, which produce very large diameter xylem vessels in the spring as well as narrow vessels in summer are thought to be at greater risk of losing xylem function due to drought-induced embolism than diffuse-porous species, which produce only narrower vessels (which gradually decrease in size from spring through summer), because the much wider vessels are likely to cavitate more readily (Zimmermann & Brown 1971, Zimmermann 1983). The advantage of wide vessels is that when water is available, they are much more efficient at water transport because the hydraulic conductivity of a vessel is related to its radius raised to the fourth power according to Poisseuille's law (Zimmermann 1983). Thus, even small increases in diameter greatly increase conductivity. Consequently, ring-porous wood anatomy is thought to be a more efficient, but "riskier" hydraulic system (Zimmermann 1983). In general, trees with ring-porous wood anatomy are expected to suffer greater percent loss of conductive function under drought conditions than diffuse-porous trees (Lechowicz 1984). A comparison of 35 North American hardwood tree species by Wang, Ives & Lechowicz (1992) found that ring-porous species did have greater loss of conductivity due to embolism caused by late-summer drought and winter freeze-thaw cycles than did diffuse-porous species, supporting this expectation.

Comparisons of the extent of water-stress induced cavitation have been made between *Acer saccharum* and two conifers (Tyree & Dixon 1986) and among four diverse species (Tyree & Sperry 1988). Khalil and Grace (1992) have examined cavitation under drought and well-watered treatments in seedlings of *Acer pseudoplatanus*. Shumway, Steiner and Kolb (1993) investigated various aspects of hydraulic architecture in *Quercus rubra* and *Liriodendron tulipifera* seedlings grown under different light and soil moisture regimes, but did not examine percent loss of conductivity *per se*. In spite of growing interest in hydraulic conductivity and drought-induced cavitation, I know of no study to date, other than the current one, that compares loss of conductivity across species under contrasting soil moisture conditions.

Summer drought can also affect wood formation, hastening the transition from the production of earlywood to the production of latewood (Zahner 1968, Creber & Chaloner 1984, Zobel & van Buijtenen 1989) and determining how much latewood is produced (Zahner 1968, Woodcock 1989, Zobel & van Buijtenen 1989). Limited studies on ring-porous species suggest that development of the wide earlywood vessels is usually completed before summer droughts typically occur and, thus, the formation of earlywood is generally not affected (Zahner 1968, Woodcock 1989). However, the paucity of data does not allow us to exclude the possibility that fewer large vessels are formed as a result of early season drought or severe drought in the previous year. If early transition to latewood production does occur, the effect on hydraulic conductivity could be substantial, especially in ring-porous species. For both ring-porous and diffuse-porous species, a high proportion of smaller latewood xylem conduits (as reported for conifers on dry sites by Zahner (1968)) would serve to decrease the risk of cavitation while maintaining adequate water transport.

On the longer term, the impact of water shortage on xylem morphogenesis is little understood. Aloni (1987) has hypothesized that narrower vessels will be produced under environmental conditions that limit growth, including drought conditions. Vessel diameter is thought to be determined by the auxin gradient established through the region of differentiation (Aloni & Zimmermann 1983). Basipetal flow of auxin from the leaves to the roots creates a gradient of decreasing auxin concentration. The distance from the leaves to the differentiating cells determines the concentration of auxin the cells experience. High concentrations result in rapid cell differentiation. Once the secondary wall is laid down, no further expansion occurs; hence, narrow vessels are formed when differentiation is rapid. A lower auxin concentration causes slower differentiation of wider vessels. This hypothesis was developed to explain the general trend of increasing xylem conduit diameter from branches to stems to roots (Aloni & Zimmermann 1983). Aloni (1987) expanded the hypothesis to include environmental effects on xylogenesis. Stunted growth due to a stressful environment results in a shorter distance between the leaves and lower stem which in turn weakens the gradient of auxin flowing from the leaves through the branches and stem. A weak gradient results in a high auxin concentration in regions basal to the leaves which results in rapid vessel differentiation and, thus, produces narrower vessels than occur under conditions that are not limiting to growth (Aloni 1987). There is some evidence that trees do produce narrower vessels on more xeric sites; Zahner (1968) found the earlywood vessels of mature *Quercus rubra* trees growing on a dry site to be 10-20% smaller in diameter than those of trees growing on moist sites. However, *Populus euphratica* in Israel and *Adesmia horrida* in Argentina produce diffuse-porous wood on moist sites and ring-porous wood on dry sites (Aloni 1991). Thus, there is contradictory evidence and the extent of morphogenetic effects in different species is largely unknown and unquantified. If there are differential morphogenetic effects among species, the impact of chronic drought on the hydraulic conductivity of ring-porous *versus* diffuse-porous species may differ from the cavitation effects of shorter-term drought events. In spite of possible morphogenetic effects, I expect to find less phenotypic plasticity in hydraulic architecture than in other traits, such as gas exchange. This proposed lack of plasticity may constrain the degree of plasticity of other traits in response to water shortage (Tyree & Sperry 1989).

In addition to its importance in water transport, wood anatomy is also related to the timing of spring budbreak and, hence, the potential seasonal duration of carbon gain. Throughout temperate forests in Europe and Asia as well as in eastern North America, there is a consistent trend for ring-porous species to leaf out later than diffuse-porous species (Lechowicz 1984). Due to loss of xylem function resulting from embolism caused by summer drought and winter freeze-thaw cycles, ring-porous species must produce new xylem vessels before water can be delivered to the buds (Zasada & Zahner 1969, Lechowicz 1984). Therefore, they break bud later than diffuse-porous species, which have functional xylem remaining from the previous season or seasons (Chaney & Kozlowski 1977). While ring-porous species depend primarily on the outermost annual ring of sapwood for water transport, in diffuse-porous species the vessels of several prior-year xylem increments conduct water (Chaney & Kozlowski 1977).

Little has been reported concerning the effects of water shortage on the timing of spring budbreak. Droughts rarely occur early in the season, but it is possible that spring drought may slow or delay budbreak, as did a severe late frost in Illinois (Bell & Johnson 1975). Hinckley *et al.* (1979) found little difference in timing of budbreak in *Quercus alba* in the year following a severe drought compared to other years. It is, however, possible that previous summer and/or winter drought might delay budbreak, especially in diffuse-porous trees if they suffer increased xylem cavitation under drought and consequently have to produce new xylem, as do the ring-porous species, in order to support a full canopy. On the other hand, if drought causes reduced growth and, hence, narrower vessels according to Aloni's hypothesis (1987) or if proximate controls of budbreak are overriding, budbreak may not be affected.

Although little is known about drought effects on budbreak, drought is known to cause premature leaf abscission (Parker 1969, Parker & Pallardy 1985), which will reduce canopy duration and, hence, potential seasonal carbon gain. Increased cavitation as summer drought progresses may cause the leaves of ring-porous species in particular to senesce early. Leaf abscission would decrease the transpirational demand of the canopy and possibly protect the tree from further xylem vessel cavitation (Zimmermann 1983, Tyree & Sperry 1988). However, if a tree is able to retain its leaves during drought, delayed senescence may in part compensate for lower net assimilation rates during the dry period.

Soil water availability also influences growth form. Extreme drought caused terminal shoot dieback in *Q. alba* (Hinckley *et al.* 1979) and may cause branch abscission in some species, such as *Eucalyptus* spp. (Sands & Mulligan 1990). The effects of water shortage on shoot growth depend partly on the species' seasonal pattern of extension growth (Spurr & Barnes 1980). Late summer drought will have little effect on shoot growth of determinate species, which complete their extension growth relatively early in the growing season. Trees with indeterminate growth, in which shoots grow for a greater part of the summer, are more likely to show reduced extension growth as a result of current season drought (Zahner 1968). Long-term effects of water shortage are such that trees growing in semi-arid regions or on xeric sites are often shrubby in appearance due to reduced extension growth and early loss of apical control resulting from repeated dieback of branches (Zimmermann & Brown 1971). Thus, growth form is fairly plastic, but within the genetic constraints of branching pattern for each species (Hallé 1978). However, it is fixed in the sense that once branches have developed, form cannot be readily changed unless branches abscise. Since branches are longer-lived organs than leaves, the effects of drought on branch development are more long-lasting than effects on leaves. Branch development is, therefore, considered less plastic than leaf development.

In addition to modifying overall growth form and reducing extension growth, water shortage may alter the display of leaves in the canopy, which influences the efficiency of light capture (Canham 1988). Leaf abscission will decrease the leaf area per unit branch length (leaf display index, LDI (Canham 1988)), resulting in less photosynthetic area for a given investment in woody tissue. This is adaptive in that it also reduces transpirational water loss, but at the expense of carbon gain. While current-year drought will have little effect on the leaf display of determinate species, apart from effects of leaf abscission, water shortage during the preceding summer may reduce the number of leaf primordia that form in the winter bud (Zahner 1968). Current-year drought during the period of extension growth of indeterminate species may result in fewer and smaller leaves spaced more closely along the branch (Zahner

1968). Thus, on the longer term, LDI would increase if drought reduced stem extension growth more than leaf area. However, since drought may also result in the production of smaller leaves (Zahner 1968, Kozlowski 1991, Witkowski & Lamont 1991), LDI may remain unchanged. The effects of water shortage on LDI and those on hydraulic conductivity may influence leaf specific conductivity (LSC, Zimmermann (1983)), the hydraulic conductivity per unit leaf area supplied by the xylem. Shumway, Steiner & Kolb (1993) found decreased LSC in seedlings of *Quercus rubra* and *Liriodendron tulipifera* grown under drought-stressed conditions for two years.

Of the leaf level responses to water shortage, stomatal regulation is considered to be the most important short-term and reversible mechanism for preventing excessive water loss (Sands & Mulligan 1990). Many tree species reduce stomatal conductance (g) in response to short-term water shortage (Davies & Kozlowski 1977, Hinckley *et al.* 1979, Parker & Pallardy 1991, Ellsworth & Reich 1992a). This generally results in increased water use efficiency (WUE, the ratio of carbon assimilated, A, to water lost through transpiration, E) (Sands & Mulligan 1990), but reduced photosynthetic gain (Hinckley *et al.* 1981, Ranney, Whitlow & Bassuk 1990). However, other species maintain stomatal conductance under conditions of water shortage and thereby maintain photosynthesis at the expense of water loss (Bunce, Miller & Chabot 1977, Hinckley *et al.* 1979, Kelliher & Tauer 1980, DeLucia & Heckathorn 1989, DeLucia & Schlesinger 1991, Ni & Pallardy 1991). I hypothesize that whether a species shows tight stomatal regulation (a "water-saver" strategy) or maintains photosynthesis in spite of water loss (a "water-spender" strategy) will be determined by its hydraulic architecture and the relationship between water-conducting capacity and the leaf area needed to be supplied (LSC), as well as by external factors such as the spatial and temporal distribution of water availability and competition with other plants for the same water supply (Cohen 1970, Bunce, Miller & Chabot 1977, Cowan 1982). I expect ring-porous species to show tighter stomatal regulation to avoid catastrophic xylem dysfunction due to cavitation (Tyree & Sperry 1988), while diffuse-porous species may be able to maintain gas exchange to much lower levels of soil water availability. Species with a greater conductive capacity per unit leaf area may also be able to maintain gas exchange longer during drought than species with relatively low leaf specific conductivity. Although photosynthetic capacity shows a genetic component (Ceulemans, Impens & Steenackers 1987, Parker & Pallardy 1991, Kubiske & Abrams 1992), gas exchange traits are considered plastic since photosynthesis and stomatal conductance can change over the course of minutes (Chazdon & Pearcy 1986, Knapp & Smith 1987).

In addition to short-term responses, trees growing under conditions of chronic water shortage may also alter their photosynthetic processes and leaf structure in more permanent ways. Leaf nitrogen concentration (N) has been shown to increase under drought stress conditions (van den Driessche 1974). With increasing N per unit leaf area, the proportion of total leaf N in soluble protein (primarily Rubisco) increases (Evans 1989). Increased investment of leaf N in Rubisco may enhance the "capture" of CO_2 in the substomatal cavity when the latter is limited due to partial stomatal closure. A similar type of compensation is seen in the increased leaf N found in plants at high altitude, where atmospheric CO_2 partial pressure, and, hence, internal CO_2 partial pressure, are lower (Körner 1989, Körner, Farquhar & Wong 1991, Hilbert, Larigauderie & Reynolds 1991). Thus, increased N may allow the greatest uptake of CO_2 possible for a given loss of water (Reich, Walter & Tabone 1989). Specific leaf mass (leaf mass per unit area, SLM) is related to insolation regime: sun leaves typically have higher SLM than shade leaves (Jurik 1986a, Ellsworth & Reich 1992b). SLM is usually discussed as an adaptation to increased irradiance and heat load, but high SLM also serves to reduce the transpiring surface area of the leaf and, thus, can be an effective means to reduce transpirational water loss in open areas, such as the experimental nursery, where evaporative demand is generally higher than under a closed canopy (Nobel 1991). When growing under conditions of limited water supply, leaves often have reduced surface area and increased thickness (Zimmermann & Brown 1971). For example, smaller and thicker leaves with higher

SLM were found in *Fraxinus pennsylvanica* populations from more xeric sites compared to those of trees from mesic sites (Abrams, Kubiske & Steiner 1990).

General expectations for tree response to chronic drought.

The considerations discussed above indicate that the overall response of a tree to water shortage depends on a whole suite of interrelated traits. Individual traits may or may not respond to water shortage. Table 1 shows a variety of reported or hypothesized responses for the traits considered in this study; no two species are likely to respond in exactly the same manner. To survive and grow under conditions of chronic intermittent water shortage, leaf physiological responses must be appropriate for the tree's hydraulic architecture (Milburn 1991) and are likely to be limited by the phylogenetic constraints of wood anatomy (Tyree & Sperry 1989, Tyree & Ewers 1991). Although the importance of leaf physiological responses in determining the ability of a species to withstand water shortage has received much attention (*e.g.* Bunce, Miller & Chabot 1977, DeLucia & Heckathorn 1989, Abrams, Schultz & Kleiner 1990), hydraulic architecture may be of equal importance (Tyree & Ewers 1991) and other traits may also be involved.

In spite of the various mechanisms to reduce the negative effects of water shortage (*e.g.* stomatal closure to reduce leaf water loss or leaf abscission to decrease canopy water loss and xylem cavitation), chronic drought generally will reduce carbon gain and, thus, reduce tree growth (Zahner 1968, Kozlowski 1991). However, there will be variation among species in the extent of growth reduction. In general, I expect trees grown under chronic drought to have reduced stomatal conductance and increased WUE compared to their well-watered counterparts (*e.g.* Davies & Kozlowski 1977, Sands & Mulligan 1990, Parker & Pallardy 1991; but see Tobiessen & Kana 1974, Abrams, Schultz & Kleiner 1990). I suspect that this response is likely to be particularly strong in species with ring-porous wood anatomy as an adaptation to avoid loss of hydraulic conductivity. I also expect ring-porous trees to be more likely to show leaf abscission under drought conditions (Parker 1969, Parker & Pallardy 1985) for the same reason. However, production of narrower vessels under drought conditions, whether due to early transition to latewood production (Zahner 1968, Creber & Chaloner 1984) and/or the effects of growth form on xylogenesis (Zahner 1968, Aloni 1987) may reduce the risk of cavitation. I suggest that trees that are able to maintain gas exchange under drought, albeit at lower rates, may have a longer canopy duration than their well-watered counterparts, which would partially compensate for reduced carbon gain due to the lower photosynthesis rates. Diffuse-porous species would seem to be the better candidates for this strategy.

That there is more than one way to successfully respond to water shortage is evidenced by the wide variety of tree species found in temperate forests in which seasonal drought occurs. Differences in plasticity of different traits (Bradshaw 1965) and among species is likely to lead to different ecological strategies (*i.e.* species constrained in the same ways, for example, by hydraulic architecture, will tend to show similarities in overall response). The existence of these different strategies allows species with different physiological, phenological and morphological traits to co-occur in temperate deciduous hardwood forests. However, some strategies will be more successful under conditions of chronic water shortage than others. The effectiveness and coordination of all aspects of response and adaptation will determine the growth realized under stress conditions. Relative growth rate under drought *versus* well-watered conditions can, therefore, be considered an indication of the extent to which responses are truly adaptive in the sense of mitigating growth losses rather than merely indicating suboptimal performance under stress conditions.

The four species chosen for this study differ in a number of the traits discussed above and, thus, are likely to vary in overall response to water shortage. *Acer saccharum* and *B. papyrifera* are diffuse-porous, while *F. americana* and *Q. rubra* have ring-porous wood anatomy (Core, Côté & Day 1979). *Betula papyrifera* has indeterminate shoot growth (Marks 1975). *Fraxinus americana* and *Q. rubra* are determinate species that may produce additional growth flushes under favourable conditions, especially when young (Borchert 1976). *Acer saccharum* has also been characterized as a determinate species (Marks 1975), although vigorous leader shoots may show an indeterminate growth pattern (Steingraeber 1982). The four species also differ in physiological traits: *A. saccharum* has low photosynthetic capacity compared to many other hardwood trees (Walters, Kruger & Reich 1993, Ceulemans & Saugier 1991, Jurik, Weber & Gates 1988), *B. papyrifera* and *Q. rubra* have relatively high photosynthetic capacity (Walters, Kruger & Reich 1993, Jurik, Weber & Gates 1988), while intermediate values have been reported for *F. americana* (Bazzaz & Carlson 1982, Jurik, Weber & Gates 1988, Ceulemans & Saugier 1991). Thus, these species are likely to demonstrate some of the possible patterns of overall response to water shortage found in deciduous hardwood trees.

There are as yet no general theories or expectations of whole tree response to water shortage. Recent studies linking leaf responses to other traits such as hydraulic architecture and conductivity (Milburn 1991, Tyree & Ewers 1991, Shumway, Steiner & Kolb 1993), leaf phenology (Koike 1987) and leaf lifespan (Kikuzawa 1991, Reich, Walters & Ellsworth 1991b, 1992) demonstrate considerable interest and progress in this area. In this paper, I examine the plasticity of a number of physiological, phenological and morphological traits in response to water shortage and the resulting growth over a five-year period with the aim of elucidating patterns of whole tree response.

Materials and Methods

1. Experimental tree nursery.

An experimental tree nursery was established at the Mont St. Hilaire Research Centre of McGill University (45°32'N, 73°8' W; 140 m). In November 1984, seed from two provenances of *Acer saccharum*, *Betula papyrifera*, *Fraxinus americana* and *Quercus rubra* was planted. The seed was obtained from various sites in eastern Canada and northeastern USA (Appendix I). Each species/provenance combination was planted in a pair of m^2 plots, consisting of raised beds of 10 cm of commercial topsoil on top of postglacial sand deposits that had been bulldozed level and free of vegetation to establish the experimental nursery. These sands were laid down as beaches of the Champlain Sea that inundated this region during the retreat of the Wisconsinan ice sheet (Occhietti 1989). The nutrient characteristics of the top 0-20 cm of sand were as follows: pH 7.53; Ca 490.3, Mg 17.5, K 41.5 and P 39.5 $\mu g\ g^{-1}$ (based on four 250 g samples taken from around the nursery on July 8, 1993 and air dried before analysis). Thus, the artificial A horizon (commercial topsoil) and the underlying sandy B horizon together comprise a reasonably good soil, except for its high drainage and poor water-holding capacity. In summer 1985, all plots were irrigated and fertilized (N-P-K: 11-41-8 in spring, 20-8-20 in early summer, 8-20-30 in late summer, Plant Products Co., Bramalea, Ontario) to enhance seedling establishment. Commencing in 1986, one plot of each species/provenance pair was irrigated, while the other received only natural rainfall. The irrigated plots were watered with lawn sprinklers for 2-4 hours whenever 2-5 days had passed without rain and the soil felt dry to about 6 cm depth. The non-irrigated plots were watered only when necessary to prevent tree mortality (judged by severe wilting and initiation of leaf fall in at least one plot), once each summer. At such times, all non-irrigated plots were watered equally with lawn sprinklers for 2-3 hours. The irrigation regime was continued for the duration of the study. All plots continued to be fertilized with slow-release fertilizer (Osmocote 14-14-14, Sierra Chemical Company, Milpitas, California, USA) once each spring and with two applications of micronutrients and 10-10-10 (Plant Products Co., Bramalea, Ontario) in late spring-early summer. The nursery was located in an open area and with the deep sand substrate this provided an environment with less moisture available than the seedlings' natural regeneration sites within the forest and along the forest edge. Consequently, although the non-irrigated plots did receive natural rainfall, lack of irrigation resulted in periods of water shortage in these plots (see Results). All four species were regenerating naturally in the vicinity of the nursery on similar sandy soils (Maycock 1961, *personal observation*).

In each of 16 plots (4 species x 2 provenances x 2 treatments), three trees were chosen randomly and individually tagged. These three trees were used for all measurements described below. Other trees were thinned from the plots as necessary to prevent overcrowding.

2. *Soil moisture measurements.*

One m^2 plot with no trees was established at the centre of the experimental nursery as a reference plot for soil moisture measurements. At each of three locations in this reference plot, four soil psychrometers (model PCT55, Wescor, Logan, Utah, USA) were installed, two at 15 and two at 30 cm depth. The means of the two psychrometers at each depth and location were used in analyses where possible (five psychrometers proved to be unreliable and were excluded from analysis). For measurement of soil moisture by the neutron method (Greacen 1981), three aluminum neutron probe access tubes were installed close to the psychrometer locations in the reference plot. An access tube was also installed in each study plot used for gas exchange measurements (see below). Psychrometer measurements were taken in late afternoon or early evening (to minimize temperature gradients through the soil) using a Wescor psychrometric microvoltmeter (model HR-33T). Prior to installation, the psychrometers were individually calibrated as outlined in Appendix II. Neutron probe measurements were taken at 15 and 30 cm depths in the study plots and the reference plot with a CPN Model 503DR Hydroprobe (Pacheco, California, USA) in conjunction with each gas exchange assay. To obtain equations to convert the study plot neutron counts to soil water potential, neutron counts taken in the reference plot were regressed on psychrometer readings for the nine days that had both psychrometric and neutron probe data (for 15 cm depth, the least squares regression $r^2 = .28$, $p= .02$; for 30 cm depth, $r^2 = .45$, $p= .0001$; Proc REG, SAS Institute, Inc., 1985a).

3. *Experimental protocols.*

a) Growth and canopy architecture. I measured relative growth rate (RGR), rather than simply comparing height growth at a single point in time (*e.g.* 5 years), as the former is a better measure of response to water regime and allows easier comparison with other studies. Since the species differed in canopy architecture, I calculated an index of relative growth rate incorporating measurements of growth in height, stem basal diameter and total branch length. Stem basal diameter was measured with calipers in two orthogonal directions and the measurements averaged. The location of the calipers was marked with paint so that repeated measurements were made at the same position. Vertical height from the ground surface was measured with a tape to the base of the terminal bud on the main stem or tallest branch. Diameter and height measurements were made each spring and fall from 1986 to 1990. A five-year relative growth rate (RGR) was calculated for both diameter and height: RGR(di)=(ln diameter 1990/ln diameter 1985)/5 , RGR(ht)=(ln height 1990/ln height 1985)/5 (Evans 1972). In May 1991, the total length of lateral branches on each tree was measured, excluding new 1991 growth. This value was used to calculate a five-year branch RGR: RGR(br)=(ln branch length 1990/5); the total branch length in 1985 was 0.0 cm since it was the seedlings' first growing season. I submitted these three values to a Principal Component Analysis (Proc FACTOR, SAS Institute Inc., 1985a) to obtain an RGR index based on diameter, height and branch growth: RGRINDEX = factor1 + 2.0 (to make all values positive). Details are given in Appendix III.

Total canopy area was calculated from a total leaf count in August 1988 and the mean leaf area for each tree (calculated from the leaf samples described below). Total canopy leaf area/tree height was calculated as a measure of whole tree leaf display and canopy architecture. Architecture at the branch level was estimated by a leaf display index, LDI (Canham 1988), calculated for each branch sampled for hydraulic conductivity measurements as the total leaf area of the branch divided by its total length.

b) Hydraulic conductivity and wood density. In late August 1990, branches of one centimeter diameter (often the main stem) were marked for winter harvest for hydraulic conductivity measurements. All leaves beyond the segment to be assayed for hydraulic conductivity were removed and total leaf area was measured in order to calculate leaf specific conductivity (LSC), the maximum conductivity (kg MPa^{-1} m^{-1} s^{-1}) per m^2 leaf area supplied. This definition of LSC differs from that of Zimmermann (1983), who defined LSC as the hydraulic conductance per unit fresh weight of leaves supplied, but is more relevant to areal losses in transpiration than is foliar mass. In March 1991, the marked branches were harvested, wrapped in plastic and kept frozen in a lab freezer. At this time they had been subjected to several natural freeze-thaw cycles as well as summer drought. This timing of collection was chosen in order to examine conductive capacity available for exploitation of the relatively high soil water availability in early spring and the relationship between hydraulic conductivity and timing of spring budbreak. The samples were assayed in completely random order. Each branch was removed to a refrigerator overnight, allowed to thaw 30 min. in water, cut to a 35 cm section and then, while immersed, trimmed to a 15 cm section, which was used for the conductivity measurements. The

15 cm section was attached to an apparatus similar to that described by Sperry, Donnelly & Tyree (1988a). Lateral branch stubs were sealed with wax and the branch segment was allowed to stabilize for 2 min. before the initial measurement. Hydraulic conductivity was assayed using a version of the technique developed by Sperry, Donnelly & Tyree (1988a) as modified by Wang, Ives & Lechowicz (1992). Conductivity was calculated as the slope of the regression of 10 consecutive water mass measurements (recorded manually at exactly 60 s intervals) on time. After measurement of initial conductivity, the sample was flushed with demineralized water passed through a micropore filter for 30 min. at a pressure of 172 kPa to remove any embolisms. Hydraulic conductivity was then assayed again to obtain a measure of maximum conductivity. Actual assays were conducted using degassed water, filtered through a micropore filter, and acidified to 1.2 - 1.9 pH with oxalic and hydrochloric acid. Percent reduction in conductivity due to embolism was calculated as [1-(preflush conductivity/postflush conductivity)] * 100. In two branches, conductivity was reduced after flushing. This was most likely due to the plugging of vessels by small particles or microorganisms already in the branch that were not flushed out. Therefore, in these cases the percent reduction in conductivity due to embolism was set to zero. The diameters of both ends of the segment were measured and used to estimate the mean cross-sectional area of the assayed segment. The reported maximum specific conductivity (MSC) is adjusted for differences in total cross-sectional area. Note that this is not a measure of conductivity for a standardized cross-sectional conducting area since it does not take into account species differences in the percent of branch cross-sectional area occupied by xylem vessels (Zimmermann 1983) or the loss of conductive function in older wood which varies among species (Chaney & Kozlowski 1977). However, it does reflect the conducting capacity per unit investment in woody tissue for branches of comparable size. The segment assayed and the rest of the branch were then dried and dry wood density determined by displacement in water.

c) Leaf phenology. Observations were made every 1-3 days during the period of leaf emergence in 1987 and 1988. Spring budbreak was recorded as the day the bud scales had totally separated and the leaves actually began to emerge and unfold. From late August through October, observations of leaf colouration and leaf fall were made at 3-5 day intervals. Since neither the earliest colouring of leaves nor the final dehiscence of all leaves provided a repeatable measure for cross-species comparisons, I used a median date of senescence for each tree based on the progression of both leaf colour and dehiscence as the date of fall senescence in 1987 and 1988. The mean date of budbreak and fall senescence for the two years is reported. For each year, canopy duration (days) was calculated as the date of senescence - date of budbreak; the two-year mean canopy duration is reported.

d) Leaf samples for SLM, leaf N and $\delta^{13}C$. Leaves were collected from each tree in early September 1988 and 1989 for determination of specific leaf mass (SLM) and leaf nitrogen (N). Leaf area (blade area excluding rachis and petiole) was measured using a LI-3100 Area Meter (LI-COR, Inc., Lincoln, Nebraska, USA). The leaves were oven-dried at 70°C, weighed, and SLM calculated for each tree as the total leaf weight/total leaf area of the leaves sampled for that tree. Leaf nitrogen (N) concentration was then determined using a standard Kjeldahl procedure. Subsamples of 0.1000 g dried leaf tissue were ground through a 40-mesh screen and digested using 5 ml of concentrated H_2SO_4 with 0.5 g K_2SO_4 and 6 selenium catalyst granules. The digest was neutralized and N concentration assayed colorimetrically with a Bausch and Lomb Spectrometer 21 (Bausch and Lomb Optical Company, Rochester, New York, USA) after Nesslerization (Middleton 1960). Nitrogen per unit leaf area (N_{area}) was calculated from SLM and mass-based N (N_{mass}, % N). The SLM and leaf N values reported are the means of the 1988 and 1989 values.

The dried 1989 leaf samples were subsampled for carbon isotope discrimination analysis, which was conducted according to the in-vial combustion technique described in Ehleringer and Osmond (1989). Carbon isotope discrimination is related to integrated internal CO_2 concentration (c_i) (Farquhar, O'Leary & Berry

1982) and is a measure of long-term, integrated water use efficiency (WUE), provided the plants and/or species being compared do not differ in vapour pressure deficit (vpd) experienced or in the proportion of carbon gain that is lost through respiration (Farquhar & Richards 1984).

In many temperate hardwood species, the majority of leaves are produced in a single spring flush from stored carbon reserves (Kozlowski 1964, Dickson 1991). In some species, including *F. americana* and *Q. rubra*, additional growth flushes may be produced under favourable conditions, particularly in young trees (Borchert 1976); however, even in such cases the majority of leaves are likely to originate in the first flush. *Acer saccharum* has been characterized as a determinate species (having a single growth flush) along with *F. americana* and *Q. rubra* (Marks 1975), although Steingraeber (1982) has reported the production of neoformed leaves in vigorous leader shoots. *Betula papyrifera* has indeterminate growth, producing a first flush of leaves from primordia in the winter bud (similar to determinate species) and later producing neoformed leaves from current photosynthate (Kozlowski & Clausen 1966, Marks 1975). However, the majority of its leaves are likely to be produced during the first flush because, as shown for *Betula pendula* by Maillette (1982), generally neoformed leaves are produced only by long shoots at the top of the canopy and not by the many short shoots towards the base of the crown. Thus, the relative contribution of carbohydrate from stored reserves *versus* current photosynthate to leaf production and shoot expansion varies among species and, in heterophyllous species like *Betula* spp., among shoots on an individual tree (Kozlowski & Clausen 1966). In general, the degree to which stored reserves *versus* current photosynthate contribute to leaf growth and shoot extension is not clear (Dickson 1991), but is relevant to carbon isotope studies since the isotopic composition of the leaves will reflect the ^{13}C discrimination at the time the constituent carbon was assimilated (Brugnoli *et al.* 1988).

In 1988, weekly phenological observations of the study trees were made from June 10 to July 25 to determine the timing of growth cessation and bud formation. Most of the *Q. rubra* trees had completed growth (and, hence, leaf production) by June 10 (two irrigated trees completed a second flush by July 25). All *F. americana* trees had completed growth by June 10, except one tree, which had formed a terminal bud by June 28. Most *A. saccharum* trees had completed growth by June 20, with one tree forming a bud by June 28 and another by July 4. Only one *B. papyrifera* had a definite bud by July 25 when observations ceased; however, leaf production had been very slow for some time and other *B. papyrifera* trees in the nursery had begun forming buds by this time. Thus, most of the leaves of all four species appear to have been produced in the first spring flush, largely from stored reserves (1987 photosynthate). For this reason, the 1989 leaf samples were used for the determination of carbon isotope ratios since these leaves would most closely reflect the isotopic composition of the carbon assimilated in 1988 when the gas exchange assays were conducted.

e) Gas exchange assays. During the late summer (when drought events were most likely) and early fall of 1988, I assayed the gas exchange of the tagged trees on 17 occasions at different times of day and under different environmental conditions. Assays were conducted twice on July 29, on August 4 and 5, twice on August 9, three times on August 10, on August 11, 30 and 31, on September 1 and 2, twice on September 7 and on September 22. Earlier studies have indicated that after an initial increase to a maximum near completion of leaf expansion in spring, gas exchange rates of hardwood trees remain fairly constant until leaf senescence when they decline rapidly (Jurik 1986b). Mature, non-senescing leaves were assayed; therefore, developmental and leaf-age effects were unlikely to confound treatment effects or species comparisons. The plot pairs were assayed in random order each time and the order of the plots within the pair and the trees within the plots was also randomized. For each assay one randomly chosen healthy leaf per tree was measured using a LI-

6200 Portable Photosynthesis System (LI-COR, Inc.). Since the objective of the study was to estimate average gas exchange, choice of leaves was not limited to those on the exterior of the canopy. Therefore, not all leaves were in full sun during measurement. However, care was taken to ensure that the LI-6200 quantum sensor was in the same light environment as the leaf enclosed in the chamber and also to ensure that conditions in the cuvette were the same as ambient when the leaf was enclosed. Measurements began as soon as the CO_2 concentration in the cuvette began to decline, within a few seconds of the leaf being clamped in the chamber. Measurements were automatically terminated after a drawdown of 3 ppm CO_2 or manually terminated at 60 seconds (2 assays) or 120 seconds (15 assays) to avoid conditions in the cuvette deviating much from ambient. The raw data were screened to remove unrealistic extreme values and measurements taken under non-ambient chamber conditions. Photosynthesis (A), stomatal conductance (g), and internal CO_2 concentration (c_i) values from each of the 17 assays were averaged for each tree to provide seasonal mean values that reflect average activity over the range of conditions encountered. I used A/E (the ratio of A to transpiration, E) calculated for each measurement by the LI-6200 as a measure of instantaneous WUE and calculated seasonal means as for the other variables. Mean values for individual trees were used in all analyses. Field A_{max} and g_{max} were calculated as the 95th percentile of A and g values for each tree. This is not necessarily the maximum rate obtained under optimal (*i.e.* light-saturated) conditions that is usually reported, but reflects the maximum rate under natural conditions. Variability in c_i was taken as the standard deviation of c_i values for each tree over the full set of 17 assays.

The gas exchange data are summarized in Appendix IV.

4. Statistical analysis.

The significance of treatment differences within species and of differences in phenology between diffuse-porous and ring-porous species was tested with Wilcoxon non-parametric t-tests (Proc NPAR1WAY, SAS Institute Inc., 1985a). Tukey tests on ranked data were used for comparisons of species means (Proc RANK, Proc GLM, SAS 1985b,a). Analysis of variance (ANOVA) on ranked data (Proc RANK, Proc GLM, SAS, 1985b,a) was used to test responses of individual traits. Relationships between plant traits were made using Spearman non-parametric rank correlations (Proc CORR, SAS 1985b). Treatment differences were considered statistically significant when probabilities were less than or equal to 0.0520. All analyses were based on the values for individual trees (except for the means presented in Table 3, which were based on the individual observations for each variable). The analyses contain only those trees for which a complete data set of all variables was obtained, n = 42 trees.

A summary of the dates of nursery establishment, treatment implementation, and data collection is presented in Table 2.

Table 2. Summary of dates of nursery establishment, treatment imposition and data collection.

hydraulic conductivity							▮
carbon isotope ratio					■		
SLM and leaf N				■	■		
canopy area				■			
gas exchange				■			
spring and fall phenology			■	■			
height and diameter growth	▮	■	■	■	■	■	
treatments imposed		■	■	■	■	■	
nursery fertilized	■	■	■	■	■	■	
seeds germinated	■						
Year	1985	1986	1987	1988	1989	1990	1991

Note: Half-filled cells indicate end of growing season measurements, or, for hydraulic conductivity, March wood collection.

Results

Soil water regime and gas exchange conditions.

The experiment was designed to test the effects of differences in soil water availability on seedling performance and growth. Therefore, to interpret the results, I must first ascertain that 1) soil water availability did indeed differ between the two experimental treatments and 2) the atmospheric environment, which also influences gas exchange, did not differ between treatments in a manner that would preclude attributing differences in seedling performance to differences in soil water availability rather than to differences in atmospheric conditions. Since the treatment plots were all in close proximity and subject only to differing irrigation regimes, I expect *a priori* that treatment differences will be in the soil moisture regime, but not the atmospheric regime. The actual observed soil water availability and atmospheric conditions in the two treatments are discussed below.

The non-irrigated plots had significantly less water available on a seasonal basis (Table 3). Soil water potential in the irrigated plots ranged from -1.80 MPa (5th percentile) to 0.00 MPa (95th percentile) and -0.73 MPa to 0.00 MPa at 15 cm and 30 cm, respectively; in the non-irrigated plots, the ranges were -2.74 to 0.00 MPa and -1.27 to 0.00 MPa at 15 and 30 cm, respectively. In the irrigated plots, soil water potential at 15 cm was <-1.5 MPa (permanent wilting point) in approximately 10% of all readings; in the non-irrigated plots, at 15 cm it was <-1.5 MPa in 50% of all readings. In neither treatment did soil water potential at 30 cm depth go below -1.5 MPa. Thus, the non-irrigated seedlings were subject to periods of moderate water shortage, primarily in the upper soil horizon, but also experienced periods of ample water availability after natural rainfall. Irrigated seedlings only occasionally were subjected to mild water shortage in the upper 15 cm of the soil profile.

I examined the primary atmospheric factors influencing leaf gas exchange.

Table 3. Environmental and gas exchange conditions during summer 1988 (mean ± SD). Probabilities based on Wilcoxon non-parametric t-tests are given for differences between treatment means. Soil water potentials based on 196 neutron probe readings (96 for each treatment); gas exchange conditions based on 642 observations (334 irrigated, 308 non-irrigated).

Variable	Treatment		
	irrigated	non-irrigated	p=
soil water potential (MPa)			
15 cm depth	-0.86 ± 0.56	-1.45 ± 0.89	.0001
30 cm depth	-0.28 ± 0.24	-0.65 ± 0.43	.0001
vapour pressure (mb)	22.2 ± 6.7	21.8 ± 6.8	.3934
rate of change of vapour pressure of air (mb s^{-1})*	.0158 ± .0339	.0125 ± .017	.7697
CO_2 concentration (ppm)	342.7 ± 9.3	342.4 ± 9.3	.7632
quantum (μmol $m^{-2}s^{-1}$)	517.6 ± 478.7	820.2 ± 543.6	.0001
t_{air} (°C)	29.5 ± 4.6	30.1 ± 5.0	.0405
t_{leaf} (°C)	28.8 ± 5.0	30.3 ± 5.8	.0006
relative humidity (%)	52.0 ± 10.1	49.3 ± 10.0	.0012
vpd (mb)	18.8 ± 7.6	23.3 ± 10.8	.0001

* dedt as calculated by the LI-6200.

During the gas exchange assays, there were no differences in ambient CO_2 concentration, vapour pressure or the rate of change of vapour pressure of air in the leaf chamber (Table 3). There were, however, significant treatment differences in mean quanta received, mean air temperature (t_{air}), leaf temperature (t_{leaf}), relative humidity (RH) and vapour pressure deficit (vpd). In biological terms, treatment differences in t_{air}, t_{leaf} and RH were negligible. Treatment differences in mean quanta received were presumably due primarily to greater self-shading within the larger saplings growing in the irrigated plots; the random sampling of leaves in the entire canopy, not just the outer layer, thus, led to greater mean irradiance during assay of the non-irrigated trees. Within species, non-irrigated trees received significantly higher quanta than irrigated trees only in *Betula papyrifera* ($p=0.04$, using the mean value for each tree). There also were no significant correlations between quanta received and gas exchange parameters; therefore, differences in gas exchange rates (discussed below) were not due to differences in light levels between treatments. Differences in vpd across species and treatments can be problematic because of the potential difficulties introduced into the interpretation of $\delta^{13}C$ data (Farquhar & Richards 1984). However, in the current data set, the higher vpd of the non-irrigated trees acts to dampen any differences in water use efficiency (WUE) estimated from $\delta^{13}C$ values (see section below on WUE and Appendix V).

Responses of individual traits to chronic intermittent drought stress and relationships among traits.

1. Relative growth rate and other aspects of growth. All species showed reduced growth (RGR Index) in the non-irrigated treatment, although growth rate was not significantly reduced in all species (Table 4, Figure 1*a*). *Betula papyrifera* and *Quercus rubra* showed significant 41.5% and 28.6% reductions, respectively; *Fraxinus americana* showed a 43.5% reduction, which closely approached significance, while *Acer saccharum* showed 19.9% reduction, which was not

Table 4. Traits studied in four deciduous hardwood species growing in an experimental nursery with and without water shortage. Means (± SD) are given for each species treatment combination along with Wilcoxon non-parametric t-test approximation probabilities for differences between treatments for each species.

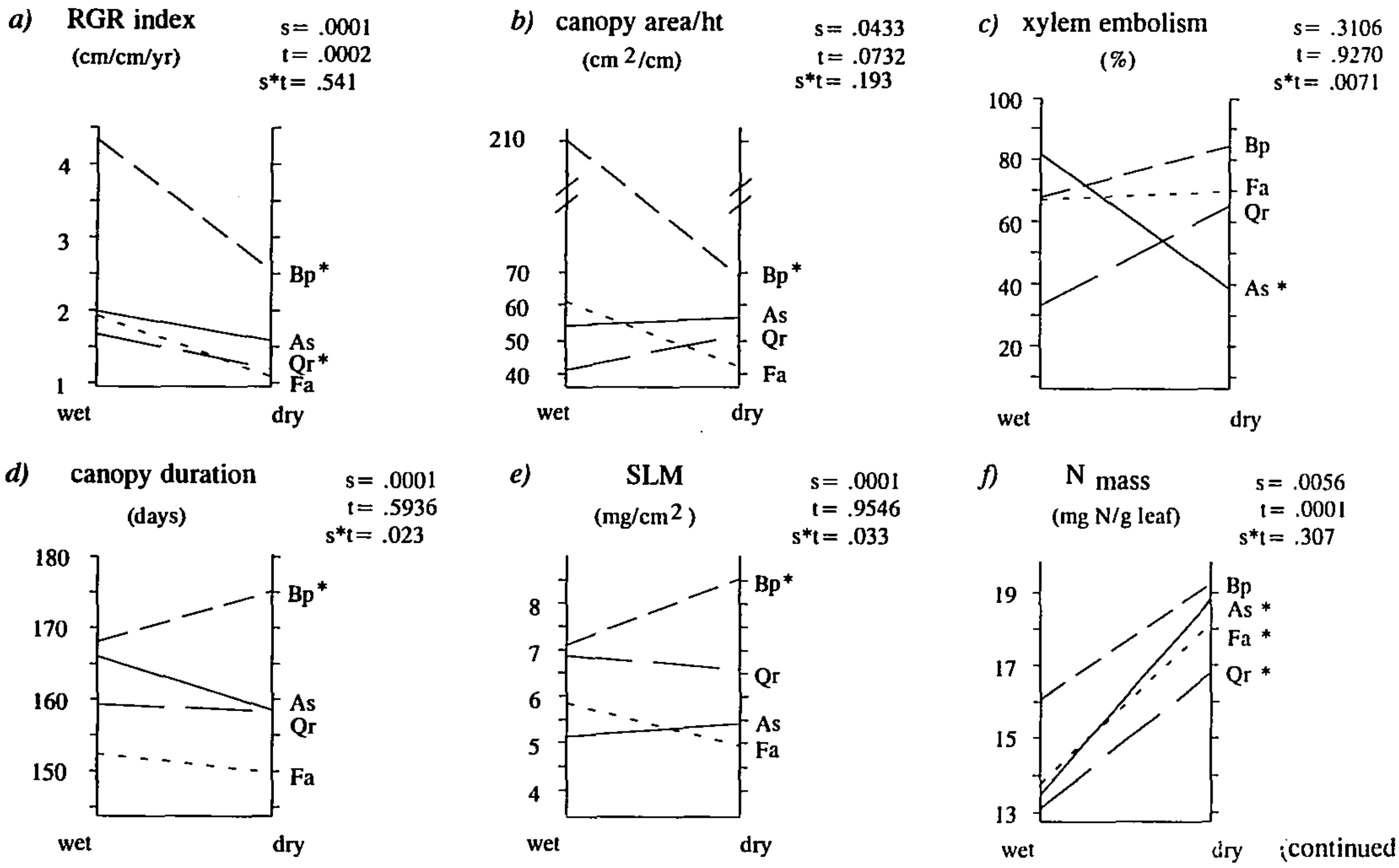
Trait	*Betula papyrifera*			*Acer saccharum*		
	irrigated (n=4 trees)	non-irrigated (n=6 trees)	p=	irrigated (n=6 trees)	non-irrigated (n=5 trees)	p=
I. <u>Growth</u>						
RGR index (cm/cm/yr)	4.34 ± .14	2.54 ± .85	.0366	1.99 ± .62	1.59 ± .60	.4305
canopy area/ht (cm^2 leaf/cm)	210.19 ± 71.92	68.78 ± 49.37	.0520	54.56 ± 18.25	57.18 ± 40.08	.7898
leaf display index, LDI (cm^2 leaf/cm branch)	6.38 ± 1.11	5.26 ± 1.86	.6069	10.71 ± 2.58	15.58 ± 5.74	.1135
wood density (g cm^{-3})	.648 ± .047	.647 ± .036	.7564	.685 ± .058	.692 ± .045	.7898
II. <u>Hydraulic conductivity</u>						
maximum specific conductivity [(kgMPa^{-1} $m^{-1}s^{-1}$)/m^2 x-sect. area]	.069 ± .033	.051 ± .018	.2711	.042 ± .019	.022 ± .005	.0842
leaf specific conductivity [(kgMPa$^{-1}m^{-1}s^{-1}$)/m^2 leaf area supplied]	1.001 ± .602	1.396 ± .648	.4746	.901 ± .355	.571 ± .202	.1517
reduction due to embolism (%)	67.60 ± 18.36	84.42 ± 7.92	.1992	81.54 ± 14.30	39.21 ± 23.60	.0244
III. <u>Leaf Phenology</u>						
budbreak (day)	116.3 ± .5	115.1 ± 1.2	.1568	118.7 ± .9	118.3 ± .9	.6488
senescence (day)	284.4 ± 1.4	290.3 ± 2.3	.0344	284.8 ± 5.6	276.7 ± 6.7	.0830
canopy duration (days)	168.1 ± 1.8	175.2 ± 1.8	.0366	166.1 ± 5.4	158.4 ± 5.9	.0842
IV. <u>Leaf Physiology</u>						
SLM (mg cm^{-2})	7.10 ± .36	8.54 ± .45	.0366	5.13 ± .91	5.43 ± .74	.5372
N_{mass} (% dry wt.)	1.61 ± .10	1.93 ± .22	.0735	1.35 ± .14	1.88 ± .28	.0244
N_{area} (mg cm^{-2})	0.114 ± 0.012	0.164 ± 0.022	.0366	0.069 ± .015	0.101 ± .015	.0334
seasonal mean A ($\mu mol\ m^{-2}s^{-1}$)	6.83 ± .63	7.28 ± 1.71	.9174	3.90 ± .66	3.17 ± .62	.0842
field A_{max} ($\mu mol\ m^{-2}s^{-1}$, 95th percentile)	14.25 ± 1.44	17.01 ± 4.33	.4746	9.29 ± 2.31	7.04 ± 1.14	.1135
seasonal mean g (mmol $m^{-2}s^{-1}$)	294.2 ± 57.6	176.5 ± 27.2	.0366	110.1 ± 22.5	51.5 ± 11.1	.0244
field g_{max} (mmol $m^{-2}s^{-1}$, 95th percentile)	455.2 ± 27.1	412.6 ± 79.0	.6069	193.7 ± 52.3	114.8 ± 16.2	.0344
seasonal mean c_i (ppm)	292.5 ± 9.9	258.7 ± 12.7	.0366	272.7 ± 6.6	239.6 ± 14.9	.0244
variability in c_i (std. dev.)	18.9 ± 2.8	42.9 ± 10.3	.0366	35.6 ± 8.7	50.8 ± 7.8	.0842
seasonal mean A/E ($\mu mol\ CO_2/mmol\ H_2O$)	1.55 ± .26	2.71 ± .25	.0366	2.40 ± .49	3.80 ± .75	.0334
$\delta^{13}C$ (0/00)	-28.40 ± .20	-25.86 ± .61	.0362	-27.55 ± .76	-25.32 ± 1.04	.0334

(continued...)

Table 4 (continued...)

Trait	*Fraxinus americana*			*Quercus rubra*		
	irrigated (n=6 trees)	non-irrigated (n=4 trees)	p=	irrigated (n=5 trees)	non-irrigated (n=6 trees)	p=
I. Growth						
RGR index (cm/cm/yr)	1.93 ± .44	1.09 ± .35	.0735	1.68 ± .25	1.20 ± .14	.0244
canopy area/ht (cm^2 leaf/cm)	60.94 ± 24.73	42.13 ± 9.31	.2711	41.14 ± 10.67	51.81 ± 22.20	.6578
leaf display index (cm^2 leaf/cm branch)	19.24 ± 6.97	13.60 ± 2.53	.1992	5.96 ± 3.45	8.78 ± 3.14	.2628
wood density (g cm^{-3})	.773 ± .054	.692 ± .047	.1034	.867 ± .049	.842 ± .050	.5372
II. Hydraulic conductivity						
maximum specific conductivity [(kgMPa^{-1} m^{-1}s^{-1})/m^2 x-sect. area]	.061 ± .044	.048 ± .034	.7228	.101 ± .057	.090 ± .083	.5372
leaf specific conductivity [(kgMPa^{-1}m^{-1}s^{-1})/m^2 leaf area supplied]	1.439 ± .964	1.471 ± 1.035	.9055	3.418 ± 1.000	2.098 ± 1.799	.2009
reduction due to embolism (%)	66.83 ± 31.73	69.65 ± 16.49	.9055	32.84 ± 37.96	64.71 ± 26.88	.1517
III. Leaf Phenology						
budbreak (day)	121.4 ± 1.3	120.8 ± 0.9	.8297	121.1 ± .5	120.3 ± .5	.0751
senescence (day)	273.7 ± 2.8	270.6 ± 5.3	.3539	280.4 ± 4.0	278.7 ± 8.5	.9999
canopy duration (days)	152.3 ± 2.9	149.9 ± 4.9	.4746	159.3 ± 3.8	158.4 ± 8.6	.7220
IV. Leaf physiology						
SLM (mg cm^{-2})	5.85 ± .69	4.94 ± .51	.1034	6.86 ± 1.04	6.59 ± .40	.5372
N_{mass} (% dry wt.)	1.38 ± .19	1.81 ± .13	.0520	1.31 ± .12	16.77 ± 1.92	.0244
N_{area} (mg cm^{-2})	0.080 ± 0.013	0.090 ± 0.016	.4746	0.089 ± 0.013	0.110 ± 0.011	.0621
seasonal mean A (μmol $m^{-2}s^{-1}$)	7.07 ± 1.72	2.77 ±.78	.0366	8.09 ± 1.35	5.21 ± .82	.0244
field A_{sat} (μmol $m^{-2}s^{-1}$, 95th percentile)	11.98 ± 2.61	6.96 ± 2.02	.0520	15.18 ± 3.73	11.41 ± 1.17	.0621
seasonal mean g (mmol $m^{-2}s^{-1}$)	262.2 ± 72.2	40.5 ± 22.7	.0366	257.0 ± 42.6	122.0 ± 35.9	.0244
field g_{sat} (mmol $m^{-2}s^{-1}$, 95th percentile)	440.0 ± 92.2	99.1 ± 83.5	.0366	392.1 ± 40.6	333.8 ± 92.6	.2009
seasonal mean c_i (ppm)	278.8 ± 8.5	220.3 ± 33.9	.0366	276.7 ± 8.5	261.5 ± 13.0	.1128
variability in c_i (std. dev.)	26.7 ± 6.0	63.1 ± 9.8	.0366	23.0 ± 7.8	51.9 ± 5.1	.0244
seasonal mean A/E (μmol CO_2/mmol H_2O)	1.83 ± .34	4.62 ± .85	.0366	1.91 ± .26	2.99 ± .23	.0244
$\delta^{13}C$ (0/00)	-28.10 ± .77	-25.61 ± .63	.0366	-28.30 ± .86	-25.99 ±.34	.0244

Figure 1. Norm of reaction diagrams for traits showing a treatment response in one or more species.
Results of ANOVA on ranked data are given for each trait (* - treatment effect significant at the .052 level).
Key: *Acer saccharum*-——— ; *Betula alleghaniensis*-— — ; *Fraxinus americana*- - - - ; *Quercus rubra*——— .



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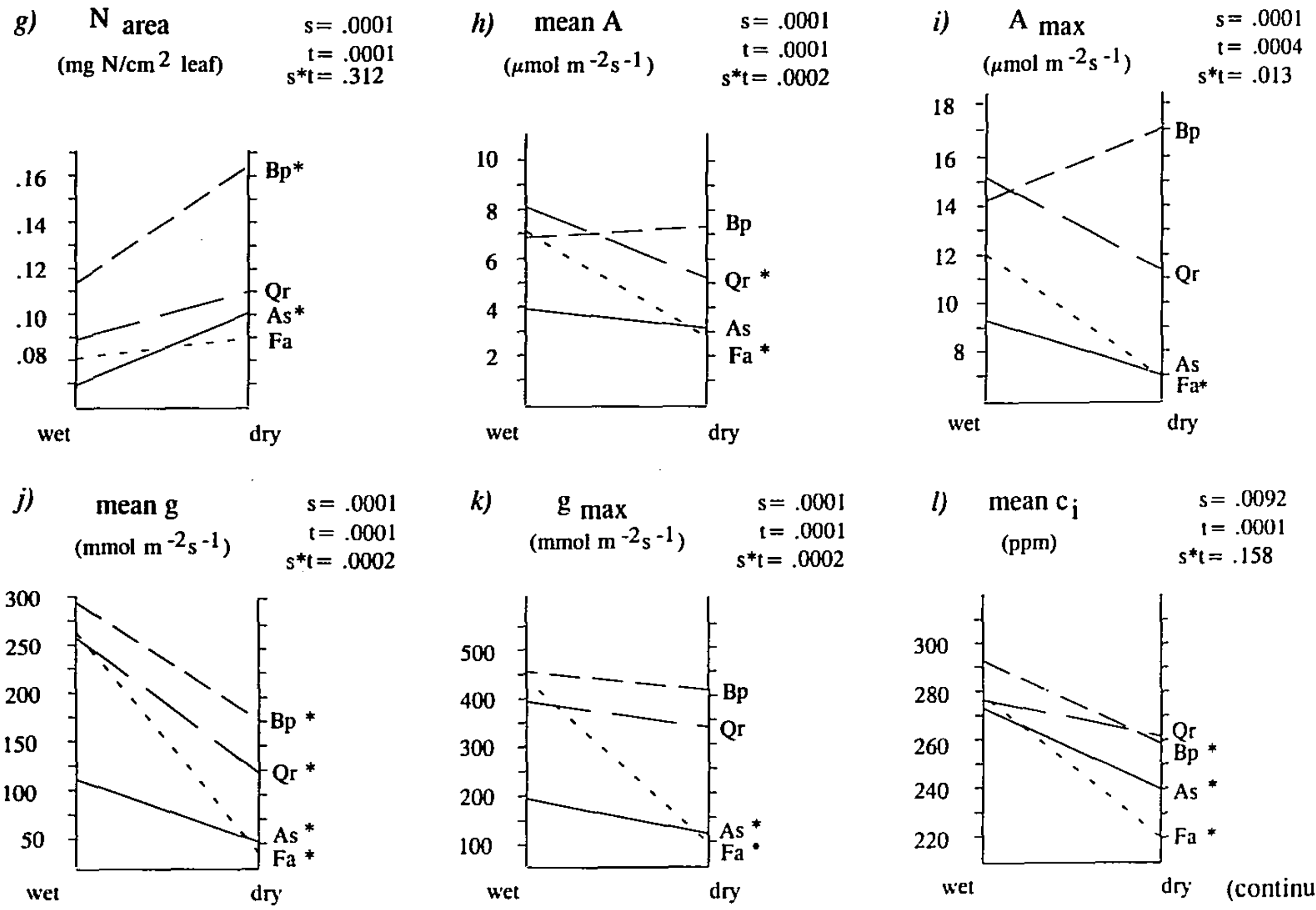

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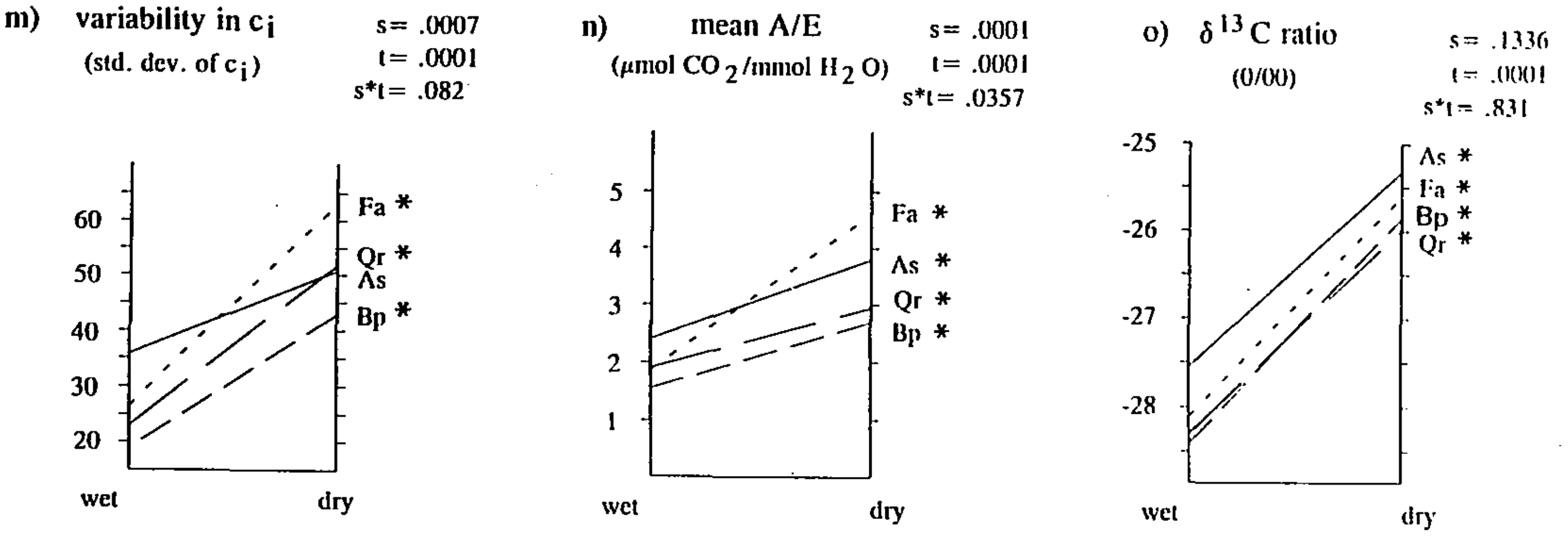


statistically significant. There were species differences in RGR in addition to treatment differences, but all species showed the same basic response (*i.e.* analysis of variance [ANOVA] showed no species x treatment interaction) (Fig. 1*a*). *Betula papyrifera* had much higher growth rates under both treatments than the other species. Growth rate in diameter and height were the two components of RGR Index that were most affected; growth rate of lateral branches was not significantly reduced under non-irrigated conditions in any species (Table 5).

Canopy area scaled to tree height (cm^2 leaf/cm height, 1988) was significantly reduced in *B. papyrifera*; the other species showed no response to water shortage in this trait (Table 4, Figure 1*b*). The reduced canopy area/height of *B. papyrifera* under non-irrigated conditions corresponded with a 72.9% decrease in canopy weight (calculated as the mean leaf weight times the total number of leaves, 1988; Wilcoxon t-test significance = .0520; data not shown). This indicates that under non-irrigated conditions *B. papyrifera* produced less leaf tissue overall; the decrease in canopy area was not solely due to increased specific leaf mass (SLM) (see below). The other species showed no significant treatment differences in canopy weight.

Responses in leaf display index, LDI (cm^2 leaf area/cm branch length, 1990), a measure of architecture at the branch level, were in the same direction as those in canopy area/height, but no treatment differences were significant (Table 4). Species differences in LDI were overriding (sp = .0001, treat = .3394, sp*treat = .1398). *Fraxinus americana* had the highest LDI (species mean ± SD = 17.0 ± 6.1) due to its compound leaves (blade area only was included in measured leaf area, rachis length was not measured), followed by *A. saccharum* (12.9 ± 4.8), *Q. rubra* (7.5 ± 3.4) and *B. papyrifera* (5.7 ± 1.6).

Dry wood density was not affected by soil water availability (Table 4). *Betula papyrifera* had the lowest density wood (0.65 g cm^{-3} ± 0.04), followed by

Table 5. Percent reduction in relative height, stem basal diameter and lateral branch length growth rates in four hardwood tree species grown under non-irrigated *versus* irrigated conditions for five years.

	Percent reduction in growth		
Species	$RGR_{(diam)}$	$RGR_{(ht)}$	$RGR_{(branch)}$
Acer saccharum	11.8 (.263)[1]	11.8 (.152)	3.3 (.929)
Betula papyrifera	34.2 (.037)	30.2 (.037)	15.4 (.200)
Fraxinus americana	25.1 (.037)	25.5 (.074)	7.5 (.362)
Quercus rubra	13.4 (.201)	13.8 (.062)	8.3 (.174)

[1] Wilcoxon non-parametric t-test approximation significance.

A. saccharum (0.69 ± 0.05), *F. americana* (0.74 ± 0.06) and *Q. rubra* (0.85 ± 0.05).

In summary, the greatest effect of chronic intermittent drought on growth and canopy architecture was reduced RGR, primarily involving reduced growth in height and diameter. Other architectural traits showed species differences but, except for canopy area/height in *B. papyrifera*, there was no response to water regime. Thus, although growth rate was reduced under drought, traits such as canopy architecture, leaf display and wood density were little affected.

2. Hydraulic conductivity. There was no significant response to chronic water shortage in maximum specific conductivity (MSC, maximum conductivity per unit branch cross-sectional area), although all species had somewhat lower rates under non-irrigated conditions (Table 4). There were also no significant effects on leaf specific conductivity (LSC, maximum conductivity per unit leaf area supplied) (Table 4). Reduction in conductivity due to embolism was significantly affected only in *A. saccharum* (Table 4, Figure 1*c*), which had slightly higher late-winter specific conductivity (data not shown) and significantly lower percent loss of conductivity under non-irrigated conditions, contrary to expectations. The other species showed a trend of slightly lower late-winter conductivity and greater percent loss of conductivity due to embolism under non-irrigated conditions, although response was not statistically significant (Table 4, Figure 1*c*). There were no consistent differences in conductivity or percent embolism between the diffuse-porous species, *A. saccharum* and *B. papyrifera*, and the ring-porous species, *F. americana* and *Q. rubra*. Surprisingly, the non-irrigated diffuse-porous *B. papyrifera* had a greater degree of embolism than the non-irrigated ring-porous *F. americana* and *Q. rubra* (Table 4).

Since there was no response to water shortage in the hydraulic conductivity variables measured, other than percent loss of conductivity in *A. saccharum*, I compared the overall species means (Table 6). The ring-porous *Q. rubra* had the highest species mean late-winter conductivity, MSC and LSC, while diffuse-porous *A. saccharum* had the lowest values; *B. papyrifera* and *F. americana* were intermediate. *Betula papyrifera* had the highest percent loss of conductivity, followed by *F. americana*, *A. saccharum*, and *Q. rubra*. All species showed greater than 50% loss of conductivity by mid-winter.

Contrary to expectations, MSC was not correlated with the degree of late winter embolism (r= -.19, p= .2341); higher potential specific conductivity did not result in greater loss of conductivity due to embolism. When individual branches were used in analysis, larger diameter branches had higher absolute maximum conductivity (r= .36, p= .0069, n= 55 branches) and also less percent loss of conductivity (r= -.53, p= .0001, n= 55). MSC and LSC were closely correlated (r= .82, p= .0001); trees with higher conductivity per unit branch cross-sectional area also had greater conductivity per unit leaf area supplied. Both MSC and LSC were significantly correlated with gas exchange rates (seasonal mean A, A_{max}, mean g, g_{max}; r values from .39 to .54, p values from .0115 to .0002). These results indicate a correspondence between the physiological activity and transpirational demands of the canopy and the ability to supply the canopy with water to meet those demands: trees with higher gas exchange rates also had high maximum rates of water delivery to the canopy. The relationships between MSC and A_{max} and g_{max} are shown in Figure 2. Thus, although hydraulic conductivity traits, in general, showed no plasticity with respect to soil water regime, these traits were functionally related to gas exchange. MSC was negatively correlated with both instantaneous water use efficiency, A/E (r= -.38, p= .0137), and long-term integrated WUE, as estimated by $\delta^{13}C$ (r= -.33, p= .0364). Trees with greater maximum rates of water transport per unit branch cross-sectional area tended to have lower water use efficiency than trees with lower rates of water transport (although there was considerable scatter in the data and the

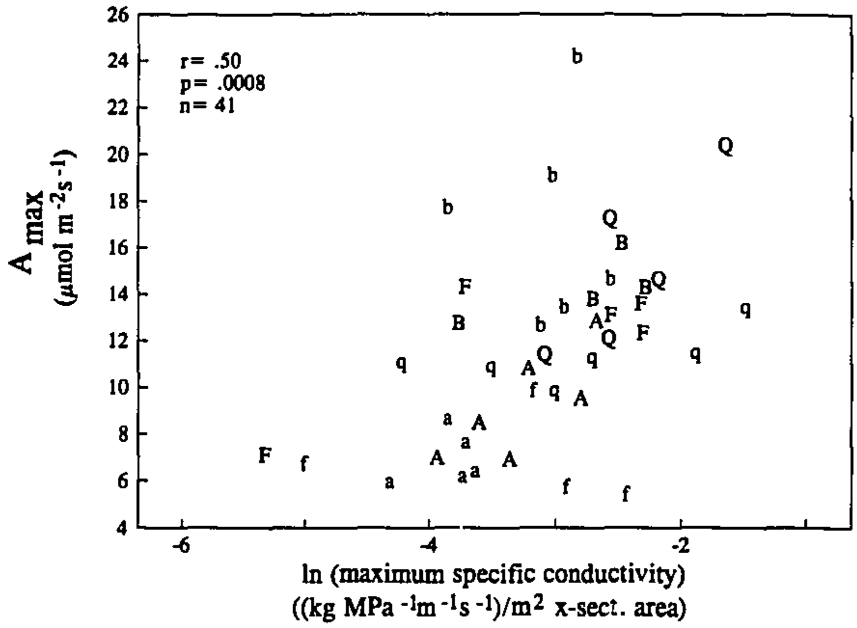
Table 6. Hydraulic conductivity of four species growing in an experimental nursery (species means ± SD). Values in the same row with different letters differ at the $p < 0.05$ level based on a Tukey comparison on ranked data.

Hydraulic conductivity[*]	*Acer saccharum*	*Betula papyrifera*	*Fraxinus americana*	*Quercus rubra*
maximum specific conductivity (MSC)	.033 ± .018 a	.058 ± .025 ab	.055 ± .038 ab	.095 ± .069 b
late-winter specific conductivity	.011 ± .008 a	.014 ± .014 a	.018 ± .019 a	.051 ± .054 a
leaf specific conductivity (LSC)	.751 ± .330 a	1.238 ± .629 ab	1.453 ± .931 ab	2.698 ± 1.579 b
% embolism	62.3 ± 28.5 a	77.7 ± 14.9 a	68.1 ± 24.7 a	50.2 ± 34.9 a

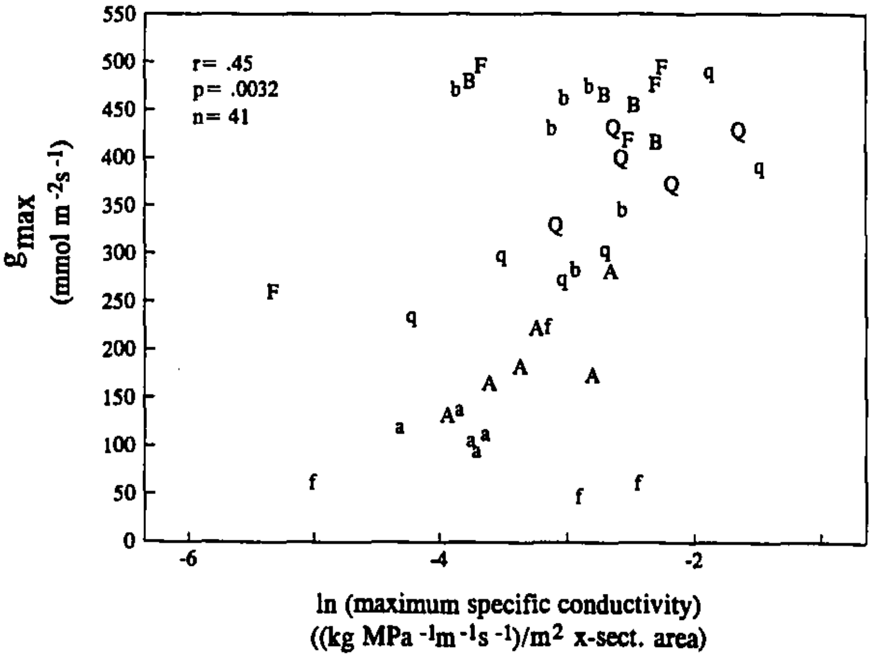
[*] Units for specific conductivity: (kg $MPa^{-1}m^{-1}s^{-1}$)/m^2 branch cross-sectional area; leaf specific conductivity: (kg $MPa^{-1}m^{-1}s^{-1}$)/m^2 leaf area supplied; % embolism: % reduction in conductivity due to embolism by late winter.

Figure 2. Relationship between maximum specific conductivity and maximum photosynthesis rate (A max) and maximum stomatal conductance (g max). Spearman correlations and probabilities are given. Uppercase letters denote irrigated trees; lowercase letters denote non-irrigated trees. *Acer saccharum* - Aa, *Betula papyrifera* - Bb, *Fraxinus americana* -Ff, *Quercus rubra* - Qq.

a) maximum photosynthesis rate



b) maximum stomatal conductance



relationship with $\delta^{13}C$, in particular, was weak).

3. Leaf Phenology. Canopy duration is determined by the timing of leaf budbreak in spring and leaf senescence in autumn. No species showed a difference in the timing of leaf budbreak between irrigated and non-irrigated trees (Table 4). However, *B. papyrifera* senesced significantly later under non-irrigated conditions resulting in a significantly longer canopy duration for non-irrigated trees in this species (Table 4, Figure 1*d*). Soil water regime had no effect on the timing of leaf senescence or canopy duration in the other species.

The diffuse-porous species, *A. saccharum* and *B. papyrifera*, leafed out significantly earlier than the ring-porous *F. americana* and *Q. rubra*, day 117.1 ± 1.8 (mean ± SD) *versus* day 120.9 ± 0.9 for diffuse-porous and ring-porous species, respectively (p= .0001). The diffuse-porous species also senesced later (day 284.3 ± 6.6 *versus* day 276.1 ± 6.5, p= .0009) and had longer canopy durations (167.2 ± 7.4 *versus* 155.2 ± 6.5 days, p= .0001). Timing of spring budbreak showed no correlation with degree of embolism (r= -.19, p= .2303) nor with MSC (r= .11, p= .50). Thus, loss of hydraulic conductivity did not result in later budbreak in these trees. Although the ring-porous *F. americana* and *Q. rubra* leafed out later than the diffuse-porous *B. papyrifera* and *A. saccharum*, they did not have significantly greater MSC or greater percent embolism (Table 6).

4. Leaf traits. Leaf level traits showed the greatest response to chronic intermittent water shortage. There were significant responses in at least one species in most of the traits examined. There were universal responses as well as species-specific differences in response. These are discussed below.

a. Specific leaf mass and leaf nitrogen. Betula papyrifera showed a significant increase in specific leaf mass (SLM, mg cm^{-2}) under non-irrigated conditions (Table 4, Figure 1*e*); the other species did not. *Acer saccharum, F. americana* and *Q. rubra* showed a significant increase in N_{mass} (% N) (Table 4, Figure 1*f*). *Betula papyrifera* followed the same trend, but the increase was not significant. *Betula papyrifera* and *A. saccharum* also showed an increase in N_{area} (mg N cm^{-2} leaf) (Table 4, Figure 1*g*); *Q. rubra* and *F. americana* followed the trend, but the differences were not significant. Thus, all species responded similarly with increased leaf N under non-irrigated conditions. In *B. papyrifera*, the concomitant increase in SLM resulted in a particularly large increase in N_{area}.

b. Photosynthesis and stomatal conductance. Seasonal mean photosynthesis (A) was significantly reduced under non-irrigated conditions in *F. americana* and *Q. rubra* (60.8 % and 35.6% reductions, respectively) (Table 4, Figure 1*h*). *Acer saccharum* had the lowest mean A under irrigated conditions and showed an 18.7% (non-significant) reduction under non-irrigated conditions. *Betula papyrifera* showed a marginal, non-significant increase (6.6%) (Table 4, Figure 1*h*) and had the highest A under non-irrigated conditions.

Maximum photosynthesis rate, field A_{max} (the 95th percentile of values for each tree), was lower under non-irrigated conditions in *A. saccharum, F. americana*, and *Q. rubra*, but the difference was significant only in *F. americana* (Table 4, Figure 1*i*). *Betula papyrifera* showed a non-significant increase. Thus, there were differences among species in A_{max} and also species differences in response to water shortage. Overall, there was a strong correlation between seasonal mean A and A_{max} (r= .91, p= .0001), indicating that average photosynthetic performance in the field reflected photosynthetic capacity.

Across species and treatments, A_{max} was positively correlated with N_{area} (r=

.45, p=.0031). A greater investment in N per unit leaf area, in general, resulted in greater photosynthetic capacity. However, within species only *B. papyrifera* actually showed an increase in A_{max} with an increase in N_{area} (Figure 3). The correlation was negative or non-significant in all other species due to their increase in N_{area} and decrease in A_{max} under non-irrigated conditions (Figure 1*g*,*i*). These results suggest that since N_{area} increased under non-irrigated conditions while A_{max} decreased in all species except *B. papyrifera*, which produced morphologically and physiologically different leaves, A_{max} was limited by factors other than N under water-limited conditions. SLM was highly correlated with both A_{max} (r= .75, p= .0001, Figure 4) and mean A (r= .67, p= .0001). SLM is, thus, a good predictor of photosynthetic capacity across species and treatments.

Seasonal mean stomatal conductance (g) was significantly reduced in all species under non-irrigated conditions due to partial stomatal closure to restrict transpirational loss (Table 4, Figure 1*j*). *Acer saccharum* and *F. americana* had very low mean g under non-irrigated conditions; they also had low maximum conductance values (g_{max}, 95th percentile) (Table 4, Figure 1*k*). *Betula papyrifera* and *Q. rubra* showed no significant decrease in g_{max} under non-irrigated conditions (Table 4, Figure 1*k*).

These results show that species differed in photosynthesis and conductance rates and that there were also differences in the way species responded to water shortage. Overall, mean A was highly correlated with mean g (r= .89, p= .0001) (Figure 5). However, *B. papyrifera* did not show the decrease in A with decreasing g as did the other species (Figure 5); its more efficient leaves under non-irrigated conditions maintained high rates of A at lower g than the leaves of irrigated trees. *Acer saccharum* showed a smaller range and generally lower values of g than the other species.

Figure 3. Relationship between maximum photosynthesis rate (A_{max}) and leaf N per unit area (N_{area}) in four deciduous tree species. n= 42 trees.

Symbols: ○ - *Acer saccharum*, ● - *Betula papyrifera*,
▽ - *Fraxinus americana*, ▼ - *Quercus rubra*.

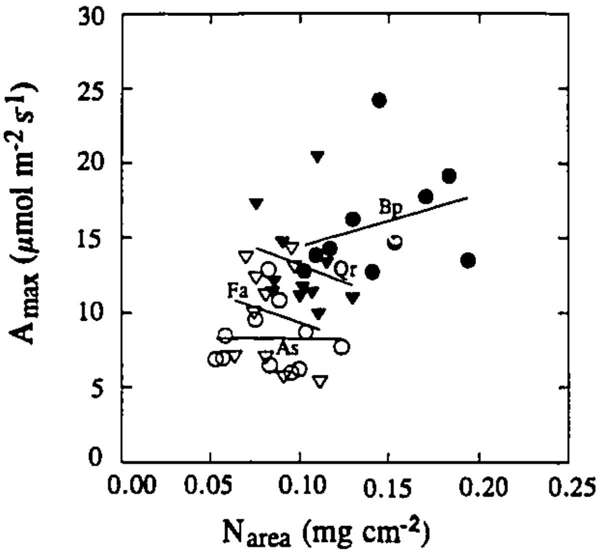


Figure 4. Relationship between maximum photosynthesis rate (A_{max}) and specific leaf mass (SLM) in four deciduous tree species. n= 42 trees. Symbols as in Figure 3.

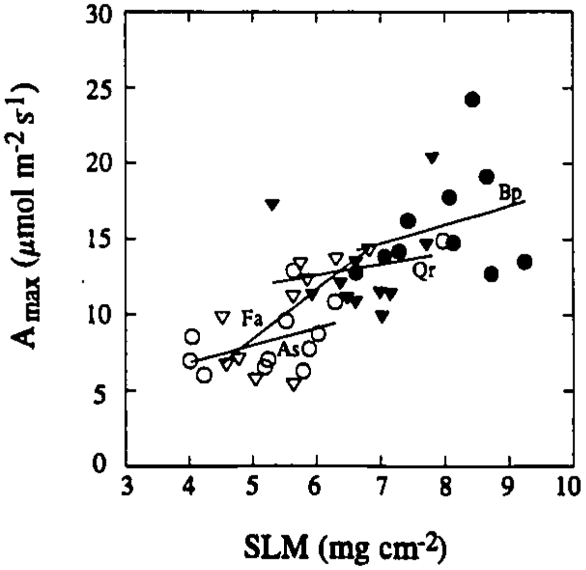
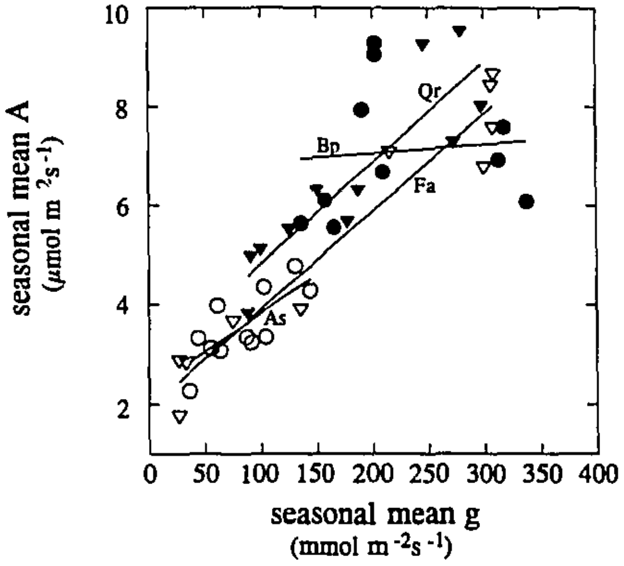


Figure 5. Relationship between seasonal mean photosynthesis (A) and stomatal conductance (g) in four deciduous tree species. n= 42 trees.

Symbols: ○ - *Acer saccharum*, ● - *Betula papyrifera*,
▽ - *Fraxinus americana*, ▼ - *Quercus rubra*.



c. Internal CO_2 concentration. Soil water availability also affected internal CO_2 concentration (c_i) (Table 4, Figure 1*l*). All species showed a similar response with lower mean c_i under non-irrigated conditions (significant in all species except *Q. rubra*). This is, in part, a short-term response of partial stomatal closure to restrict water loss. However, not only the means, but also the 75th and 25th percentile values were lower (Appendix IV) indicating that the non-irrigated plants tended to operate at a lower c_i and that the lower mean values were not entirely due to low c_i when small stomatal aperture greatly limited CO_2 diffusion. This suggests long-term adjustment to growing under the experimental conditions for three years (*i.e.* a lowering of the c_i setpoint). Maximum c_i values (95th percentile) were higher under non-irrigated conditions in all species; these values most likely result from direct inhibition of photosynthesis when water availability was lowest. Although species differed in mean c_i, they all responded similarly to chronic intermittent water shortage (Figure 1*l*).

All species showed an increase in mean c_i with an increase in mean g (overall, $r= .75$, $p= .0001$) (Figure 6). Increase in stomatal aperture allowed greater diffusion of CO_2 into the substomatal cavity. Overall, there was a positive correlation between seasonal mean c_i and seasonal mean A ($r= .46$, $p= .0021$) (Figure 7). All species showed an increase in mean A with increasing mean c_i, except for *B. papyrifera*, which showed a decrease (Figure 7). This reflects the greater photosynthetic efficiency of the thicker leaves of non-irrigated *B. papyrifera* trees (high A_{max}, low c_i) compared to the leaves of their irrigated counterparts (lower A_{max}, higher c_i). In *A. saccharum*, c_i increased more sharply for a given increase in g than it did in the other species (Figure 6) and its response in A to increasing c_i (Figure 7) was less than that of *F. americana* and *Q. rubra*. These factors indicate the limited photosynthetic capacity of *A. saccharum*. *Quercus rubra* and *F. americana* show similar slopes in the A-c_i plot, but the ranges in A and c_i are very different between the two species. *Quercus rubra* showed a relatively low range of A and c_i values, while *F. americana* showed great variability in c_i along with its great range in A.

Figure 6. Relationship between seasonal mean internal CO_2 concentration (c_i) and stomatal conductance (g) in four deciduous tree species. n= 42 trees.

Symbols: ○ - *Acer saccharum*, ● - *Betula papyrifera*,
▽ - *Fraxinus americana*, ▼ - *Quercus rubra*.

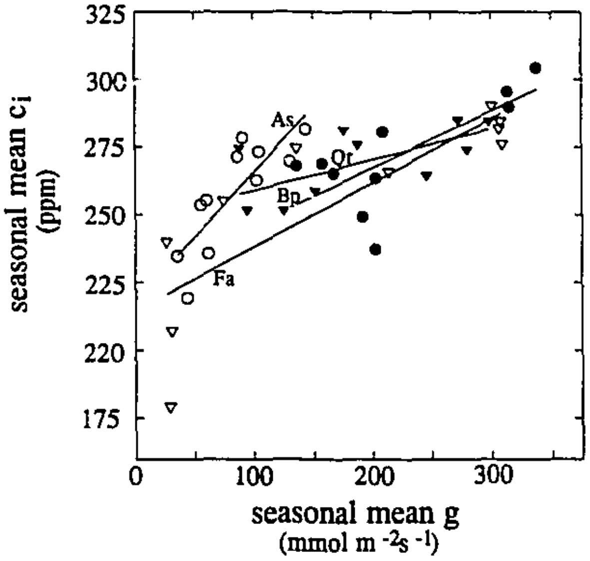
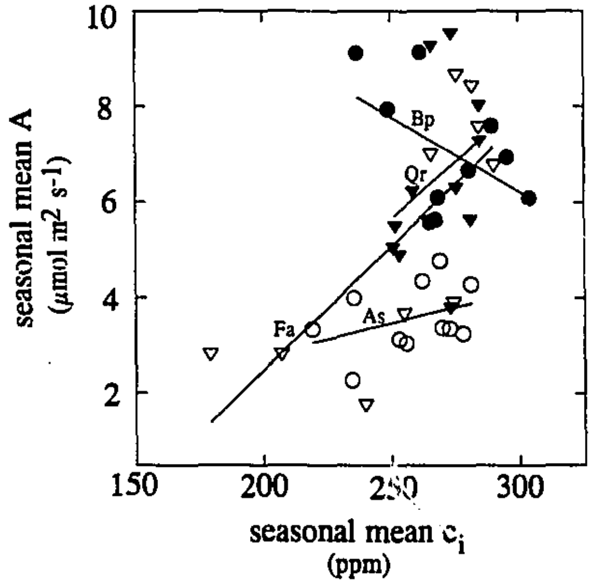


Figure 7. Relationship between seasonal mean photosynthesis (A) and internal CO_2 concentration (c_i) in four deciduous tree species. n= 42 trees. Symbols as in Figure 6.



When analysed by treatment, the correlation between mean A and mean c_i was significant for non-irrigated trees only (r= .50, p= .0223), indicating that CO_2 was not the only factor limiting A under irrigated conditions when g was higher; non-stomatal factors were also responsible for species differences in A.

Variability in c_i was represented as the standard deviation of c_i values obtained throughout the summer. Higher variability in c_i indicates greater differences in c_i across the 17 sampling times, while lower variability in c_i indicates greater similarity among c_i measurements over time. Variability in c_i differed among species and between treatments (Table 4, Figure 1*m*). *Fraxinus americana, Q. rubra* and *B. papyrifera* trees receiving adequate water had significantly more stable c_i on a seasonal basis than non-irrigated trees. *Acer saccharum* followed the same trend, although the treatment difference was not significant. Seasonal mean c_i was negatively correlated with its standard deviation (r= -.68, p= .0001) so this treatment difference is not a statistical artifact resulting from the standard deviation increasing with the mean.

Overall, variability in c_i was negatively correlated with seasonal mean g (r= -.81, p= 0.0001). Trees that maintained high mean g had higher A and also more stable c_i over the season than did trees with lower mean g. Non-irrigated *A. saccharum* and *F. americana* had low mean g and low g_{max} (Figure 1*j,k*), but showed seasonal variability in c_i similar to that of *Q. rubra* and *B. papyrifera* (Figure 1*m*). This suggests that in *A. saccharum* and *F. americana*, c_i fluctuated while g remained low and stable, indicating changes in rates of CO_2 assimilation. In *Q. rubra* and *B. papyrifera*, on the other hand, although mean g was lower under non-irrigated conditions, g_{max} was similar to that under irrigated conditions so increased variability in c_i could result from greater fluctuations in g under non-irrigated conditions rather than, or in addition to, changes in carboxylation rate (Figure 1*j,k,l*). Although there is some question of the reliability of c_i measurements when g is low, the values presented here are deemed reliable based on the analyses and discussion presented in Appendix V.

d. Water use efficiency. All species showed a significant increase in instantaneous WUE, A/E, under non-irrigated conditions (Table 4, Figure 1*n*). *Acer saccharum* had high A/E under both treatments, related to its overall conservative gas exchange pattern. *Fraxinus americana* had the highest A/E under non-irrigated conditions due to its great reduction in mean g and g_{max}. There were species differences in A/E as well as treatment differences, with *F. americana* differing from the other species in having a particularly strong increase in A/E under non-irrigated conditions (Figure 1*n*). An analysis of variance (ANOVA) and a Tukey means test showed no species differences in seasonal mean vpd within treatments (data not shown); hence, the $\delta^{13}C$ values of species within treatments describe their relative long-term water use efficiencies. Three species showed significant treatment differences in vpd with higher vpd in the non-irrigated treatment (*B. papyrifera*, p= .0366; *F. americana*, p= .0520; *Q. rubra* p= .0456; overall treatment vpd shown in Table 3). However, in this case these differences in vpd do not compromise the interpretation of treatment differences in $\delta^{13}C$ as differences in long-term WUE (as explained in Appendix V). The higher vpd values experienced by non-irrigated plants would be expected to result in lower WUE for those plants compared to their irrigated counterparts. However, the opposite result was found. Hence, I interpret differences in $\delta^{13}C$ as differences in long-term WUE. Furthermore, there was a strong negative correlation between $\delta^{13}C$ and instantaneous c_i (r= -.78, p= .0001) and a strong positive correlation between $\delta^{13}C$ and A/E (r= .84, p= .0001), further supporting the interpretation of $\delta^{13}C$ as WUE. Thus, all species showed significant increases in both instantaneous and long-term WUE under non-irrigated conditions. There were no species differences in $\delta^{13}C$ and they all showed a similar drought response (Figure 1*o*).

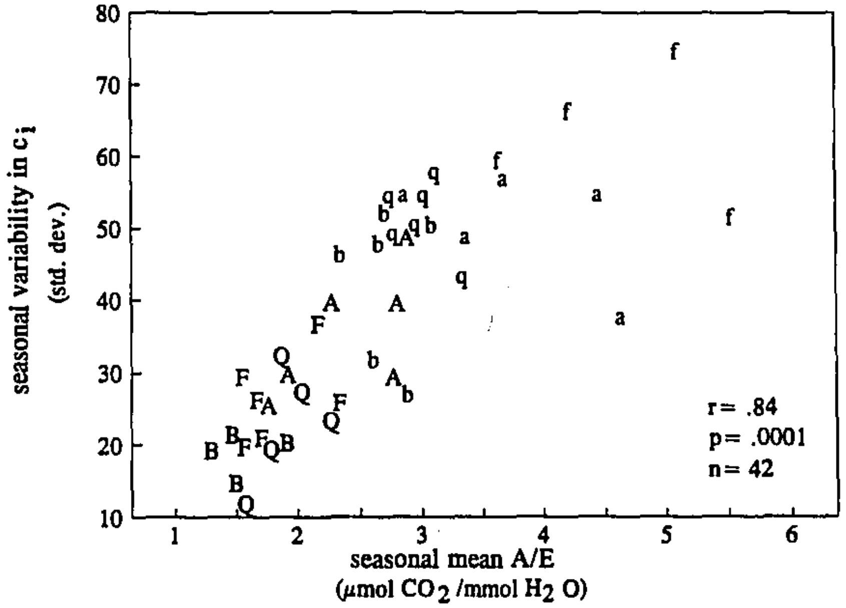
SLM, which showed a strong positive correlation with A_{max} (Figure 4), showed no relationship with c_i or $\delta^{13}C$ and a rather weak negative correlation with A/E (r= -.31, p= .0435). Hence, under the conditions of this study, high SLM, while strongly correlated with photosynthetic capacity, was not directly related to water conservation in these species. N_{mass}, however, was strongly correlated with both A/E (r= .56, p= .0001) and $\delta^{13}C$ (r= .65, p= .0001).

An unforeseen relationship was found between WUE and variability in c_i. Variability in c_i over the season was strongly correlated with both A/E and $\delta^{13}C$ (r= .84, p= .0001 and r= .79, p= .0001, respectively) (Figure 8*a,b*). Thus, WUE is related not only to seasonal mean c_i (which can be thought of as the c_i setpoint), but also with the extent to which c_i deviates from that setpoint over time. Variability in c_i was negatively correlated with seasonal mean A (r= -.67, p= .0001). Mean A was also negatively correlated with A/E (r= -.66, p= .0001) and $\delta^{13}C$ (r= -.47, p= .0018). These relationships indicate a trade-off between carbon gain and WUE at the leaf level and suggest that instability in c_i over time may result in lower mean A, but is part of the overall response that results in higher WUE. *Betula papyrifera* was the one species that had higher A as well as less negative $\delta^{13}C$ (higher WUE) under non-irrigated conditions (Figure 1*h,o*) and, thus, its ability to produce more efficient leaves of greater SLM circumvents the trade-off between A and WUE.

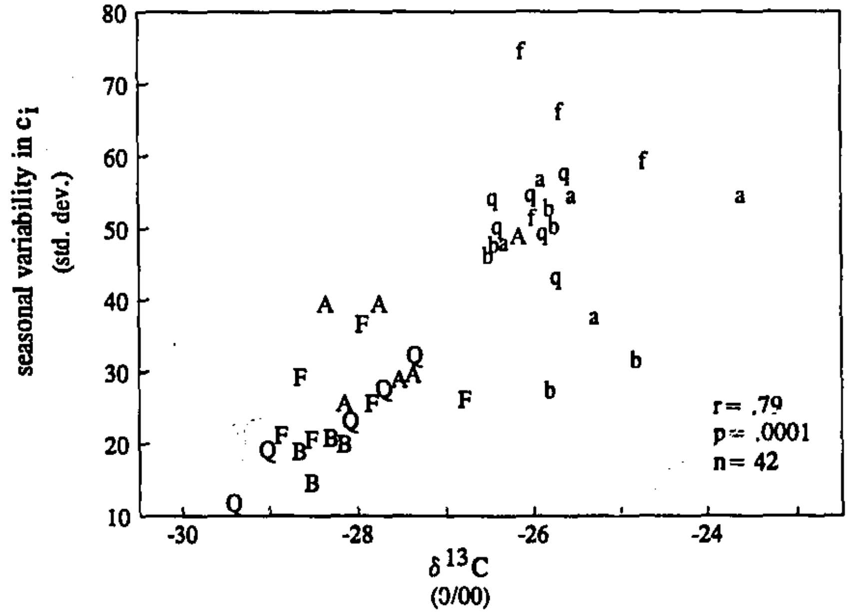
In summary, gas exchange response was such that each species showed greater WUE under non-irrigated conditions. This was related to a decrease in seasonal mean g and mean c_i (non-significant in *Q. rubra*) and an increase in N_{mass}. However, the uniformity and strength of the $\delta^{13}C$ response is striking (all species showed a similar significant response), given the species differences and differential responses in mean A, A_{max}, mean g, g_{max} and A/E and the species differences in c_i and variability in c_i. These results suggest that although A and g differed across species and were modified in species-specific ways in response to water shortage, the overall effects of these adjustments were such that the species showed similar responses in c_i, variability in c_i and, especially, $\delta^{13}C$.

Figure 8. Relationships between seasonal variability in internal CO_2 concentration (c_i) and seasonal mean A/E and carbon isotope ratio ($\delta^{13}C$). Spearman correlations and probabilities are given. Uppercase letters denote irrigated trees; lowercase letters denote non-irrigated trees. *Acer saccharum* - Aa, *Betula papyrifera* - Bb, *Fraxinus americana* - Ff, *Quercus rubra* - Qq.

a) seasonal mean A/E

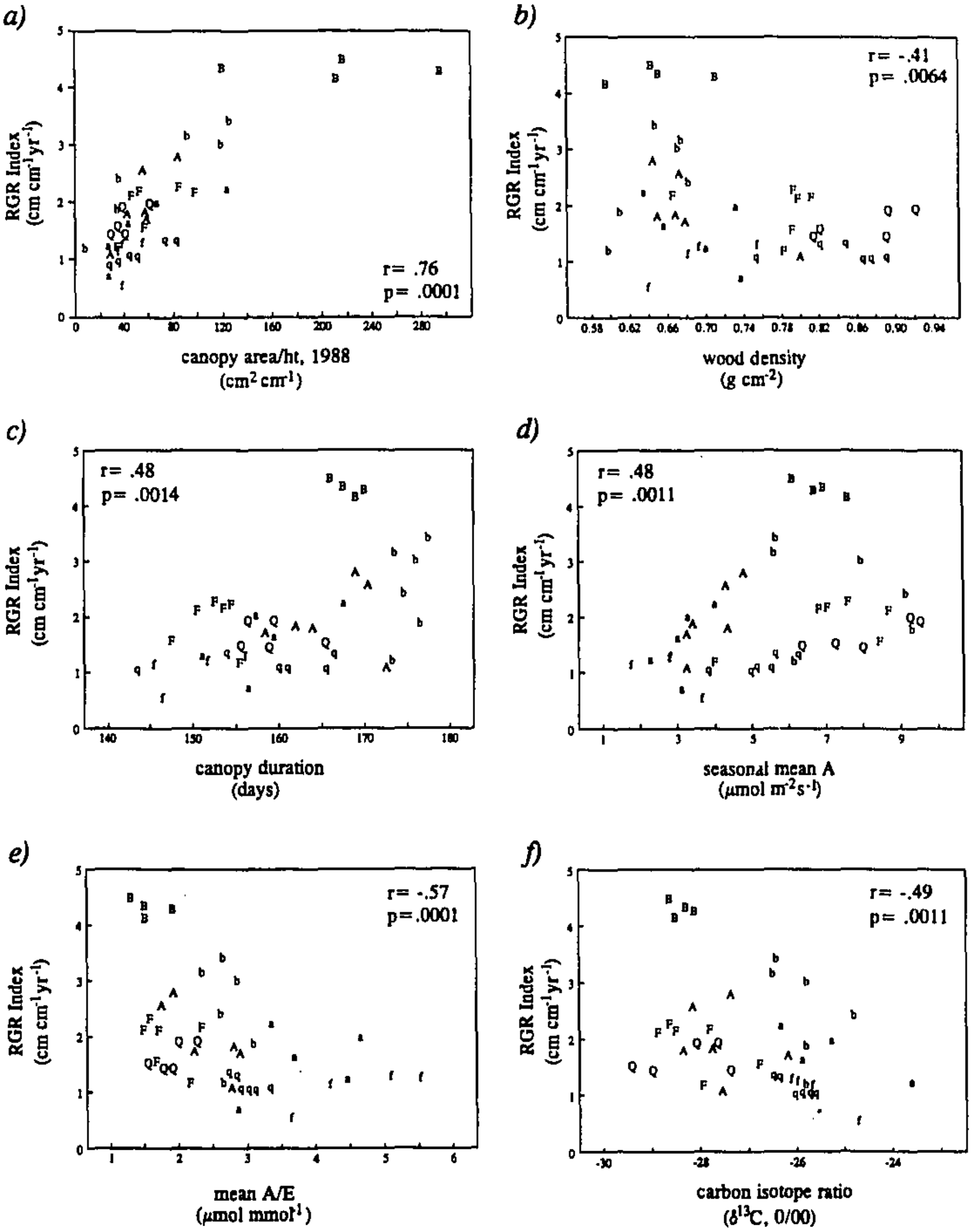


b) carbon isotope ratio ($\delta^{13}C$)



5. Relationships between RGR and other traits. RGR was directly related to a number of traits including traits that showed no treatment response and traits that did respond to different soil water regimes. RGR was positively correlated with canopy area (r=. 87, p= .0001) and canopy area/height (r= .76, p= .0001, Figure 9*a*). Not surprisingly, fast-growing (and, therefore, larger) trees had larger canopy area, but they also had greater canopy area per unit height, indicating greater proportional investment in leaves for a given height compared to more slowly growing trees. Although these correlations were strongly influenced by the high RGR and canopy area/height of irrigated *B. papyrifera*, the correlations were still highly significant when irrigated *B. papyrifera* was omitted (r= .82, p= .0001 and r= .68, p=.0001 for canopy area and canopy area/height, respectively). Greater investment in leaves, therefore, was related to higher RGR. On the contrary, wood density was negatively correlated with RGR (r= -.41, p= .0064; Figure 9*b*). *Betula papyrifera* had the lowest wood density, while *Q. rubra* had the highest. RGR was positively correlated with canopy duration (r= .48, p= .0014; Figure 9*c*) and seasonal mean photosynthesis rate (r= .48, p= .0011; Figure 9*d*). Both the high mean A and long canopy duration of *B. papyrifera* were related to the high RGR of this species. The other species had lower photosynthetic rates and/or were photosynthetically active for a smaller proportion of the available season. There were negative correlations between RGR and both A/E (r= -.57, p= .0001; Figure 9*e*) and $\delta^{13}C$ (r= -.49, p= .0011; Figure 9*f*), suggesting a trade-off between maximizing carbon gain and minimizing water loss at the whole plant level in these species.

Figure 9. Relationships between RGR and other traits among four broadleaved species grown irrigated (uppercase letters) and non-irrigated (lowercase letters). *Acer saccharum* - Aa, *Betula papyrifera* - Bb, *Fraxinus americana* - Ff, *Quercus rubra* - Qq. n= 42 trees.



Discussion

Universal responses to chronic intermittent drought.

Despite differences among the four species in the traits studied and the plasticity of those traits, plasticity at the leaf level was such that under conditions of chronic intermittent water shortage all species had increased water use efficiency (WUE), both on the short-term (A/E) and over the long-term ($\delta^{13}C$). This corroborates the results of a number of studies (Davies & Kozlowski 1977, Hinckley *et al.* 1979, Ranney, Whitlow & Bassuk 1990, Sands & Mulligan 1990, Parker & Pallardy 1991, Ellsworth & Reich 1992a, but see Tobiessen & Kana 1974, Abrams, Schultz & Kleiner 1990). Higher WUE was achieved primarily by reduced seasonal mean stomatal conductance (g) in non-irrigated seedlings *versus* irrigated seedlings. Reduced g and increased WUE were related to decreased seasonal mean internal CO_2 concentration (c_i) and also increased variability in c_i over the growing season. Seasonal variability in c_i has not been examined in this context before; however, it appears to be of considerable importance in plant carbon and water relations. In these four hardwood tree species, attaining high WUE appears to involve allowing c_i to deviate from its setpoint. This appears to have a negative effect on photosynthesis (A) as variability in c_i was strongly inversely related to seasonal mean A. This adds another element to the trade-off between maximizing carbon gain and minimizing water loss at the leaf level, in addition to lower g generally resulting in reduced A. When water is in short supply, all species conserve water at the expense of maintaining a stable c_i. Even *Betula papyrifera*, which had a higher photosynthetic capacity under drought conditions than when well-watered, had more variable c_i under non-irrigated conditions.

The uniformity of these leaf physiological responses (reduced seasonal mean g, lower and more variable ci, and higher WUE) across all four species was remarkable, given the species differences and differential responses in gas exchange rates.

Although A and g differed among species and were modified in species-specific ways in response to water shortage, the net result of these adjustments were such that all species showed increased instantaneous WUE (A/E) and uniform increases in long-term integrated WUE ($\delta^{13}C$).

Overall patterns of response and interrelationships among traits.

Overall, the greatest degree of plasticity in response to soil water regime was seen at the leaf level. There was no treatment response in architectural traits with the exception of canopy area/height in *B. papyrifera.* Lateral branch growth rate, leaf display index (LDI) and wood density showed no response, indicating little phenotypic plasticity in these traits under the conditions of this study. Hydraulic architecture was also little affected by water regime. Neither maximum specific conductivity (MSC) nor leaf specific conductivity (LSC) showed a treatment response in any species. This suggests that hydraulic architecture is rather stable across different soil moisture regimes. Any effects of water shortage on the timing of transition from production of earlywood to production of latewood (Zahner 1968, Creber & Chaloner 1984) or on xylogenesis (Aloni 1987, Bissing 1982) were insignificant in terms of the trees' xylem transport capacity. Aloni's (1987) hypothesis concerns the effects of reduced growth resulting in production of narrower vessels due to increased auxin concentrations along the shorter distances between auxin source (leaves) and regions of xylem differentiation. The relative decrease in leaf-to-stem distance in five-year-old saplings grown under non-irrigated *versus* irrigated conditions may not be great enough to cause differences in xylem vessel diameter sufficient to affect xylem transport capacity. The only response concerning hydraulic conductivity was a decrease in percent embolism in non-irrigated *Acer saccharum.* This response was unexpected and might suggest some plasticity in this species. However, *A. saccharum* showed the least reduction in RGR under non-irrigated conditions of all species and, therefore, based on Aloni's hypothesis, would be the least expected to show a morphogenetic response. More extreme water shortage may, however, affect architectural and hydraulic conductivity traits. For example, Shumway, Steiner & Kolb (1993) found decreased leaf area, potentially functional xylem area and LSC in *Quercus rubra* and *Liriodendron tulipifera* seedlings grown for two years under drought-stressed *versus* well-watered conditions. Their drought treatment was more extreme than the non-irrigated treatment in the current study, as their water-stressed seedlings received no natural rainfall. Khalil and Grace (1992) found increased xylem cavitation (detected as ultrasonic acoustic emissions) in *Acer pseudoplantanus* seedlings from which water was withheld for eight weeks compared to that in well-watered seedlings. Again, their study involved more extreme water shortage than that here.

Although hydraulic conductivity traits were, overall, not responsive to soil moisture conditions, they were related to gas exchange. Both MSC and LSC were positively correlated with stomatal conductance and photosynthesis, while MSC was negatively correlated with WUE. The water transport system is designed to meet the transpirational demands of the canopy. This coordination between the water conducting system and the canopy has been reported by Kaufmann and Troendle (1981), who found leaf dry weight and area to be closely related to sapwood area, although the ratio leaf area:sapwood area varied considerably among the species studied (three conifers and *Populus tremuloides*).

Although intraspecific variability was very high, the assays of hydraulic conductivity suggest that while ring-porous wood can provide a very efficient water conducting system (*Q. rubra*), this is not always the case, at least not for young saplings grown under the conditions of this study (*Fraxinus americana*). Furthermore, diffuse-porous species, such as *B. papyrifera* may be able to attain the conduction rates of some ring-porous species. In addition, ring-porosity alone is not totally responsible for high degrees of cavitation during late-summer drought or winter freeze-thaw cycles, nor does diffuse-porosity necessarily confer safety. Here, *Q. rubra* (with the largest diameter vessels; French 1923) had the lowest species mean loss of conductivity due to embolism, while the diffuse-porous *B. papyrifera* had the greatest loss. All species showed at least 50% embolism by March. Similarly high levels of embolism by late winter have also been reported by Sperry, Donnelly & Tyree (1988b), Cochard & Tyree (1990), Wang, Ives & Lechowicz (1992) and Tognetti & Borghetti (1994). Thus, substantial embolism seems quite common. The current study indicates that both ring-porous and diffuse-porous species are affected. *Acer saccharum* appears able to recover from embolism in spring (Sperry, Donnelly & Tyree 1988b); however, the genus *Acer* is unique in the production of positive xylem pressures in spring which refill the embolised vessels (Sperry, Donnelly & Tyree 1988b). We do not know how widespread the recovery phenomenon is among other hardwoods. In most species, embolism appears to permanently incapacitate the vessels (Milburn 1991). Although not much is known about recovery in other species, presumably there is sufficient recovery or a sufficient number of unembolised vessels in diffuse-porous species to permit budbreak before new xylem vessels are produced.

The lack of correlation between wood anatomy and both MSC and percent embolism by late winter emphasizes the importance of the number of vessels as well as vessel diameter for both maximizing conductivity and minimizing the impact of embolism on water delivery (Bass 1986, Tyree & Sperry 1989). The fact that larger diameter branches, in general, had higher MSC and lower percent embolism gives further evidence of this. A single cavitation event in a large diameter branch with more vessels would have a smaller impact on total conductivity than a single cavitation in a small branch with fewer vessels. In addition, the lack of correspondence between MSC and percent embolism highlights the fact that other xylem features, particularly pit membrane pore size, also influence susceptibility to cavitation (Tyree & Sperry 1989). In contrast to the results of this study, in a survey of 35 hardwood and 8 conifer species, Wang, Ives & Lechowicz (1992) found species with higher MSC had significantly higher loss of conductive capacity by late winter, supporting the theory that larger xylem conduits are more efficient, but "riskier" (discussed by Carlquist 1975, Baas 1986, Zimmermann 1983 and others). Such a correlation is not necessarily to be expected among young saplings of four hardwood species growing under contrasting water regimes.

In the current study, the ring-porous species did leaf out later than the diffuse-porous species as expected (Lechowicz 1984). However, timing of spring budbreak was not affected by chronic intermittent water shortage. Also, there was no correlation between date of budbreak and percent loss of conductivity due to embolism in contrast to that found in the broader range of variation represented by the 35 hardwood species studied by Wang, Ives & Lechowicz (1992). The proximate control of budbreak in temperate trees is usually the cumulative heat sum to which the buds are exposed after a prerequisite cold period (Ahlgren 1957, Kramer & Kozlowski 1979, Hunter & Lechowicz 1992) and, in some cases, also daylength (Bell & Johnson 1975, Heide 1993). The lack of correlation in the current study suggests that hormonal response to the proximate cues of budbreak in the young trees overrides the potential effects of xylem embolism on hydraulic conductivity. Thus, although timing of spring budbreak is linked to wood anatomy in an evolutionary sense, the actual timing of budbreak is triggered by environmental cues and is not directly affected by percent embolism. Although soil water shortage has been shown to be related to early leaf fall (Escudero & del Arco 1987) and severe drought to cause premature leaf abscission (Parker & Pallardy 1985), timing of fall senescence was affected only in *B. papyrifera*, which showed later senescence and, hence, longer canopy duration under non-irrigated conditions.

Across species and treatments, relative growth rate (RGR) was positively related to proportional allocation to leaves (estimated as canopy area/height), seasonal mean photosynthesis rate and canopy duration. Proportional allocation to leaf tissue *versus* stem and roots (measured as leaf area ratio, the ratio between total leaf area and total plant weight) was determined to be the primary factor contributing to variation in RGR in 24 herbaceous species (Poorter & Remkes 1990). Interspecific variation in RGR among seedlings of five deciduous tree species (including *A. saccharum, B. papyrifera* and *Q. rubra*) was also positively correlated with allocation to leaves (Walters, Kruger & Reich 1993). Photosynthetic rate measured on single leaves is often a poor indicator of growth rate (Körner 1991, Poorter & Remkes 1990, Poorter, Remkes & Lambers 1990). However, some studies have shown a positive relationship such as shown here (*e.g.* Walters, Kruger & Reich 1993). The negative relationship seen between RGR and wood density indicates a trade-off between rapid growth and investment in structural support and defense against pathogens (Loehle 1988). Higher wood density is related to increased tensile strength (Niklas 1994), which decreases susceptibility to windthrow (King 1986) and also increases pathogen resistance (Loehle 1988). High wood density is typical of late successional, long-lived canopy dominant trees, such as *A. saccharum* (King 1986, Lei & Lechowicz 1990). The negative relationship between RGR and WUE suggests that the reduced carbon gain that generally results from increased WUE has a long term impact on plant performance. Another possibility is that characteristics necessary to maximize growth rate (*e.g.* large canopy leaf area, high gas exchange rates) and those that are necessary for high WUE (*e.g.* low transpirational surface area, tight stomatal regulation of water loss) are mutually exclusive (Schuster *et al.* 1992).

Species-specific characteristics and responses to chronic intermittent water shortage.

Although the four species investigated in this study differ somewhat in geographic range and the site characteristics with which they are most commonly associated (Burns & Honkala 1990), they are found growing together on both good and poor sites and under various soil moisture regimes (Curtis 1959, Lambert &

Maycock 1963, Burns & Honkala 1990, Anderson *et al.* 1990). However, even though they do co-occur, they differ in longevity and do not all occur in late-successional forests. *Betula papyrifera* has a lifespan of <140 years (Loehle 1988). The other three species persist in late-successional forests with lifespans of 200-400 years (Loehle 1988). Of these three species, *Acer saccharum* is most successful at regenerating under a closed canopy because of its ability to form good root systems at low light levels and to grow fairly rapidly even in small gaps (Runkle 1984). Like *A. saccharum*, *F. americana* may have large numbers of seedlings present in the understory, but very few persist into larger size classes as they require more light to outcompete the *A. saccharum* seedlings and do well only in larger gaps (Runkle 1984). *Quercus rubra* appears least successful at regenerating under a closed canopy, establishing most successfully after large scale disturbance, such as fire, and along forest edges (Crow 1988, Burns & Honkala 1990, Abrams 1992). These differences in life history characteristics shed light on the different autecologies of these four species and the differences in the degree and nature of their response to chronic intermittent drought.

These diverse co-occurring species do to some degree have shared responses to drought (as discussed above); however, they also show species-specific responses to water shortage that are related to their differences in life history and in other traits. The early successional, shade intolerant *B. papyrifera* stands out from the other species in a number of ways. First of all, under well-watered conditions in the experimental nursery, *B. papyrifera* attained a high RGR (more than double those of the other species). Higher relative growth rates (RGR) are expected in early successional, shade intolerant species such as *B. papyrifera*, which must grow quickly to avoid overtopping by other species and reach reproductive maturity at an early age in order to colonize newly disturbed sites (Bazzaz 1979, Walters, Kruger & Reich 1993). This high RGR was achieved by the combination of a number of traits. *Betula papryifera* had a proportionally larger investment in canopy leaf area per unit height than the other species. This suggests it had a proportionally greater investment in leaves *versus* woody tissue. Greater allocation to leaves *versus* other tissue has been shown to correlate consistently with high RGR (Poorter & Remkes 1990, Lambers & Poorter 1992, Walters, Kruger & Reich 1993). *Betula papyrifera* also maintained high seasonal mean A and g rates, which were related to high specific leaf mass (SLM) and high investments in leaf N relative to the other species. High seasonal mean g allowed high seasonal mean internal CO_2 concentration (c_i), which would allow *B. papyrifera* to make efficient use of its photosynthetic machinery. *Betula papyrifera* appears to have an efficient diffuse-porous hydraulic system: it was able to sustain high stomatal conductance rates by having high MSC and LSC, similar to those of the ring-porous *F. americana*. In addition to having a high proportional investment in leaves, leaves with a high photosynthetic capacity and a hydraulic architecture that could support high gas exchange rates, *B. papyrifera* also had the longest canopy duration of the four species studied. Thus, it also made maximal use of the season available for photosynthesis. These characteristics show *B. papyrifera* to be well adapted to rapid establishment and growth in open, disturbed sites where light is not limiting.

Under conditions of chronic intermittent drought, *B. papyrifera* also displayed responses that set it apart from the other three species. It maintained a much higher RGR than the other species, even though its RGR was reduced nearly 42%. *Betula papyrifera* was also the only species to show plasticity in canopy architecture, having reduced canopy area/height and less leaf tissue under non-irrigated conditions. This decrease in canopy area/height resulted from the non-irrigated trees having fewer branches (*B. papyrifera* had the greatest percent reduction in branch RGR), rather than the spacing of leaves on those branches (LDI). *Betula papyrifera* also was plastic in leaf morphology, producing leaves of higher SLM under non-irrigated conditions than under irrigated conditions. This increase in SLM resulted in a particularly large increase in N_{area} in non-irrigated *B. papyrifera* and also much greater N_{area} than in the other species. The combined effect of increased SLM and N_{area} was a considerably higher A_{max} (although the increase was not statistically significant) and also the maintenance of reasonably high WUE under drought conditions (due to reduced transpirational leaf area). In a study of 26 hardwood species, Abrams & Kubiske (1990) found that all species produced leaves of higher SLM when grown in sun *versus* shade. Of four species in the current study (which were all included in Abrams & Kubiske's study), *B. papyrifera* had the greatest difference in SLM between sun and shade plants, although the others also showed a response. In spite of this generally plastic response to light regime, *B. papyrifera* was the only species to show a similar response in relation to drought in this study. *Betula papyrifera*'s indeterminate growth pattern (Marks 1975) would allow more rapid adjustment to current conditions compared to species with determinate growth and apparently allowed the production of leaves that were not only better suited to maintaining photosynthesis under drought conditions, but which were also able to persist longer into the fall relative to those of the other species and irrigated *B. papyrifera*. This longer canopy duration would partially compensate for potential gain lost due to drought conditions. The other species, producing all or almost all of their leaves in a single spring flush, would be unable to respond during the current growth season. However, since the drought treatment was imposed for five years, the lack of response suggests a lack of plasticity in leaf morphology in response to chronic intermittent drought in the later successional species.

Even though *B. papyrifera*'s seasonal mean g was reduced under non-irrigated conditions, it still had higher g than *A. saccharum*, *F. americana* and *Q. rubra*. Thus, it may be considered a "water spender" compared to the later successional species. However, like the other species, *B. papyrifera* had higher WUE (both A/E and $\delta^{13}C$) under non-irrigated conditions due to decreased seasonal mean g. Although it had relatively low WUE, its WUE did not differ markedly from that of the other species. Therefore, *B. papyrifera* does not fit the picture of a water spender such as

Populus tremuloides (another shade intolerant, early successional species), which appears to have little or no stomatal closure in response to soil water shortage (Tobiessen & Kana 1974). *Betula papyrifera* showed the same pattern of increasing WUE under drought conditions as did *A. saccharum, F. americana* and *Q. rubra*. Although it has diffuse-porous wood anatomy, *B. papyrifera* attained MSC and LSC values similar to those of the ring-porous *F. americana*, indicating that diffuse-porous wood anatomy does not necessarily constrain the rate of water transport. Its high seasonal mean g and rapid growth, even under drought conditions, relative to the other species suggest that *B. papyrifera* is efficient at extracting large quantities of water from the soil and, thus, may deplete soil moisture reserves to the detriment of neighbouring species (Cohen 1970, Bunce, Miller & Chabot 1977).

Overall, *B. papyrifera* is a species geared to maximizing carbon gain under both irrigated and non-irrigated conditions. Under non-irrigated conditions, it maintained high A and WUE through plastic adjustments in SLM and N_{area}, which together with the ability to maintain an active leaf canopy for longer than under irrigated conditions, helped mitigate the negative effects of chronic intermittent drought. Although its physiological and morphological adaptations to water shortage did not entirely buffer growth losses, it still had the highest RGR of the species studied. *Betula papyrifera* is, thus, able to successfully compete on the dry-mesic sites on which it is commonly found (Curtis 1959), growing rapidly to maturity and reproducing before being overtopped and replaced by longer-lived, more shade tolerant species.

The three species that persist in late successional forests differed from the short-lived *B. papyrifera*, but also from one another. The experimental nursery provided a fairly high light environment and when ample water was available, *A. saccharum, F. americana* and *Q. rubra* all grew steadily and at comparable rates. *Quercus rubra* had a slightly lower RGR by the size-based RGR Index used here, but its denser wood suggests the three species would be roughly equivalent in RGR if measured on a biomass-basis. These results parallel those of Walters, Kruger & Reich (1993), who found first-year seedlings of *Q. rubra* had slightly lower whole-plant mass-based RGR than *A. saccharum* seedlings, while both species had much lower RGR than *B. papyrifera*. Although the three species attained similar RGR under irrigated conditions, they achieved this comparable growth in different ways that are related to their wood anatomy type and life history characteristics.

Acer saccharum is distinguished from the other later succesional species in having diffuse-porous wood anatomy and in being very shade tolerant and able to survive for long periods in the low light levels of the forest understory (Canham 1985, Burns & Honkala 1990). It maintained a relatively slow, steady growth rate by means of comparatively low gas exchange rates over a long period of canopy duration. Under irrigated conditions, *A. saccharum* had leaf N_{mass} similar to that of *F. americana* and *Q. rubra*, but lower SLM. Similarly, lower SLM in both open and understory sites was found in shade tolerant *versus* intolerant trees in a comparison of 26 hardwood species (Abrams & Kubiske 1990). Similar N_{mass} but lower SLM resulted in somewhat lower N_{area} in *A. saccharum* relative to *F. americana* and *Q. rubra*. Lower N_{area} was related to the limited photosynthetic capacity of *A. saccharum* under irrigated conditions relative to the other two species. Although, its seasonal mean A and g, as well as maximum A (A_{max}) and maximum g (g_{max}), were much lower than those of *F. americana* and *Q. rubra*, *A. saccharum* operated at a similar internal CO_2 concentration (c_i setpoint). Its low mean g under irrigated conditions, coupled with its low A, suggests carboxylation capacity rather than water availability limited photosynthesis in this species. Other studies, such as those by Lei & Lechowicz (1990), Jurik (1986a,b) and Ellsworth & Reich (1992a,b) have also demonstrated the low photosynthetic capacity of *A. saccharum*. Under non-irrigated conditions, *A. saccharum* maintained its low A rates, but at reduced g, resulting in lower seasonal mean c_i and higher WUE. *Acer saccharum* has been shown to have little photosynthetic plasticity when growing under contrasting light regimes (understory, gap and clearing) (Ellsworth & Reich 1992a) as well as under different soil water regimes. Thus, *A. saccharum* appears to be conservative in leaf physiology under a range of environmental conditions. This supports the hypothesis put forward by Bazzaz & Carlson (1982) that late successional species have low photosynthetic plasticity compared to that of early successional species. Although their study included a wide range of plant types from early successional annuals to late successional trees, the pattern also seems to hold among tree species of different successional status. In addition, Tyree & Sperry (1988) suggest that the conservative g rates of *A. saccharum* are related to its apparent high vulnerability to catastrophic xylem dysfunction ("runaway" embolism in which xylem embolism causes increased tension in the remaining vessels, which then embolise, increasing tension further). Their model predicted that catastrophic xylem dysfunction would occur after only 5% loss of hydraulic conductance in *A. saccharum*, compared to after >15% loss in the three other species studied (Tyree & Sperry 1988). *Acer saccharum*'s conservative physiology and ability to maintain relatively slow, but steady growth under a range of environmental conditions (sun, shade, ample moisture and chronic intermittent drought) are tied to its ability to persist for long periods in the low-light, highly competitive environment of the forest understory.

Fraxinus americana and *Q. rubra* are similar to each other in having ring-porous wood anatomy (Core, Côté & Day 1979, Lechowicz 1984) and tap roots, at least as seedlings (Burns & Honkala 1990). These characteristics suggest that these species may be able to acquire and transport large quantities of water to their leaf canopies. Under irrigated conditions, *F. americana* and *Q. rubra* had much higher rates of A and g than *A. saccharum*; in fact, their rates were similar to those attained by *B. papyrifera*. Consistent with other studies of leaf phenology (Lechowicz 1984, Wang, Ives & Lechowicz 1992), the ring-porous *F. americana* and *Q. rubra* leafed out later than the diffuse-porous *A. saccharum* and *B. papyrifera* and also senesced earlier. Thus, while *F. americana, Q. rubra* and *A. saccharum* attained similar growth rates, *A. saccharum* accomplished this by maintaining low photosynthesis rates over a longer canopy duration, while *F. americana* and *Q. rubra* had higher photosynthesis rates which compensated for a shorter period of leaf activity.

The impact of the above-mentioned differences in gas exchange rates and wood anatomy between *A. saccharum*, on the one hand, and *F. americana* and *Q. rubra*, on the other, becomes more apparent under conditions of water shortage. *Fraxinus americana* and *Q. rubra* were more affected in terms of RGR (44% and 29% reduction under non-irrigated conditions in *F. americana* and *Q. rubra*, respectively) than *Acer saccharum* (20%), although the reduction in growth under non-irrigated conditions was statistically significant only in *Q. rubra*. *Fraxinus americana* and *Q. rubra* had significantly reduced seasonal mean A under drought conditions, in contrast to *B. papyrifera* and *A. saccharum*, the former maintaining high A by producing drought-adapted leaves and the latter maintaining its conservative physiological patterns. The reductions in seasonal mean A in *F. americana* and *Q. rubra* were accompanied by particularly steep declines in seasonal mean g suggesting that these ring-porous species were at greater risk of drought-induced xylem cavitation (Tyree & Sperry 1988, Tyree & Ewers 1991) than *A. saccharum* and *B. papyrifera* and, therefore, needed to reduce transpirational water loss by stomatal closure to the extent of significant reductions in A and seasonal carbon gain. *Fraxinus americana* showed the most visible damage due to water shortage, with premature leaf dehiscence in some trees under non-irrigated conditions. Not only were its seasonal mean A and g greatly reduced, but A_{max} and g_{max} were as well, indicating that non-irrigated *F. americana* were unable to take full advantage of favourable soil moisture conditions when they did occur (after natural rainfall). It had lower MSC and LSC and somewhat higher loss of conductivity due to embolism than *Q. rubra* (although the scatter in the data precluded statistically significant differences), suggesting that *F. americana* may be especially constrained in its gas exchange under drought due to the need to protect its hydraulic system (Tyree & Ewers 1991). Tight stomatal control resulted in its having the highest WUE of all species, but also resulted in the greatest reduction in growth rate (43.5%). As a species most common to wet-mesic sites (Curtis 1959, Maycock & Curtis 1963), it was least able to withstand chronic intermittent water shortage.

Unlike *F. americana, Q. rubra* maintained the capacity for high gas exchange rates under non-irrigated conditions, which would enable this dry-mesic species (Maycock & Curtis 1963) to take advantage of water when it was available. *Quercus rubra* seems to have a very efficient, but also relatively "safe" water delivery system; it had the highest species mean MSC and LSC of the four species, but also the lowest percent embolism (although the interspecific differences were, in general, not stastically significant), despite having much larger diameter xylem vessels in both earlywood and latewood (more than double the diameters of *F. americana* vessels) (French 1923). *Quercus rubra* was also found to have high MSC and comparatively low percent embolism relative to other ring-porous species in the study of 35 deciduous hardwood species by Wang, Ives & Lechowicz 1992. Low percent embolism (measured in late winter as in Wang, Ives & Lechowicz (1992) and the current study) is likely to be related not only to xylem features but also to the coordination of hydraulic architecture and stomatal regulation of water loss (Tyree & Ewers 1991) and features that might affect vulnerability to winter freezing-induced embolism and ability to recover from winter embolism, in addition to drought-induced embolism.

In summary, all four species are able to survive in the same successional forests under conditions of ample soil water and chronic intermittent drought. However, their means of doing so differ considerably and are related to their longevity and successional status and also to their wood anatomy and leaf physiological and phenological traits. *Betula papyrifera* stands out in having greater phenotypic plasticity in response to water shortage, which corresponds with an emphasis on maximizing carbon gain and RGR in order to successfully outgrow the longer-lived, more shade tolerant species. *Acer saccharum* represents the other extreme, maintaining slow, steady growth through a conservative physiology under different soil moisture regimes and also different light regimes (Ellsworth & Reich 1992a). This strategy enables *A. saccharum* to persist in the understory until it is able to reach the canopy after a series of release episodes initiated by the creation of small canopy gaps (Runkle 1984, Canham 1985, Ellsworth & Reich 1992a). *Fraxinus americana* and *Q. rubra* are similar to *A. saccharum* in growth rate and longevity, but are capable of higher gas exchange rates over their shorter periods of canopy duration and show a greater relative reduction in both seasonal mean A and RGR than *A. saccharum* under conditions of water shortage. These species require larger gaps or more open areas to reach reproductive maturity and are better adapted to take advantage of high light environments.

In conclusion, the differential responses of the four hardwood species studied to conditions of chronic intermittent water shortage reflected their life history characteristics and were related to their canopy and hydraulic architecture. Leaf-levels traits were related to successional status and shade tolerance, but the responses of the leaf traits were also related to hydraulic architecture. To fully understand interspecific variation in leaf-level response to water shortage, it is necessary to examine other aspects of plant structure and function and how whole-tree response is reflected in growth under well-watered conditions *versus* conditions of water shortage. Despite interspecific variation in number of traits, leaf traits showed the greatest plasticity in all species and all species showed the uniform response of increased WUE under drought conditions. Thus, not only do leaves appear to be the primary regulators of response to water shortage (Dickson & Isebrands 1991), but across these deciduous tree species, leaves have evolved similar mechanisms of response to water shortage.

CHAPTER 2

A comparison of gas exchange characteristics in 22 species of deciduous hardwood trees grown under chronic drought

Abstract

I examined the gas exchange characteristics and functionally related leaf traits of 22 deciduous hardwood tree species grown under chronic intermittent drought for four years. My focus was on the performance of the different species under natural conditions in the field. Repeated gas exchange measurements over two summers allowed comparison of long-term responses to water shortage integrated with short-term responses. The average physiological activity of each species under varying environmental conditions was examined by comparison of seasonal mean photosynthesis (A) and stomatal conductance (g) rates and internal CO_2 concentration (c_i), in addition to field maximum photosynthesis (A_{max}) and conductance (g_{max}) rates. The relationships of these traits to specific leaf mass (SLM), leaf nitrogen concentration (N) and carbon isotope ratio ($\delta^{13}C$), an indicator of long-term integrated water use efficiency (WUE), were examined. Across species, there was a strong trend of increasing A_{max} with concurrent increases in SLM and N_{area}, suggesting an underlying design for species-to-species variation in these traits. Seasonal mean A and g were strongly correlated, with variability in the relationship related to species differences in seasonal mean c_i. In turn, seasonal mean c_i was related to SLM and N per unit leaf area (N_{area}); species with higher SLM and N_{area} tended to have lower seasonal mean c_i. Species with higher N per unit leaf mass (N_{mass}), suggesting greater investment in photosynthetic enzymes, had higher long-term WUE estimated from $\delta^{13}C$ values. N_{mass} is shown to set an upper limit on the WUE ($\delta^{13}C$) a species can attain. Species with higher leaf N concentration appeared to be capable of greater WUE than species with low N concentration, although not all high N species had high WUE.

In addition to interspecific variation in seasonal mean c_i, the extent to which c_i varied over the season also differed among species. Although c_i is generally considered a conservative character, it does vary under different environmental conditions. The present study suggests that variability in c_i over time is related to both instantaneous WUE (A/E) and long-term WUE ($\delta^{13}C$). Species with less stable c_i over time appeared to be more efficient in their use of water than species with less variable c_i. Thus, stomatal regulation that allows c_i to vary results in greater WUE than regulation such that c_i remains relatively constant. However, greater variability in c_i was negatively correlated with A and g. Species with high gas exchange rates attained those rates at the expense of WUE, suggesting a trade-off between maximizing carbon gain and minimizing water loss in deciduous hardwood species.

Gas exchange rates appeared to be related to species' light requirements or shade tolerance, while water use characteristics were more closely related to habitat moisture preference. Under the conditions of the study, some species appeared to be geared towards maximizing carbon gain, having high gas exchange rates, relatively low and/or stable c_i, and low WUE under chronic drought conditions. Many of these species were species generally found in wet to wet-mesic habitats, *e.g. Populus deltoides, P. tremuloides* and *Juglans nigra*. Other species were more conservative in their water use and tended to have lower A and g and higher and/or more variable c_i. These species, including *Acer saccharum, A. rubrum* and *Prunus serotina*, tended to be mesic to dry species. However, there were exceptions to these general trends. Patterns of gas exchange under conditions of chronic intermittent drought were not entirely explained by traditional classifications of species by shade tolerance or habitat moisture preference.

Introduction

Co-occurring tree species in the northeastern deciduous forest region of North America differ in their habitat moisture preferences. Although most encounter periods of water shortage, commonly on a seasonal basis (Keever 1973, Spurr & Barnes 1980, Hinckley *et al.* 1981), they differ in their ability to withstand drought. Overall response to water shortage is the result of the integration of a number of plant traits and the responses of those individual traits (Chapter 1). Most studies have focussed on the short-term response of leaf traits to imposed or naturally occurring drought (*e.g.* Bunce, Miller & Chabot 1977, Davies & Kozlowski 1977, Abrams, Schultz & Kleiner 1990, Ranney, Whitlow & Bassuk 1990, Ni & Pallardy 1991, Ellsworth & Reich 1992a); however, survival and growth are related to long-term response. Although adaptations to extremely xeric conditions have been studied (Field, Merino & Mooney 1983, DeLucia & Heckathorn 1989, DeLucia & Schlesinger 1991, Smedley *et al.* 1991), little is known about long-term whole-tree responses to the common water shortages that are encountered by temperate forest trees and which determine species distributions along a moisture gradient within the temperate forest (Curtis 1959, Keever 1973, Peet & Loucks 1977, Burns & Honkala 1990). In this paper, I focus on the integration of long- and short-term gas exchange responses and functionally related leaf traits under chronic intermittent water shortage. The gas exchange responses of trees to drought have been shown to be varied (Chapter 1, Bunce, Miller & Chabot 1977, Davies & Kozlowski 1977, Hinckley *et al.* 1979, Abrams, Schultz & Kleiner 1990, Ni & Pallardy 1991). There appears to be no one way trees respond to water shortage. I will now briefly review the short-term and then the long-term leaf level responses to water shortage that have been reported for trees. One must bear in mind that the responses of a given species are likely to be related to both the habitat in which it is found and to other characteristics of that species that may constrain gas exchange response (Bradshaw 1965, Tyree & Sperry 1989). The relationship of gas exchange patterns to other traits, including leaf phenology and water transport capacity, is discussed in the following chapter.

Partial stomatal closure is a common and reversible short-term response to water shortage (Sands & Mulligan 1990). It reduces transpirational water loss, but also restricts the entry of CO_2 into the leaf and, hence, carbon fixation. However, due to the higher diffusive conductivity of CO_2 compared to water, transpiration (E) is reduced more than photosynthesis (A), resulting in greater water use efficiency (WUE, calculated as the ratio A/E). Other relatively short-term responses include changing leaf angle to reduce heat load (Sands & Mulligan 1990), rolling or folding leaves to reduce leaf surface area (Spurr & Barnes 1980), osmotic adjustment to maintain cell turgor at low tissue water potential (Hinckley *et al.* 1981, Abrams 1990) and allow a low water potential threshold for stomatal closure (Dougherty & Hinckley 1981, Abrams 1990), and producing leaves of higher specific leaf mass (SLM) (Zimmermann & Brown 1971, Abrams, Kubiske & Steiner 1990) and other xeromorphic characteristics (Zimmermann & Brown 1971, Spurr & Barnes 1980, Abrams 1990). The ability to rapidly recover physiological activity when water stress is relieved is also thought to indicate drought tolerance (Davies & Kozlowski 1977, Hinckley *et al.* 1981, Hicks & Chabot 1985). Under more extreme drought, leaf or branch abscission may occur (Parker & Pallardy 1985, Kozlowski, Kramer & Pallardy 1990, Sands & Mulligan 1990).

Many of the responses to drought events are also characteristics of trees found in dry environments and, thus, are involved in adaptation to xeric habitats as well as being short-term responses. Many trees in dry environments do have well-developed stomatal regulation of water loss (Sands & Mulligan 1990) and this has been hypothesized to be of importance in surviving drought. A number of studies have shown that trees adapted to more xeric conditions have higher A/E than more mesic species (*e.g.* Wuenscher & Kozlowski 1971, Davies & Kozlowski 1977, Field, Merino & Mooney 1983). Conversely, detailed studies of *Quercus alba* by Hinckley, Dougherty and co-workers (Hinckley *et al.* 1978, Hinckley *et al.* 1979, Dougherty & Hinckley 1981) have suggested that the ability to continue photosynthesis (and, hence, transpiration) under drought conditions may be involved in drought tolerance. Other studies have found that species from more xeric sites are less water use efficient than species from mesic habitats, suggesting that the ability to maintain high gas exchange rates and, hence, carbon gain, may be advantageous, especially in situations where other trees may be competing for the same water supply (*e.g.* Cohen 1970, Bunce, Miller & Chabot 1977, DeLucia & Schlesinger 1991). However, most comparative studies have involved species from xeric rather than more mesic or wet habitats (*e.g.* Abrams 1990, DeLucia & Heckathorn 1989, DeLucia & Schlesinger 1991) or, in studies of eastern hardwoods, species not differing greatly in habitat moisture preference (*e.g.* Abrams 1988a, Abrams, Schultz & Kleiner 1990). There has been little in the way of broad comparison across temperate hardwood species ranging from xeric to wet in habitat moisture preference. Thus, it is unclear which strategy (conservative or prolifigate water use) is most common in hardwood trees found in drier habitats or what other plant traits support each strategy. I hypothesize that there is a continuum among species rather than two distinct strategies and that the placement of a species along that continuum will be based on a number of factors, including carbon (C) and nitrogen (N) allocation, leaf phenology, growth type (determinate or indeterminate), and the ability to take up and transport water to the leaves. Before linking gas exchange characteristics to these other traits, we must first come to a better understanding of gas exchange patterns in hardwood trees under natural conditions.

Gas exchange response involves a number of interrelated traits including stomatal sensitivity, photosynthetic capacity and internal CO_2 concentration. The interrelationships among them are usually described in terms of the mechanistic model of C_3 photosynthesis developed by Farquhar, von Caemmerer and associates (Farquhar, von Caemmerer & Berry 1980, Farquhar & Sharkey 1982). The basic equations are summarized here to demonstrate the mathematical interdependence of photosynthesis (A), stomatal conductance (g) and internal CO_2 concentration (c_i) and how these relationships allow the use of carbon isotope ratio as an estimate of long-term integrated c_i and WUE. Photosynthesis rate is related to c_i and g according to the following equation (Ehleringer & Osmond 1989):

$$A = (c_a - c_i)\ g/1.6 \qquad (1)$$

where c_a and c_i are atmospheric and internal CO_2 concentrations, respectively, g is stomatal conductance and 1.6 is the ratio of the diffusivities of water vapour and CO_2 in air. Transpiration is related to conductance as follows:

$$E = \Delta wg \qquad (2)$$

where Δw is the leaf to air water vapour gradient. From these equations, instantaneous water use efficiency can be calculated:

$$A/E = (c_a - c_i)/(1.6\ \Delta w) \qquad (3)$$

Internal CO_2 concentration can be found by rearranging equation (1):

$$c_i = c_a - 1.6\ A/g \qquad (4)$$

Carbon isotope ratio ($\delta^{13}C$) has become popular as a measure of integrated ecophysiological function because, as shown by Farquhar, O'Leary & Berry (1982), it is related to c_i:

$$\delta^{13}C_{leaf} = \delta^{13}C_{air} - a - (b - a)\ c_i/c_a \qquad (5)$$

where $\delta^{13}C_{air}$ is about 8‰, a is the fractionation due to the slower diffusion of $^{13}CO_2$ relative to $^{12}CO_2$ (4.4‰) and b is the fractionation caused by discrimination against $^{13}CO_2$ by RuBP carboxylase (about 27-30‰) (Farquhar, Ehleringer & Hubick 1989). Provided that the vapour pressure deficit (vpd) is the same across plants and/or species and environments being compared and the plants do not differ in the fraction of carbon gain that is respired, $\delta^{13}C_{leaf}$ (henceforth, $\delta^{13}C$) is also a measure of integrated WUE, based on equation (3) (Farquhar & Richards 1984, Ehleringer, Phillips & Comstock 1992). If the assumptions concerning vpd and respired C are met, species with higher long-term WUE are expected to have higher (less negative) $\delta^{13}C$ values (*i.e.* show less discrimination against ^{13}C).

From the above equations, it is apparent that c_i and both instantaneous and long-term WUE are determined by the relationships among the rate of influx of CO_2 into the substomatal cavity, the rate of carbon fixation at the carboxylation sites, and the rate of efflux of water vapour out of the leaf. They are affected both by environmental factors that influence A and g and by internal factors, such as carboxylation efficiency. Other leaf traits that are inherently related to A, g and c_i include specific leaf mass (SLM) and leaf N content. SLM is generally positively correlated with photosynthetic capacity (Jurik 1986, Ellsworth & Reich 1992b, Shipley & Lechowicz *in review*) and, as mentioned above, increased SLM may be a response to drought stress or an adaptation to drought conditions (Zimmermann & Brown 1971, Abrams, Kubiske & Steiner 1990). By reducing the leaf surface area to volume ratio, transpirational area is reduced. Thus, leaves of higher SLM may have higher WUE, all else being equal. Leaf N is also correlated with photosynthetic capacity (Field & Mooney 1986, Reich, Walters & Ellsworth 1991a, 1992, Ellsworth & Reich 1992b) since much of the nitrogen in the leaf is in photosynthetic enzymes (Evans 1989). Both high SLM and high leaf N concentration might be expected to be correlated with lower c_i; a leaf with high SLM will have less surface area for CO_2 entry and greater diffusive resistance than a leaf of the same mass but lower SLM, while a leaf with more carboxylation sites due to a higher investment of N in photosynthetic enzymes will be able to draw down CO_2 within the leaf more rapidly than a leaf of lower N concentration. Thus, c_i is determined proximately by A and g, but is ultimately affected by SLM and leaf N. Each of these traits may vary among species and under different environmental conditions. Hence, a full understanding of gas exchange patterns requires examination of SLM and N in addition to environmental effects on A and g. There is interspecific variation in these traits; thus, the interactions among traits and the effect of these interrelationships on response to water shortage are especially well suited for comparative study.

To investigate gas exchange responses of hardwood trees to drought, I examined patterns in a wide range of sympatric species grown under more or less natural conditions in an experimental nursery under a regime of chronic intermittent water shortage. Theoretical models and experiments performed under controlled conditions have greatly increased our understanding of gas exchange in response to specific environmental factors, such as light (Weber *et al.* 1985, Wong, Cowan & Farquhar 1985a, Jurik, Weber & Gates 1988), transient light (Wong, Cowan & Farquhar 1985b, Chazdon & Pearcy 1986, Pearcy 1988, Knapp & Smith 1987), CO_2 (Pearcy & Björkman 1983, Wong, Cowan & Farquhar 1985a), temperature (Jurik, Weber & Gates 1988), humidity (Schulze 1986, Aphalo & Jarvis 1991), salinity (Ball & Farquhar 1984a,b), drought (Wong, Cowan & Farquhar 1985c, Schulze 1986, Abrams, Kubiske & Steiner 1990, Wise *et al.* 1990, Ni & Pallardy 1991) and mineral nutrition (Wong, Cowan & Farquhar 1985a, Reich, Walters & Tabone 1989). Recently, attention has turned to examination of plant performance under natural and varying conditions (Lechowicz & Ives 1989, Cheeseman *et al.* 1991, Ellsworth & Reich 1992a). I chose to examine response under varying field conditions to determine the average performance of the different species. This focus differs from the more traditional approach of examining photosynthetic capacity under optimal (or at least, light-saturated) conditions. My primary interest is in gas exchange in the field under the conditions the trees normally encounter, which are very often not optimal. There is likely to be great variability in such field data. The approach I have taken is to assay gas exchange repeatedly over a range of conditions (which cannot be completely described or quantified), thus, incorporating much of the variation that exists (see Cheeseman *et al.* 1991). I have used seasonal mean values for gas exchange characteristics as a measure of the average activity of each tree under the range of conditions it encounters. My questions concern how the species are actually performing relative to each other in their often less than optimal environments rather than examining the physiological capacities of the different species, although the sampling method does allow estimation of the latter. The regime of chronic intermittent drought represents one meaningful environment. Examination of performance in other naturally encountered environments would further enrich our understanding of gas exchange patterns in deciduous trees and would help bring out the full nature of the trade-offs among traits and implications for habitat preferences and competitive ability in this set of species; however, such study was beyond the scope of the current work.

The instantaneous gas exchange measurements taken on 47 occasions over two summers show performance under the conditions of the assay, but also incorporate longer term responses to drought conditions. They, therefore, describe integrated gas exchange response which will be linked (in Chapter 3) to other aspects of tree ecology to provide a better understanding of whole plant response and function under drought conditions. There are as yet no general expectations for whole tree response to water shortage. The questions I attempt to answer include: How do realized A, g and c_i compare across tree species under chronic intermittent drought? How are these traits related to leaf investments in C and N? What are the relationships between these traits and WUE, both instantaneous (A/E) and long-term ($\delta^{13}C$)? Are patterns that emerge, if any, related to traditional classification of the species according to habitat moisture preference or shade tolerance?

Materials and Methods

1. *Experimental tree nursery.*

An experimental tree nursery was established at the Mont St. Hilaire Research Centre of McGill University (45°32'N, 73°8'W; 140m). The nursery was set in an open area on deep sand and consisted of 1 m^2 raised plots topped with 10 cm of commercial topsoil. The sand is a glacial sea deposit (Occhietti 1989), circumneutral to slightly alkaline in pH, with quite a good clay fraction; it, thus, has a higher nutrient binding capacity than typical sand. The artificial A horizon (commercial topsoil) and the underlying sandy B horizon together comprise a reasonably good soil, except for its high drainage and poor water-holding capacity (see Chapter 1). In November 1984, seed of 17 species was broadcast into the plots (one species per plot) and covered with soil to the depth required for germination. In May and June 1985, seed of the remaining 5 species was broadcast into single plots. In summer 1985, the plots were irrigated and fertilized (N-P-K: 11-41-8 in spring, 20-8-20 in early summer, 8-20-30 in late summer, Plant Products Co., Bramalea, Ontario). Commencing in 1986, the plots received only natural rainfall. The nursery environment provided less moisture than the seedlings' natural regeneration sites within the forest and along the forest edge; consequently lack of irrigation resulted in periods of intermittent water shortage (Chapter 1). The plots were watered only when necessary to prevent tree mortality (judged by severe wilting and initiation of leaf fall in at least one plot), once each summer. At such times, all plots were watered equally (with lawn sprinklers for 2-3 hours). They continued to be fertilized with slow-release fertilizer (Osmocote 14-14-14, Sierra Chemical Company, Milpitas, California, USA, or 10-10-10, Centre Agricole Harnois, Inc., Québec) once each spring and with two applications of micronutrients and 20-20-20 (Plant Products Co.) in late spring-early summer each year.

Seedlings were thinned as necessary to avoid overcrowding in the plots. In each plot, three seedlings were chosen randomly and individually tagged. These seedlings were used for all measurements described below.

2. *Soil moisture measurements.*

In the centre of the experimental nursery, a reference plot was established (described in Chapter 1) in which soil water potential at 15 and 30 cm depth was measured with soil psychrometers (model PCT55, Wescor, Logan, Utah, USA). Prior to installation, the psychrometers were individually calibrated against saline solutions of known water potential as described in Appendix II. Psychrometer measurements were taken in early morning and/or late afternoon-early evening (to minimize temperature gradients through the soil) using a Wescor psychrometric microvoltmeter (model HR-33T). Neutron probe measurements were taken at the same depths in the adjacent access tubes with a CPN model 503DR Hydroprobe (Pacheco, California, USA) and in the study plots in conjunction with gas exchange assays. In 1987, neutron probe measurements were taken in the study plots on 30 days (32 sets of readings); in 1988, neutron probe measurements were taken on 6 days (6 sets of readings in conjunction with the gas exchange assays conducted after July 7).

Neutron probe measurements were taken in the reference plot both before and after readings in the study plots (about 1.5 hr apart). In 1988, the means of the "before" and "after" readings were regressed with late-afternoon/early evening psychrometer readings (since most neutron probe measurements were taken in the afternoon) and these regressions used to convert the neutron counts obtained in the study plots to soil water potential (for 15 cm depth, $r^2 = .28$, $p = .02$; for 30 cm depth, $r^2 = .45$, $p = .0001$; Proc REG, SAS Institute, Inc. 1985a). In 1987, there were no consistent correlations between reference plot psychrometer and neutron probe values (due to inconsistent behaviour among the psychrometers); therefore, it was not possible to use the 1987 psychrometer values to convert the study plot neutron counts to soil water potential and the 1988 regression equations were used instead. The calculated overall seasonal mean soil water potentials at 15 cm and 30 cm for each year across the 22 study plots are presented in Table 1.

Precipitation was recorded with a WeatherMeasure Recording Rain Gauge, Model P501 (WeatherMeasure Corporation, Sacramento, California, USA) located in the experimental nursery.

3. *Gas exchange assays.*

I assayed the gas exchange of the tagged saplings on 34 occasions in 1987 (July 23 - Oct. 7) and 13 occasions in 1988 (June 14 - Sept. 16) at different times of day and under different environmental conditions (morning and afternoon, clear days, overcast days, cool, warm and hot days, days following rainfall and days during dry spells). The species and saplings within species were assayed in random order and the order re-randomized for each assay. For each assay, one randomly chosen healthy leaf from each sapling was measured using a LI-6200 Portable Photosynthesis System (LI-COR, Inc., Lincoln, Nebraska, USA). Care was taken to ensure that conditions in the cuvette were the same as ambient when the leaf was enclosed (Table 1). Measurements began as soon as the CO_2 concentration in the cuvette began to decline, within a few seconds of the leaf being clamped in the chamber. Measurements were terminated after a drawdown of 3 ppm CO_2 or after 60 seconds (in a few instances, 40 or 120 seconds) to avoid conditions in the cuvette deviating substantially from ambient. This protocol gives a point-in-time view of gas exchange under the conditions of the current assay. The photosynthesis (A), stomatal conductance (g) and internal CO_2 concentration (c_i) values used were those calculated by the LI-6200. The raw data were screened to remove unrealistic extreme values and measurements taken under non-ambient conditions. A, g, and c_i were averaged over the two years for each tree to provide mean values that reflect average activity

Table 1. Environmental and chamber conditions during gas exchange measurements (mean ± SD). Soil water potential values are based on readings over 30 days (1987, n= 704 observations) and 6 days (1988, n= 131 observations). Means of leaf chamber conditions based on 2557 observations.

Variable		Overall mean ± SD
1987 soil water potential (MPa)	15 cm	-1.72 ± 0.81
	30 cm	-0.59 ± 0.41
1988 soil water potential (MPa)	15 cm	-1.43 ± 0.70
	30 cm	-0.51 ± 0.33
quantum (μmol m^{-2} s^{-1})		885.5 ± 580.1
CO_2 concentration (ppm)		338.7 ± 9.1
t_{air} (°C)		25.4 ± 5.3
range in t_{air} (°C)		0.4 ± 0.3
t_{leaf} (°C)		25.8 ± 5.6
range in t_{leaf} (°C)		0.7 ± 0.5
relative humidity (%)		43.5 ± 11.0
range in relative humidity (%)		1.2 ± 1.3
vapour pressure of air in chamber (kPa)		1.47 ± .58
range in vapour pressure (kPa)		0.46 ± 0.39
vapour pressure deficit (kPa)		2.01 ± 0.83

over the range of conditions encountered. Water use efficiency was calculated as A/E (photosynthesis/ transpiration: μmol CO_2 (mmol $H_2O)^{-1}$). Since transpiration values measured in a cuvette may differ substantially from true transpiration rates (McDermitt, 1990), A/g was also calculated. A/E and A/g were calculated for each measurement and two-year means calculated as for the other variables. Mean values of A, g, c_i, A/E and A/g for individual trees were used for all analyses. Field A_{max} and g_{max} were calculated as the 95th percentile of A and g values for each tree. This is not the maximum rate obtained under optimal (*i.e.* light-saturated) conditions as is usually reported, but reflects the maximum rate under natural conditions. Variability in c_i was taken as the standard deviation of c_i values for each tree. Only individual trees assayed both years were included in analyses.

4. *Leaf samples for SLM, N, $\delta^{13}C$.*

Leaf samples were collected Sept. 7-9 in 1988 and 1989. Eleven (1988) or 15 (1989) healthy leaves were chosen randomly from each tree and harvested. Leaf area (blade excluding rachis and petiole) was measured using a LI-3100 Area Meter (LI-COR, Inc.). The leaves were dried at 70°C, weighed, and specific leaf mass (SLM, mg cm^{-2}) determined from the bulk leaf sample for each tree. Leaf nitrogen (N) concentration was then determined using a standard Kjeldahl procedure (as described in Chapter 1). Nitrogen per unit leaf area (N_{area}) was calculated from SLM and mass-based N (N_{mass}, % N).

Carbon isotope ratio was determined according to the in-vial combustion technique described by Ehleringer & Osmond (1989). Subsamples of 2-3 mg of ground dried leaf tissue were combusted at 850° for 6h in sealed, evacuated Vycor tubes containing cupric acid and silver foil and then slowly cooled to room temperature. The CO_2 produced by combustion was purified cryogenically and its $\delta^{13}C$ value measured on a delta S Finnegan MAT isotope ratio mass spectrometer (San

Jose, California, USA).

The SLM and leaf N values, and carbon isotope ratios reported are the means of the 1988 and 1989 values. Since most likely the majority of leaves in these species are produced in spring from stored carbon reserves (Chapter 1, Kozlowski 1964, Dickson 1991) leaves sampled in 1988 and 1989 would most closely reflect the isotopic composition of the carbon assimilated in 1987 and 1988 when gas exchange was assayed. For a few trees (8), only one year's data were available for one or more variables. In these cases, the single year value was used in analyses.

5. *Statistical analysis.*

All measurements were taken on individual trees as my focus is on whole tree physiology. Comparisons were made at the tree level using Spearman non-parametric rank correlations (Proc CORR, SAS Institute Inc., 1985b). For all analyses $n=64$ trees, except for those including $\delta^{13}C$, for which $n=62$ (due to two missing samples for *Prunus pensylvanica*). Species values are, thus, the means of the values of the three saplings of each species (two of *Fraxinus americana* and *Ulmus americana* due to mortality). In Table 1, mean values for gas exchange conditions are based on the 2557 observations entering into analyses. Species differences in vpd were tested with analysis of variance and a Tukey means test (Proc GLM, SAS Institute Inc., 1985a).

Results

1. *Environmental conditions.*

Table 2 gives the total annual precipitation at St. Hubert, Québec (45°31'N, 73°25'W), near the Mont St. Hilaire Research Centre, from 1985, when the nursery was established, through 1990, when the full study was completed. The 53-year average annual precipitation is also presented (all data from Atmospheric Environment Service, Environment Canada). The years of the gas exchange assays were very dry; 1988 was the driest year on record since 1929 with 24.3% less precipitation than the 53-year mean of 1003 mm. 1987 was the fifth driest year, receiving 838 mm of precipitation, 16.4% less than average. Potential evapotranspiration (PET) (Pereira & Paes de Camargo 1989) and the ratio of PET to precipitation are also given in Table 2. Higher ratios of PET/precipitation indicate greater relative water shortage; 1987 and 1988 had considerable greater PET relative to precipitation as well as less precipitation than the other years of the study and the 53-year average (Table 2).

Although June 1987 had higher than average precipitation, July and August had less than half of the average for those months (Figure 1). Summer 1988 was dry from May through July, but had higher than average precipitation in August before returning to below average values for September. In 1987, the gas exchange measurements were concentrated mainly in the driest portions of the summer (Figure 2). In 1988, gas exchange assays were interspersed among days with moderate rain (10 to 25 mm).

Seasonal mean soil water potential values at 15 cm and 30 cm were calculated from the neutron probe measurements taken in the study plots (using regressions calculated from 1988 reference plot psychrometer and neutron probe data) and are presented in Table 1. Seasonal mean soil water potential was near or exceeding the permanent wilting point (-1.5 MPa) at 15 cm depth, while more soil moisture was

Table 2. Total annual precipitation (mm), potential evapotranspiration, PET (mm), and the ratio PET/ppt at St. Hubert, Québec. Percent deviation from the 53-year mean is given in parentheses.

Year	Total precipitation	PET	PET/ppt
1985	971.6 (-3.1%)	260.0 (-2.7%)	0.268 (+0.8%)
1986	1109.1 (+10.6%)	261.3 (-2.2%)	0.236 (-11.3%)
1987	838.1 (-16.4%)	257.2 (-3.7%)	0.307 (+15.4%)
1988	759.4 (-24.3%)	259.9 (-2.7%)	0.342 (+28.6%)
1989	895.6 (-10.7%)	248.5 (-7.0%)	0.227 (-14.7%)
1990	1214.6 (+21.1%)	262.8 (-1.7%)	0.216 (-18.8%)
53-year mean	1002.9	267.2	0.266

Figure 1. Monthly precipitation and potential evapotranspiration (PET) at St. Hubert, Québec, for April-October 1987-88 and 53-year mean values (capital letters).

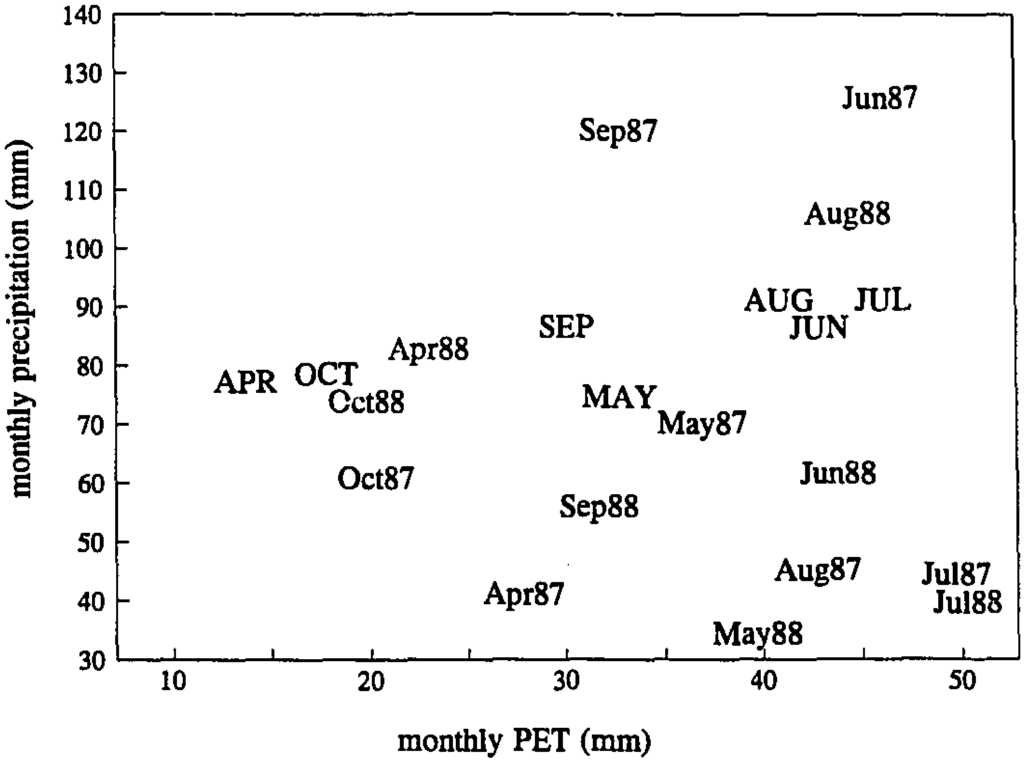
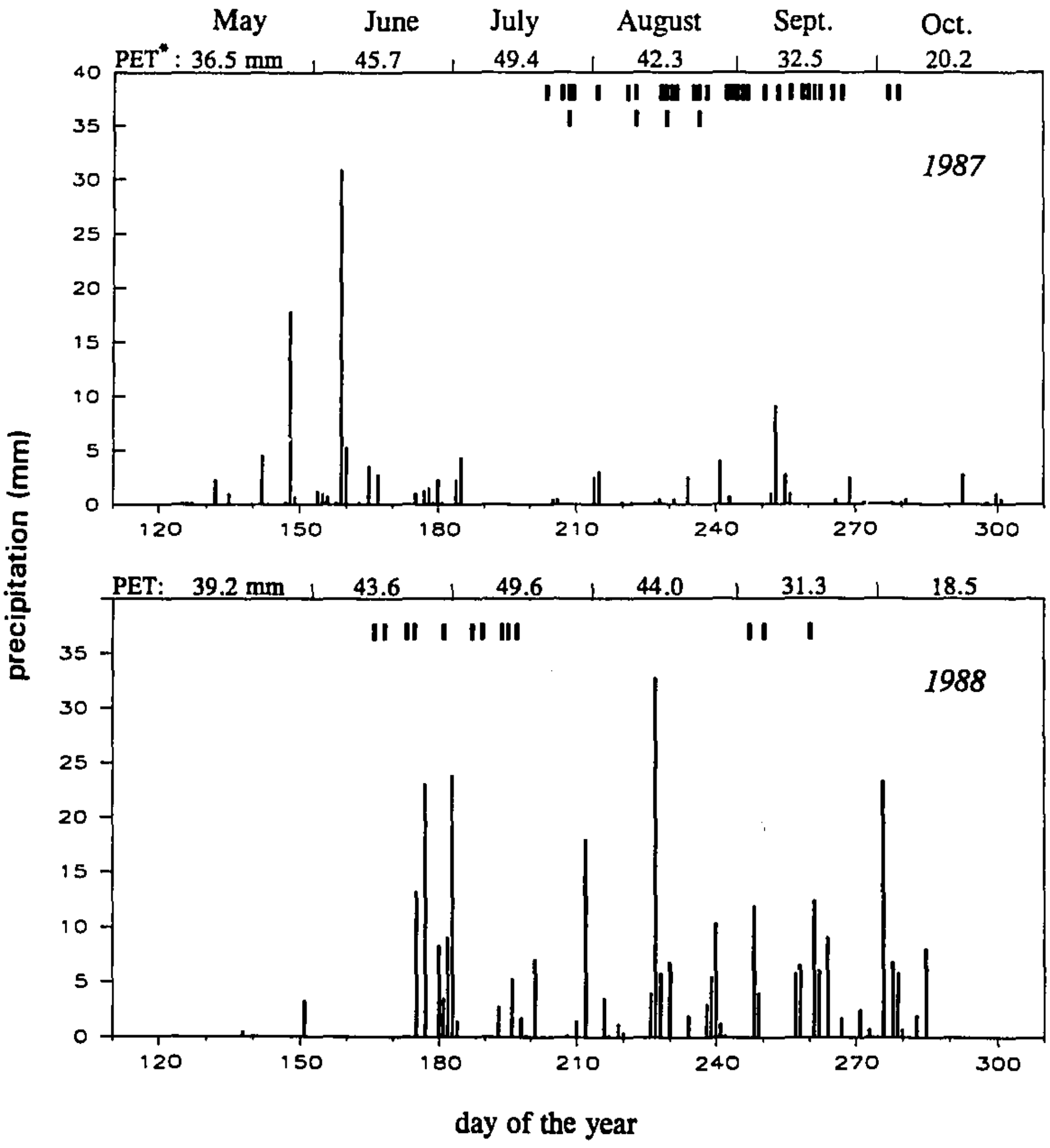


Figure 2. Summer rainfall at Mont St. Hilaire, Québec, 1987 and 1988. Gas exchange assays indicated by |.



* - monthly potential evapotranspiration

available at 30 cm depth.

The overall chamber conditions during the gas exchange assays are presented in Table 1. There were species differences in mean vapour pressure deficit (vpd) experienced; however, a Tukey means test showed great overlap of species (data shown in Appendix V). Therefore, differences in carbon isotope ratios ($\delta^{13}C$) can be interpreted as differences in long-term water use efficiency (WUE) as long as care is taken when making comparisons between specific species. Similar analyses of leaf temperature (data shown in Appendix V) and relative humidity (data not shown) showed even greater overlap among species further supporting interpretation of $\delta^{13}C$ as long-term WUE. Thus, species with higher (less negative) $\delta^{13}C$ values had higher long-term WUE.

2. *Gas exchange traits and species responses.*

Photosynthesis, conductance and internal CO_2 concentration.

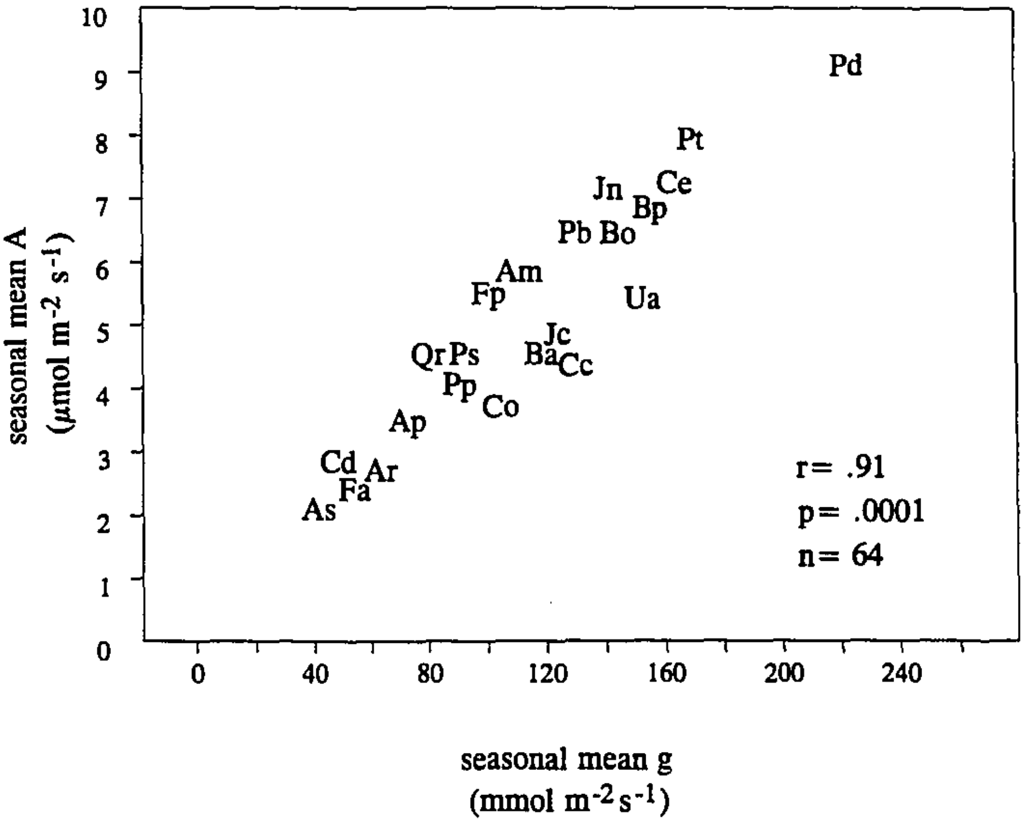
Mean photosynthesis (A) and stomatal conductance (g) were highly correlated (Table 3) indicating a tight link between photosynthetic activity and stomatal regulation across species and over the varying conditions encountered over the two seasons during which gas exchange was assayed. Mean photosynthesis increased linearly with mean g across species (Figure 3). High mean A and mean g characterized *Populus deltoides, P. tremuloides, Celtis occidentalis, Juglans nigra, Betula papyrifera, P. balsamifera* and *B. populifolia. Acer saccharum, Fraxinus americana, A. rubrum, Castanea dentata* and *A. pensylvanicum* had low A and g. Box plots showing the range, mean and median values for A, g and internal CO_2 concentration (c_i) for each species are presented in Appendix IV.

Although overall A and g were tightly correlated, greater variability in the relationship was found among species of median A and g than in those at the high or

Table 3. Spearman correlations among gas exchange parameters across 22 species of deciduous hardwood trees, r (probability). n=64, except correlations with $\delta^{13}C$, where n=62. Correlations significant at the 0.05 level are printed in bold type. Units: mean A, A_{max} - μmol m^{-2} s^{-1}; mean g, g_{max}, g at A_{max} - mmol m^{-2} s^{-1}; mean c_i, c_i at A_{max} - ppm; SD of c_i - std. dev. of c_i values; mean A/E - μmol CO_2/mmol H_2O; $\delta^{13}C$ - ‰; SLM - mg cm^{-2}; N_{area} - mg cm^{-2}; N_{mass} - % dry wt.

Trait	mean A	A_{max}	ci at A_{max}	g at A_{max}	mean g	g_{max}	mean c_i	SD of c_i	mean A/E	$\delta^{13}C$	SLM	N_{mass}
N_{area}	**.38 (.002)**	**.43 (.0005)**	-.06 (.64)	.22 (.07)	**.30 (.02)**	**.36 (.004)**	**-.34 (.006)**	.15 (.23)	.17 (.19)	.08 (.54)	**.63 (.0001)**	**.65 (.0001)**
N_{mass}	-.15 (.22)	-.15 (.25)	-.14 (.26)	-.20 (.10)	-.16 (.22)	-.08 (.53)	-.02 (.86)	.16 (.21)	-.03 (.80)	**.34 (.008)**	-.11 (.39)	
SLM	**.67 (.0001)**	**.70 (.0001)**	.06 (.64)	**.48 (.0001)**	**.54 (.0001)**	**.56 (.0001)**	**-.44 (.0002)**	.12 (.36)	**.30 (.02)**	-.22 (.09)		
$\delta^{13}C$	**-.62 (.0001)**	**-.46 (.0001)**	**-.42 (.0007)**	**-.56 (.0001)**	**-.74 (.0001)**	**-.65 (.0001)**	-.10 (.44)	**.36 (.004)**	.11 (.39)			
A/E	.14 (.28)	.09 (.48)	-.14 (.28)	-.04 (.76)	-.14 (.28)	-.08 (.52)	**-.78 (.0001)**	**.45 (.002)**				
SD of c_i	**-.37 (.003)**	-.21 (.09)	**-.30 (.02)**	**-.33 (.007)**	**-.44 (.0003)**	**-.28 (.02)**	-.15 (.23)					
mean c_i	**-.40 (.001)**	**-.34 (.006)**	.14 (.29)	-.15 (.25)	-.07 (.57)	-.08 (.55)						
g_{max}	**.83 (.0001)**	**.79 (.0001)**	**.40 (.001)**	**.77 (.0001)**	**.91 (.0001)**							
mean g	**.91 (.0001)**	**.82 (.0001)**	**.38 (.002)**	**.78 (.0001)**								
g at A_{max}	**.73 (.0001)**	**.76 (.0001)**	**.71 (.0001)**									
ci at A_{max}	**.26 (.04)**	.23 (.07)										
A_{max}	**.90 (.0001)**											

Figure 3. Seasonal mean photosynthesis (A) *versus* seasonal mean stomatal conductance (g) in 22 deciduous hardwood species.



Species:

Ap - *Acer pensylvanicum*
Ar - *A. rubrum*
Am - *A. saccharinum*
As - *A. saccharum*
Ba - *Betula alleghaniensis*
Bp - *B. papyrifera*
Bo - *B. populifolia*
Cc - *Carya cordiformis*
Co - *C. ovata*
Cd - *Castanea dentata*
Ce - *Celtis occidentalis*
Fa - *Fraxinus americana*
Fp - *F. pennsylvanica*
Jc - *Juglans cinerea*
Jn - *J. nigra*
Pb - *Populus balsamifera*
Pd - *P. deltoides*
Pt - *P. tremuloides*
Pp - *Prunus pensylvanica*
Ps - *P. serotina*
Qr - *Quercus rubra*
Ua - *Ulmus americana*

low extremes. This variability arises, at least in part, from functionally related variability in c_i. Across species, mean c_i ranged from 229 to 269 ppm (Table 4). This range of species means indicates that over the long-term under field conditions, species tend to operate at different species-specific c_i, which can be thought of as the species' c_i "setpoint". Figure 4 shows the relationship among the three variables. Species attaining similar mean A at different mean g (Figure 3) differed in their c_i setpoints in a predictable way: the species with higher g for a given A also had higher seasonal mean c_i (Figure 4, Table 5). For example, *Ulmus americana* had similar A to *Fraxinus pennsylvanica*, but had both higher mean g and mean c_i. The same pattern is seen in comparisons of *Carya cordiformis versus Prunus serotina* and *Betula alleghaniensis versus Quercus rubra* (Figure 4, Table 5). Overall, species with lower mean c_i tended to have higher mean A, although the moderate correlation coefficient (Table 3) indicates that other factors also influence the relationship. There was no correlation between mean c_i and mean g (Table 3) indicating that the c_i setpoint for each species is controlled more by carboxylation than by stomatal conductance. However, both A and g are involved because c_i is affected by both carboxylation rate and stomatal conductance and is, in fact, defined by their ratio (equation 4). The lack of correlation between mean g and mean c_i results in part from the differential effects of low and high g on c_i and A. At moderate to high g (>50 mmol m^{-2} s^{-1}), c_i decreased with decreasing g (reduced stomatal aperture limited diffusion of CO_2 into the leaf), while as g decreased below 50 mmol m^{-2} s^{-1}, A also appeared to be limited and reduced carboxylation caused c_i to increase again (the effects of low *versus* high g on c_i are discussed further in Appendix V).

Although there was no correlation between mean c_i and mean g for the reasons given above, c_i at A_{max} was strongly correlated with g at A_{max} (Table 3). High g at A_{max} would allow c_i to approach the external CO_2 concentration, which, in turn, would permit a higher carboxylation rate. There was no correlation between mean c_i and c_i at A_{max}, suggesting that some species were operating at non-optimal c_i at least some of

Table 4. Leaf characteristics of 22 deciduous hardwood tree species (mean ± SE).

Species	mean A (μmol m^{-2} s^{-1})	A_{max} (μmol m^{-2} s^{-1})	ci at A_{max} (ppm)	g at A_{max} (mmol m^{-2} s^{-1})	mean g (mmol m^{-2} s^{-1})	g_{max} (mmol m^{-2} s^{-1})
Acer pensylvanicum	3.49 ± 0.34	8.59 ± 0.17	233.3 ± 7.5	157.0 ± 15.8	73.3 ± 9.4	211.2 ± 51.4
A. rubrum	2.66 ± 0.82	8.64 ± 2.03	235.3 ± 13.0	145.9 ± 46.6	59.3 ± 12.5	169.7 ± 23.9
A. saccharinum	5.63 ± 0.40	11.16 ± 0.12	262.3 ± 14.6	245.1 ± 29.7	106.9 ± 3.1	251.3 ± 27.3
A. saccharum	2.12 ± 0.23	4.64 ± 0.58	207.1 ± 11.6	65.8 ± 10.1	41.8 ± 1.6	95.2 ± 3.1
Betula alleghaniensis	4.62 ± 0.52	9.95 ± 0.87	259.1 ± 4.0	240.6 ± 34.5	120.9 ± 15.1	264.1 ± 35.0
B. papyrifera	6.87 ± 1.06	12.88 ± 0.86	254.8 ± 9.7	262.9 ± 34.4	154.2 ± 14.4	373.7 ± 31.9
B. populifolia	6.47 ± 0.63	12.53 ± 0.68	240.6 ± 4.2	260.6 ± 30.4	143.7 ± 18.5	359.0 ± 27.8
Carya cordiformis	4.39 ± .25	9.96 ± 0.63	257.6 ± 36.4	244.2 ± 92.9	125.9 ± 4.8	282.1 ± 44.8
C. ovata	3.70 ± 0.41	8.56 ± 0.48	265.0 ± 18.6	223.8 ± 79.4	103.1 ± 15.9	264.6 ± 37.3
Castanea dentata	2.80 ± 0.42	8.47 ± 1.16	218.0 ± 12.6	127.4 ± 18.8	48.7 ± 7.4	126.7 ± 19.4
Celtis occidentalis	7.25 ± 0.89	13.17 ± 0.52	239.9 ± 3.1	259.5 ± 14.1	163.1 ± 26.1	336.2 ± 45.0
Fraxinus americana	2.56 ± 0.65	7.57 ± 1.41	226.3 ± 36.0	99.6 ± 5.3	57.3 ± 13.4	206.2 ± 30.4
F. pennsylvanica	5.53 ± 1.26	10.57 ± 2.38	262.0 ± 5.4	229.2 ± 50.2	106.7 ± 18.4	271.6 ± 24.5
Juglans cinerea	4.83 ± 0.13	10.11 ± 0.63	231.7 ± 10.0	174.2 ± 3.2	122.1 ± 3.5	342.5 ± 20.8
J. nigra	7.11 ± 0.44	13.87 ± 0.50	266.4 ± 10.1	397.4 ± 56.2	140.8 ± 10.6	357.2 ± 34.5
Populus balsamifera	6.41 ± 0.55	16.31 ± 0.63	228.4 ± 23.6	297.2 ± 50.7	129.8 ± 8.3	340.4 ± 15.4
P. deltoides	9.08 ± 0.67	17.57 ± 0.70	237.1 ± 11.0	354.0 ± 43.7	222.6 ± 20.3	469.3 ± 11.4
P. tremuloides	7.90 ± 0.32	14.75 ± 1.04	257.8 ± 15.5	356.7 ± 43.8	168.6 ± 8.8	379.9 ± 12.8
Prunus pensylvanica	4.01 ± 0.24	9.19 ± 1.12	210.3 ± 17.0	129.2 ± 5.24	90.7 ± 3.8	205.2 ± 15.3
P. serotina	4.47 ± 0.56	10.94 ± 0.72	251.0 ± 23.9	282.0 ± 93.6	90.0 ± 13.6	261.3 ± 46.8
Quercus rubra	4.54 ± 0.64	8.16 ± 0.61	198.9 ± 18.6	107.8 ± 19.0	80.8 ± 9.8	199.6 ± 16.0
Ulmus americana	5.40 ± 0.06	10.95 ± 0.33	277.0 ± 27.9	326.7 ± 97.3	150.6 ± 9.3	334.9 ± 60.7

(continued...)

Table 4 (continued)

Species	mean c_i (ppm)	variability in c_i (SD c_i)	mean A/E (μmol mmol^{-1})	$\delta^{13}C$ (0/00)	SLM (mg cm^{-2})	N_{mass} (% dry wt)	N_{area} (mg cm^{-2})
Acer pensylvanicum	239.4 ± 1.6	42.5 ± 1.8	3.42 ± 0.15	-25.71 ± 0.27	5.96 ± 0.42	1.33 ± 0.03	0.080 ± 0.004
A. rubrum	258.3 ± 11.0	51.9 ± 3.2	3.13 ± 0.33	-25.44 ± 0.33	6.16 ± 0.36	1.43 ± 0.04	0.089 ± 0.003
A. saccharinum	232.7 ± 5.4	42.8 ± 2.7	3.69 ± 0.15	-27.02 ± 0.04	6.96 ± 0.28	1.51 ± 0.12	0.107 ± 0.007
A. saccharum	246.9 ± 7.1	48.7 ± 4.3	3.20 ± 0.22	-24.26 ± 0.39	4.92 ± 0.50	2.06 ± 0.12	0.100 ± 0.012
Betula alleghaniensis	254.7 ± 3.3	39.3 ± 0.8	2.53 ± 0.10	-26.50 ± 0.29	6.34 ± 0.36	1.56 ± 0.04	0.100 ± 0.006
B. papyrifera	238.4 ± 9.6	45.3 ± 1.2	3.69 ± 0.37	-26.20 ± 0.25	9.33 ± 0.96	1.87 ± 0.14	0.175 ± 0.029
B. populifolia	238.3 ± 0.8	44.4 ± 1.1	3.62 ± 0.16	-27.11 ± 0.24	7.45 ± 0.09	1.38 ± 0.04	0.103 ± 0.003
Carya cordiformis	268.6 ± 4.3	39.3 ± 1.7	2.49 ± 0.13	-26.86 ± 0.32	5.93 ± 0.28	1.89 ± 0.13	0.113 ± 0.009
C. ovata	263.8 ± 4.9	40.5 ± 1.8	2.52 ± 0.23	-26.31 ± 0.41	6.37 ± 0.37	1.83 ± 0.05	0.117 ± 0.006
Castanea dentata	239.8 ± 0.8	49.8 ± 0.7	3.44 ± 0.18	-22.76 ± 0.09	5.98 ± 0.06	2.23 ± 0.18	0.128 ± 0.008
Celtis occidentalis	245.6 ± 4.0	36.9 ± 5.9	3.10 ± 0.13	-26.75 ± 0.39	8.40 ± 0.17	1.27 ± 0.09	0.111 ± 0.007
Fraxinus americana	254.4 ± 7.1	41.8 ± 5.7	2.98 ± 0.24	-24.77 ± 0.41	5.53 ± 1.02	1.62 ± 0.03	0.090 ± 0.014
F. pennsylvanica	230.9 ± 6.2	40.3 ± 2.3	3.82 ± 0.05	-26.31 ± 0.09	6.34 ± 0.81	1.88 ± 0.05	0.120 ± 0.016
Juglans cinerea	246.8 ± 6.3	47.1 ± 1.6	3.20 ± 0.13	-27.12 ± 0.46	7.33 ± 0.07	1.84 ± 0.10	0.136 ± 0.006
J. nigra	230.7 ± 3.1	39.9 ± 2.5	3.60 ± 0.08	-26.67 ± 0.33	7.27 ± 0.22	1.49 ± 0.22	0.108 ± 0.013
Populus balsamifera	239.0 ± 4.8	44.2 ± 3.6	3.10 ± 0.13	-25.47 ± 0.39	9.13 ± 0.61	1.63 ± 0.14	0.149 ± 0.012
P. deltoides	245.7 ± 1.3	38.2 ± 2.0	2.86 ± 0.15	-27.25 ± 0.75	7.14 ± 0.50	2.08 ± 0.02	0.148 ± 0.011
P. tremuloides	232.0 ± 1.8	43.7 ± 1.6	3.45 ± 0.21	-27.24 ± 0.09	7.91 ± 0.16	1.56 ± 0.04	0.124 ± 0.001
Prunus pensylvanica	246.5 ± 2.1	48.0 ± 1.9	3.96 ± 0.27	-27.80 ± .	6.34 ± 0.29	1.38 ± 0.03	0.087 ± 0.005
P. serotina	233.1 ± 3.2	61.2 ± 1.1	4.11 ± 0.08	-25.27 ± 0.52	8.86 ± 0.68	1.81 ± 0.11	0.162 ± 0.017
Quercus rubra	229.0 ± 4.1	40.7 ± 1.2	3.48 ± 0.12	-25.48 ± 0.18	6.36 ± 0.22	1.83 ± 0.08	0.117 ± 0.007
Ulmus americana	265.6 ± 2.8	32.9 ± 4.0	2.69 ± 0.08	-27.73 ± 0.56	5.22 ± 0.27	1.16 ± 0.06	0.059 ± 0.002

Figure 4. Relationships among seasonal mean photosynthesis rate (A), stomatal conductance (g) and internal CO $_2$ concentration (c_i) in 22 deciduous hardwood species. Species acronyms are the same as in Figure 3.

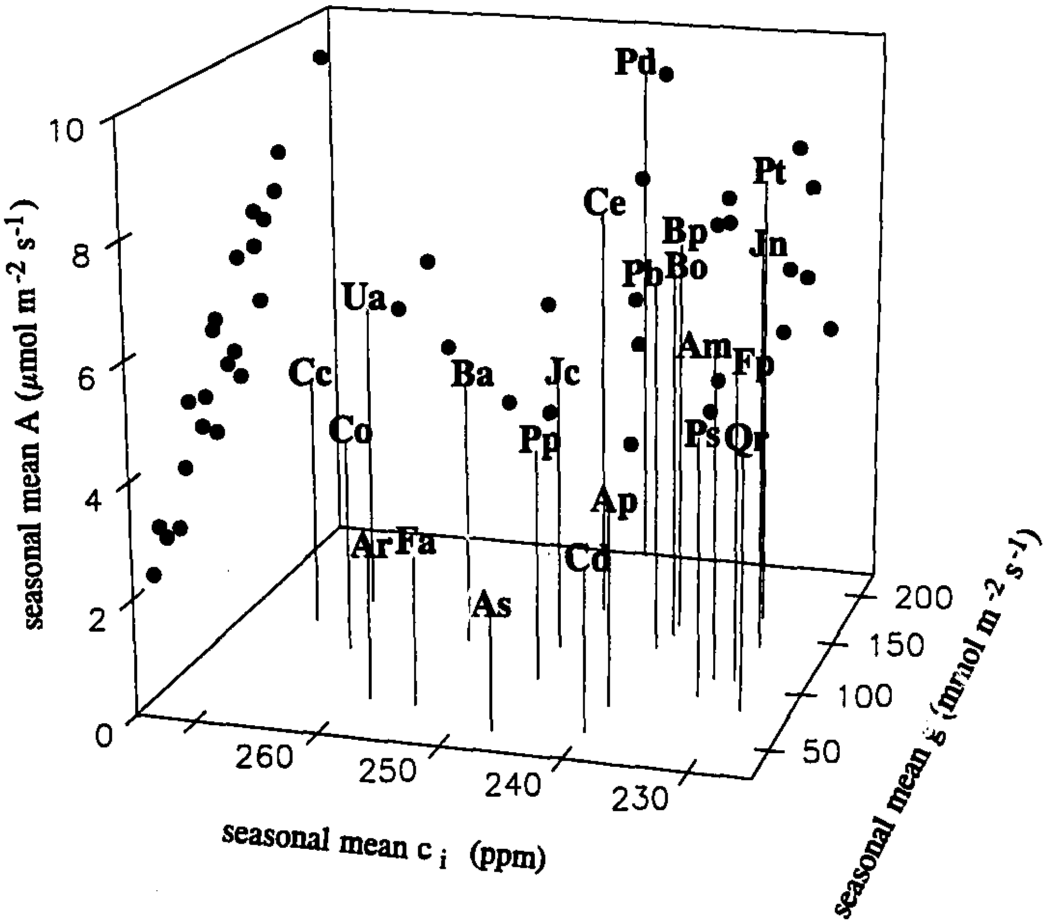


Table 5. Comparison of c_i, SLM, N_{area}, A/E and $\delta^{13}C$ in pairs of species with similar A, but differing g.

Species	Moisture class[1]	A	g	c_i	SLM	N_{area}	A/E	$\delta^{13}C$
1. Ua	WM	5.40	150.6	265.6	5.22	0.059	2.69	-27.73
Fp	W	5.53	106.7	230.9	6.34	0.120	3.82	-26.31
2. Cc	WM	4.39	125.9	268.6	5.93	0.113	2.49	-26.86
Ps	M	4.47	90.0	233.1	8.86	0.162	3.96	-25.27
3. Ba	WM	4.62	120.9	254.7	6.34	0.100	2.53	-26.50
Qr	DM	4.54	80.8	229.0	6.36	0.117	3.48	-25.48

[1] Moisture class: W - wet, WM - wet-mesic, M - mesic, DM - dry-mesic.

the time (*i.e.* either stomatal limitation or biochemical limitations to photosynthesis predominated rather than together co-limiting A (Farquhar & Sharkey 1982)). However, a more rigorous determination of c_i at A_{max} would be necessary to make a firm conclusion (c_i at A_{max} and g at A_{max} were taken as the values associated with the 95th percentile A values).

Species with high A and g and low c_i tended to be very intolerant to intermediate in shade tolerance (*e.g. P. deltoides, P. tremuloides, C. occidentalis, B. papyrifera, B. populifolia* and *J. nigra*) (Table 6, Figure 4), whereas species with low A and g and higher c_i tended to be intermediate to very shade tolerant (*A. saccharum, A. rubrum, A. pensylvanicum, F. americana* and *Carya ovata*). There were exceptions to these general trends: *Carya cordiformis* had high mean c_i, but is considered shade tolerant, while *Acer saccharinum* had high A and g and low c_i for a shade tolerant species. There was no apparent trend in terms of gas exchange rates in relation to habitat moisture preference.

Specific leaf mass and leaf N.

Leaf investments in N and carbon (SLM) reflected photosynthetic potential (A_{max}) more closely than realized photosynthetic activity under varying and often sub-optimal environmental conditions (seasonal mean A) (Table 3). I, therefore, examined the relationships among A_{max}, SLM and leaf N. I defined A_{max} as the 95th percentile of values taken over the two years for each tree. This field A_{max} and the two-year mean photosynthesis (A) were closely correlated (Table 3). This close correlation and the large number of assays taken under field conditions that included times when environmental conditions were likely to be optimal or near-optimal give us reasonable assurance that the A_{max} values do reflect photosynthetic capacity and, thus, are analogous to the A_{max} values that are usually reported in the literature. In other words, high A_{max} values reflect high photosynthetic capacity, which is realized

Table 6. Shade tolerance and habitat moisture preference of 22 deciduous hardwood tree species. Species acronyms are the same as in Figure 3.

Shade tolerance[1]	Habitat moisture preference[2]				
	dry	dry-mesic	mesic	wet-mesic	wet
very intolerant	(Bo)[3]	(Pt), Pp		(Pt)	Pb, Pd, (Bo)
intolerant		Bp	Ps	Cc, Jc, Jn	
intermediate	(Ce)	Cd, (Co), Qr		Ba, (Ce), (Co), Fa, Ua	Fp
tolerant		(Ar)		(Ar)	Am
very tolerant			As, Ap		

[1] based primarily on foresters' tolerance tables (Baker 1949, Fowells 1965, Burns & Honkala 1990).

[2] based primarily on descriptions by Curtis (1959), Maycock & Curtis (1960), Maycock (1963), Fowells (1965), Lambert & Maycock (1968), Hosie (1979), and Burns & Honkala (1990).

[3] species with bimodal moisture distributions are shown in parentheses in both moisture classes and are underlined in the class with greatest prevalence.

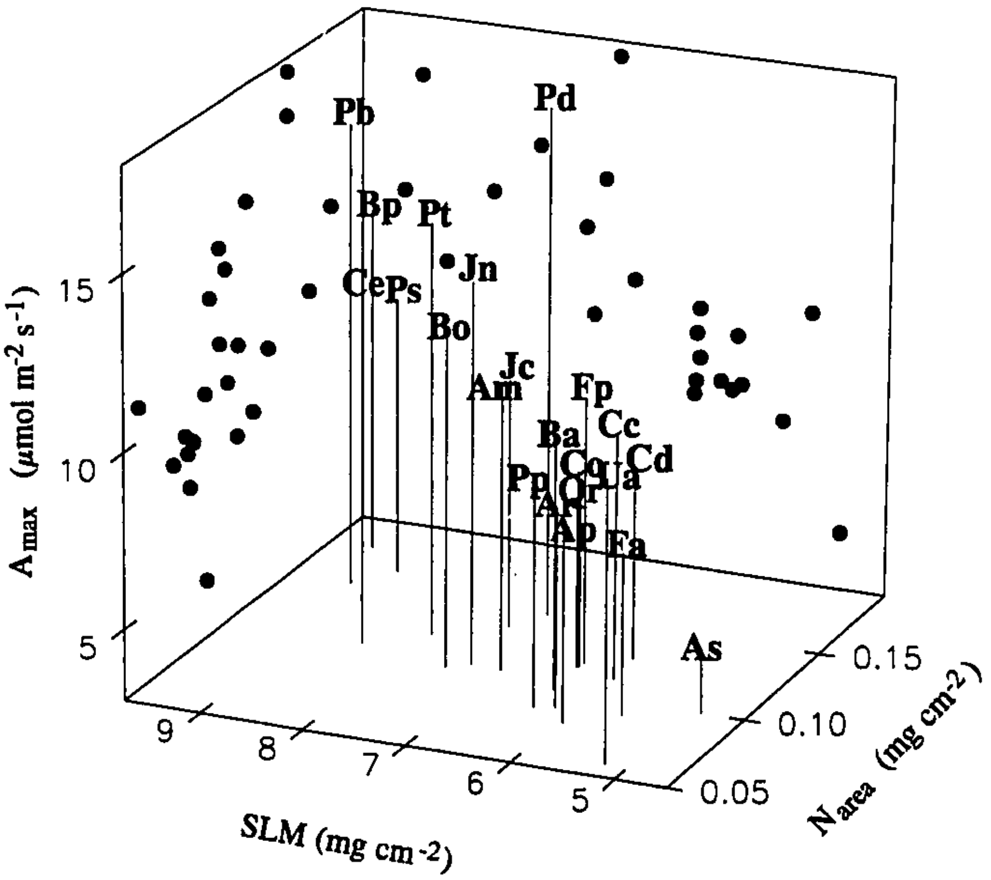
as high mean A.

Photosynthetic capacity, A_{max}, was positively correlated with specific leaf mass (SLM, mg cm^{-2}) and with leaf investment in N measured on an areal basis (N_{area}, mg N cm^{-2} leaf) (Table 3, Figure 5). A_{max} (which was measured on an area basis) was not correlated with N measured on a mass basis, N_{mass} (Table 3), due to interspecific differences in SLM. Overall, there was a strong trend of increasing A_{max} with increasing SLM and N_{area} (Figure 5). *Populus balsamifera, B. papyrifera,* and *P. tremuloides* had high A_{max}, SLM and N_{area}. Species with low A_{max}, SLM and N_{area} included *A. pensylvanicum, A. rubrum* and *F. americana.* In general, high A_{max} was the result of concurrent investment in SLM and N_{area}. However, there was some variability in the relationships. *Populus deltoides*, in particular, stands out as the species with the highest A_{max}, which was achieved at high N_{area}, but only moderate SLM. *Ulmus americana* had the lowest N_{area} and second lowest SLM, yet attained a moderate A_{max}, while *Acer saccharum* had the lowest A_{max} and low SLM, but moderate N_{area}.

Interspecific variation in seasonal mean c_i (the c_i setpoint) was related to both SLM and species investment in leaf N (N_{area}). In general, high SLM and high N_{area} were associated with low c_i (Table 3). Returning to the earlier examples of species pairs with similar A, but different g and c_i (Table 5), the species with the lower c_i values also had higher SLM and N_{area} than did their counterparts with higher c_i.

Species with higher A_{max}, SLM and N_{area} were generally intolerant or very intolerant of shade, while species at the lower end of the distribution were generally of intermediate tolerance or were tolerant or very tolerant of shade (Table 6). Exceptions to these groupings were *C. cordiformis* and *Prunus pensylvanica*, which are classed as intolerant and very intolerant of shade, respectively, yet had relatively

Figure 5. Relationships among maximum photosynthesis rate (A_{max}), specific leaf mass (SLM) and leaf N per unit area (N_{area}) in 22 deciduous hardwood species. Species acronyms are the same as in Figure 3.



low A_{max}, SLM and N_{area}. *Celtis occidentalis* had high A_{max} and SLM compared to other species of intermediate or greater shade tolerance.

In summary, gas exchange response is defined by a trio of interrelated traits, A, g and c_i, that are determined by leaf investment in N (N_{area}) and carbon (SLM) as well as by environmental effects on stomatal aperture. The relationships among this suite of traits and between these traits and environmental conditions determine water use efficiency on both a short-term (A/E) and long-term ($\delta^{13}C$) basis. These relationships are discussed in the next section.

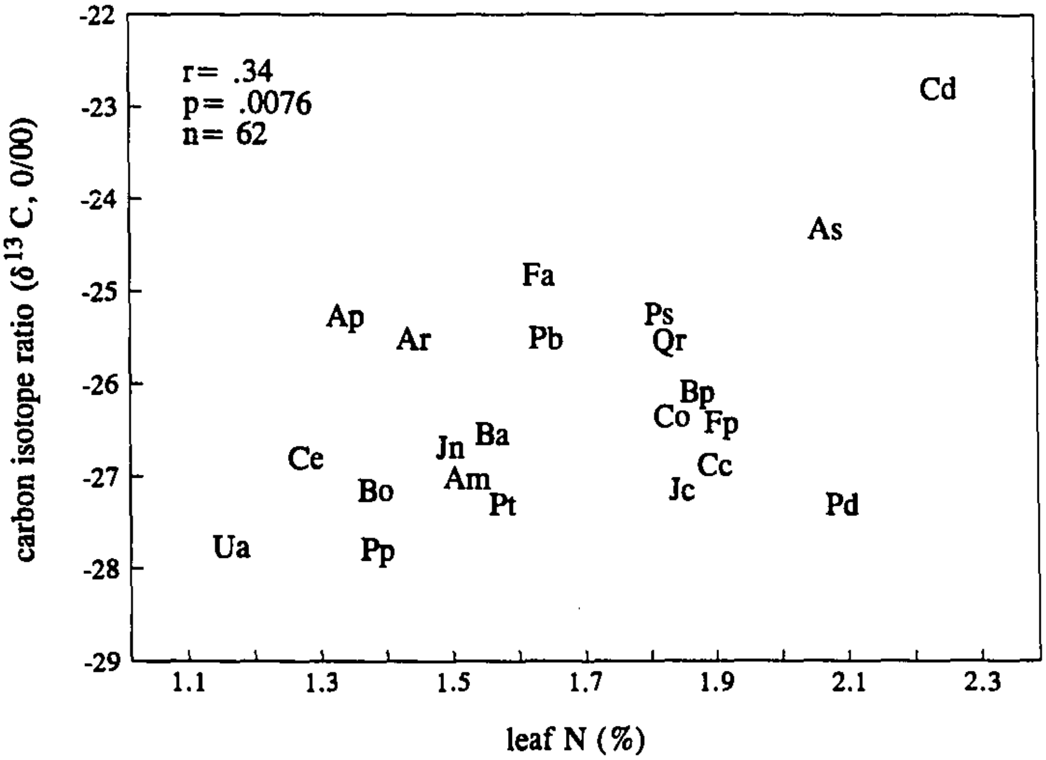
Water use efficiency.

Instantaneous water use efficiency (WUE) was calculated as both A/E and A/g. The two variables were highly correlated ($r= 0.82$, $p= 0.0001$) and correlations between them and the other traits measured were generally similar (data not shown). Since A/g is a nearly complete surrogate of c_i (equation 4), I have chosen to report A/E as a measure of instantaneous WUE, while remaining aware of the potential problems associated with chamber A/E measurements (McDermitt 1990). Mean A/E was correlated with neither A (Table 3) nor E (data not shown), reflecting the fact that it is based on the ratio of A to E rather than their absolute values. As expected from equation 3, A/E was strongly negatively correlated with c_i; species with low c_i had high short-term WUE. More interestingly, it was also positively correlated with variability in c_i (measured as the standard deviation of the values for c_i taken over the two growing seasons, Table 3), suggesting that species that allow c_i to deviate from its setpoint tend to be more efficient in their instantaneous water use.

Carbon isotope ratio ($\delta^{13}C$) is related to WUE through its relationship to c_i (equations 3, 5). In the present data set, there was no correlation between $\delta^{13}C$ and mean c_i (Table 3). This result was unexpected (see equation 5). However, $\delta^{13}C$ was negatively correlated with c_i at A_{max} across the 22 species (Table 3). More carbon will be assimilated when A is high than when it is low, therefore, the isotopic composition of the tissue will be weighted towards that of the carbon assimilated when A is high. Since mean c_i was not correlated with $\delta^{13}C$, the importance of peak events (when A is maximum) to total carbon gain is emphasized. Similarly, $\delta^{13}C$ was not correlated with mean A/E because while $\delta^{13}C$ is weighted towards times of high A, A/E is the seasonal mean of point-in-time measurements. Since the autocorrelations among A, g and A/E can confound biological interpretation of the data, I focus on $\delta^{13}C$ as an independent estimate of WUE.

Among the 22 species, there was a trend of increasing long-term WUE (less negative $\delta^{13}C$ values) with increasing N per unit leaf mass (N_{mass}), which combines SLM and N_{area} (Table 3, Figure 6). Considerable scatter in the relationship indicates that other aspects of the trees' organization are involved and the statistical significance of the correlation is driven by *C. dentata* (omitting *C. dentata*, r= .29 and p= .0271). However, the trend and placement of species is of interest. Most of the wet to wet-mesic species (*P. deltoides, C. cordiformis, F. pennsylvanica, J. cinerea, J. nigra, U. americana* and *A. saccharinum*) and species of bimodal moisture distributions tending to have greater prevalence in their wetter classification (*Betula populifolia, P. tremuloides* and *C. occidentalis*) had low long-term WUE, regardless of N_{mass}, while mesic to dry species (*A. saccharum, A. pensylvanicum, P. serotina, Q. rubra, C. dentata, B. papyrifera* and *C. ovata*, which appears to be more prevalent in its drier classification) had higher $\delta^{13}C$ values. Exceptions to this general trend were *A. rubrum* (a bimodal species), *F. americana* and *P. balsamifera*, which had higher $\delta^{13}C$ (higher WUE) than other wet species, and *P. pensylvanica*, which had lower $\delta^{13}C$ than other dry-mesic species. *Acer rubrum* is found on dry-mesic sites as well as on wetter sites. *Fraxinus americana* had very low values of A and g, along with low SLM and N_{area}, but moderate N_{mass}; it appears quite intolerant of drought conditions (see Chapter 1). *Populus balsamifera* had among the highest SLM and N_{area} values,

Figure 6. Carbon isotope ratio ($\delta\ ^{13}C$) *versus* leaf N (%) in 22 deciduous hardwood species. Species acronyms are the same as in Figure 3.



indicating a leaf structure that would tend to have lower transpiration rates. *Prunus pensylvanica* had unusually low δ^{13}C for a dry habitat species; however, this value is based on a single sample. Another tree in the same plot that was not included in the analyses had a δ^{13}C of -26.33 indicating that *P. pensylvanica* may not be as low in δ^{13}C as the single value presented suggests. *Castanea dentata*, apparently a dry-mesic species, had the highest δ^{13}C along with the highest leaf investment in N (N_{mass}). It had low g and moderately low c_i, resulting in a low seasonal mean A (Figure 4). The prime value of high N_{mass} in *C. dentata*, thus, appears to be high water use efficiency rather than a high mean A. In *A. saccharum*, a high leaf investment in N was also related to conservative use of water and low A. In *P. deltoides*, high N_{mass} did not lead to high WUE, but instead, coupled with high g, led to high mean A and A_{max}.

Species with less negative δ^{13}C values (indicating greater WUE), in general, had lower c_i at A_{max} (Table 3, Figure 7). More interesting than the negative correlation, however, is the appearance of a boundary line. As c_i at A_{max} increases, the upper limit to δ^{13}C decreases (see back wall projection in Figure 7). Many species fall below this upper limit. Species with high c_i at A_{max} appear unable to attain high WUE. Species with lower c_i at A_{max} may or may not have high WUE (again, note the value for *P. pensylvanica* should not to be weighed too heavily). This appears to be, in part, due to positive correlations between c_i at A_{max} and mean g and g_{max}. Species requiring high c_i to attain their maximum A rates tend to have relatively high g and, thus, greater water loss through transpiration.

The upper limit to δ^{13}C seen in Figure 7 is related to the degree of variability in c_i over the season (Figure 8). In addition to having different c_i setpoints, species differed in the extent that c_i varied over time. When variability in c_i was taken as the standard deviation in c_i, species with a more stable (less variable) c_i had lower mean WUE (A/E as well as δ^{13}C) (Table 3). As variation in c_i increased, so did the potential WUE. Thus, species with fairly stable c_i over time, such as *U. americana,*

Figure 7. Relationships among carbon isotope ratio ($\delta^{13}C$), internal CO_2 concentration (c_i) at A_{max} and % leaf N (N_{area}) in 22 deciduous hardwood species. Species acronyms are the same as in Figure 3.

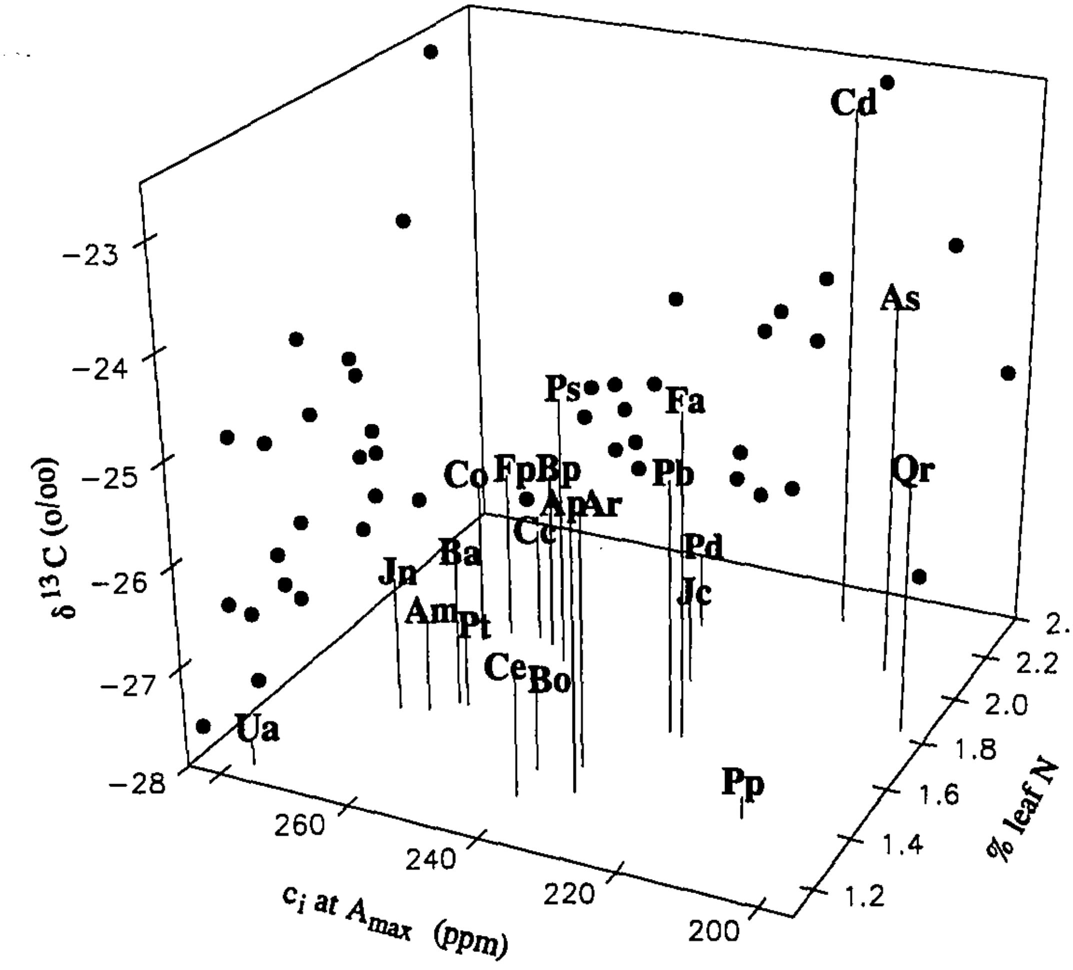
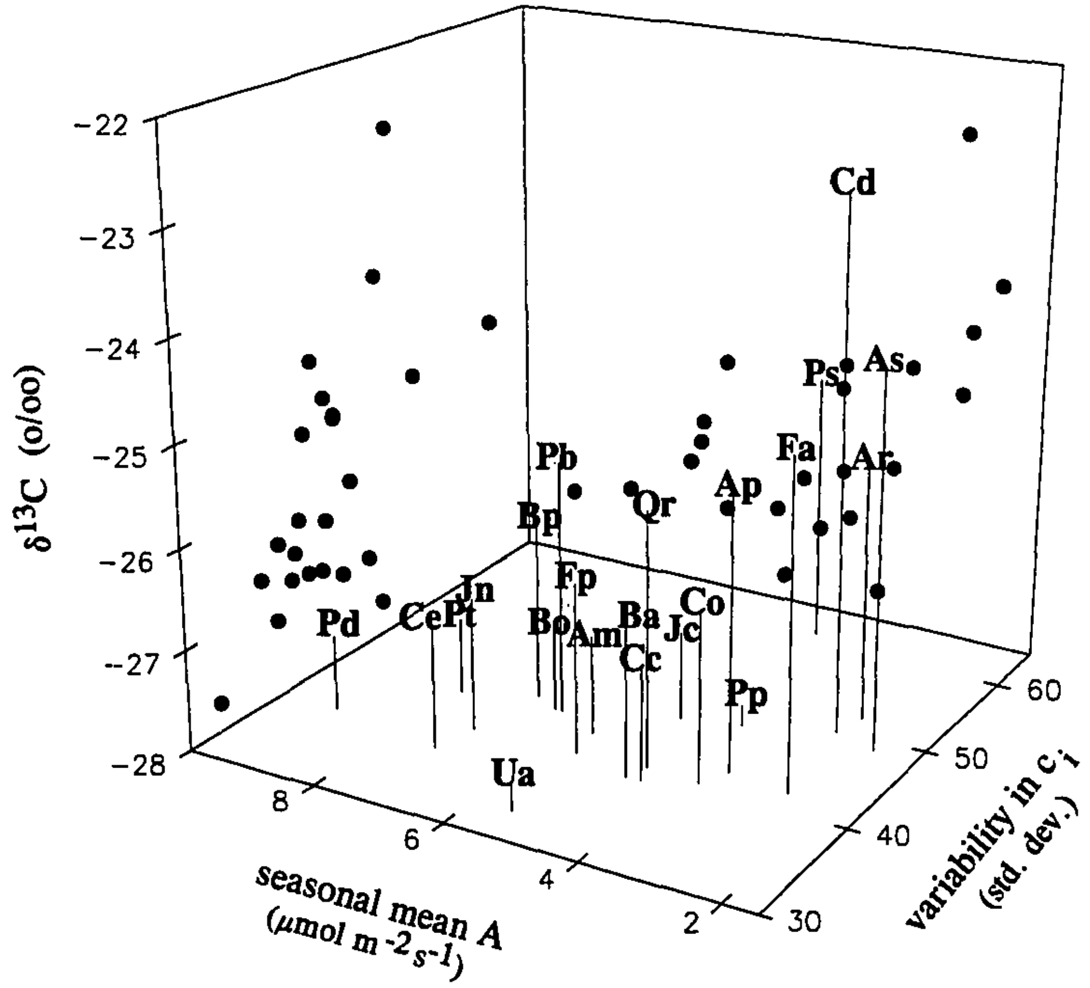


Figure 8. Relationships among seasonal mean photosynthesis (A), variation in c_i, and carbon isotope ratio ($\delta^{13}C$) in 22 deciduous hardwood species. Species acronyms are the same as in Figure 3.



P. deltoides, C. occidentalis, J. nigra, P. tremuloides and *B. populifolia* had low $\delta^{13}C$ values, while *C. dentata, A. saccharum* and *A. rubrum* had more variable c_i and higher $\delta^{13}C$ values. There appears to be an upper boundary imposed on WUE by variability in c_i. Not all species with more variable c_i had high WUE; for example, *Juglans cinerea, P. tremuloides* and *B. populifolia* had fairly variable c_i, but low $\delta^{13}C$ values. The standard deviation of c_i is not correlated with the mean and, therefore, is not a statistical artefact resulting from the standard deviation increasing with the mean, but rather, reflects true differences in stability of c_i over the growing season.

Variability in c_i was also negatively correlated with seasonal mean A (Table 3); thus, species with more stable c_i tended to have higher seasonal mean A. For example, *C. occidentalis, P. deltoides, P. tremuloides,* and *J. nigra* had high A, relatively stable c_i and low WUE, while *C. dentata, A. saccharum, P. serotina* and *A. rubrum* had low A, variable c_i and high WUE (Figure 8). However, in spite of an overall negative correlation between variability in c_i and mean A, at low values of variability in c_i mean A could be high or relatively low (Figure 8). For example, *C. ovata*, *F. pennsylvanica* and *J. nigra* had similar variability in c_i, but ranged from 4.4 to 7.1 μmol $m^{-2}s^{-1}$ in mean A. The strong negative relationship between $\delta^{13}C$ and seasonal mean A suggests a trade-off between maximizing carbon gain and minimizing water loss. This relationship appears to involve seasonal variation in c_i, as variability in c_i was correlated with both mean A and $\delta^{13}C$.

A number of species had relatively high g, low variability in c_i and low integrated WUE ($\delta^{13}C$). Under conditions of chronic intermittent drought these species maintained high g, which generally allowed more stable c_i and higher A, but resulted in lower long-term WUE (Figures 3, 8). These species were, in general, those found most abundantly on wet (*P. deltoides*) or wet-mesic (*J. nigra, B. papyrifera*) sites or which showed bimodal distributions (*P. tremuloides, B. populifolia* and *C. occidentalis*). Towards the other end of the continuum are species with lower A and g, somewhat higher variability in c_i and higher integrated WUE under chronic drought conditions. These species are found in mesic (*P. serotina, A. pensylvanicum, A. saccharum*) and dry-mesic (*Q. rubra, B. papyrifera* and *C. dentata*) habitats or with bimodal distribution (*A. rubrum*). *Fraxinus americana* was an exception, having low A and g and high WUE, despite its wet-mesic habitat preference.

The placement of species along this continuum (from high A, low WUE to low A, high WUE) appears to be most closely related to habitat moisture preference. Shade tolerance does not appear to be a determining factor; for example, *A. saccharum* (very tolerant) and *P. serotina* (intolerant) are both at the high WUE end of the continuum, while *P. deltoides* (very intolerant) and *U. americana* and *C. occidentalis* (both intermediate) are at the other extreme.

Discussion

In this study, I have compared gas exchange and functionally related leaf traits across 22 species of deciduous hardwood trees grown under a regime of chronic intermittent drought. The average soil water potential over the 1987 and 1988 growing seasons when gas exchange was assayed approached or exceeded permanent wilting point at 15 cm depth, but was less negative at 30 cm depth. This soil moisture regime was similar to or slightly drier than that reported for a dry ridge-top site near Ithaca, New York (soil water potential at 20 cm depth ranging from 0.0 to -1.75 MPa over July and August) by Bunce, Miller & Chabot (1977) and considerably drier than during a very dry summer in lower Michigan (soil water potential reaching a minimum of -1.5 MPa at 10 cm depth; Briggs, Jurik & Gates 1986). However, soil water shortage was not so extreme as to indicate severe drought such as that reported by Hinckley *et al.* (1979) during which soil water potential averaged -2.61 MPa in the upper 45 cm of the soil profile. The mean amount of light received (855 μmol $m^{-2}s^{-1}$) was above light saturation point for these hardwood trees (Jurik, Weber & Gates 1988, Ceulemans & Saugier 1991, Ellsworth & Reich 1992b). Thus, the nursery represented a relatively high light environment in which soil water availability was relatively low. This regime, therefore, represents one meaningful environment of many and is similar to one in which individuals of each species may be found in the wild.

The current study focuses on variation among species growing together in one particular environment rather than being a comparison of responses to different environments. Although all species received the same drought treatment, they did not experience the same degree of stress. In addition to the plant traits examined in this study, performance (carbon gain and survival) under chronic intermittent drought will also be influenced by the extent and depth of the rooting system (Hinckley *et al.* 1979, Sands & Mulligan 1990), the trees' ability to take up and deliver water to the leaf canopy (Tyree & Sperry 1989, Tyree & Ewers 1991), the vulnerability of xylem to drought-induced cavitation (Tyree & Ewers 1991, Tyree *et al.* 1994), the extent of leaf osmotic adjustment (Bahari, Pallardy & Parker 1985, Abrams 1988b, Ellsworth & Reich 1992a), the timing of leaf production (Spurr & Barnes 1980) and canopy duration (Kozlowski 1964, Hicks & Chabot, 1985). The value of such a comparative study is that it allows us to examine functional relationships among leaf traits across a broad range of deciduous hardwood species. The use of multiple assays of gas exchange over two growing seasons gives insight into long-term performance under the varying environmental conditions encountered. It is this actual gas exchange performance (*versus* potential performance) that is related to growth and survival. Differences in gas exchange and leaf investments in carbon and nitrogen (N) also provide the basis for interspecific variation in short- and long-term water use efficiency (WUE).

The interrelationships among photosynthesis (A), stomatal conductance (g), internal CO_2 concentration (c_i), specific leaf mass (SLM) and leaf nitrogen (N) give insight into the underlying design of hardwood tree leaves and hypothesized trade-offs between carbon gain and water loss. These interrelationships describe much of the interspecific variation in 1) photosynthetic capacity, and 2) short- and long-term WUE. The functional linkages among these traits as they relate to WUE have implications for a species' habitat moisture preference or requirements.

Photosynthetic capacity appears geared toward the light environment to which a species is adapted. Seasonal mean A (the average of 47 assays over two summers) was highly correlated with A_{max}, indicating that photosynthetic capacity was well matched to the rates actually attainable under the conditions of the study. Saplings of shade tolerant to moderately tolerant species that naturally grow where light is limiting (*e.g. Acer* spp., *Carya ovata, Castanea dentata* and *Quercus rubra*) generally had lower seasonal mean A than saplings of shade intolerant species (*e.g. Populus* spp., *Betula papyrifera, B. populifolia* and *Juglans nigra*), even in the relatively high light levels of the experimental nursery. Although tree species and leaves have been shown to adjust their gas exchange capacity to the light levels prevailing during growth (*e.g.* McMillen & McClendon 1983, Jurik, Weber & Gates 1988, Ellsworth & Reich 1992a,b), the response of shade tolerant species was not enough to allow them to attain the rates of intolerant species, at least not under the conditions of the study. There were exceptions to this general trend; for example, *Prunus pennsylvanica* had low mean A compared to other very shade intolerant species, while *Acer saccharinum* and *Celtis occidentalis* had high mean A for species ranked as shade tolerant and intermediate, respectively.

There was no apparent direct relationship between habitat moisture preference and seasonal mean A across these 22 species. For example, both *P. deltoides* and *A. saccharinum* are wet habitat species (Table 6), but *P. deltoides*, which is very intolerant of shade, had much a higher A_{max} (17.6 μmol m^{-2} s^{-1}) than the shade tolerant *A. saccharinum* (11.2 μmol m^{-2} s^{-1}). High A_{max} was found in wet and wet-mesic habitat species such as *P. deltoides* and *P. tremuloides*, but also mesic species (*C. occidentalis*) and dry-mesic species (*B. papyrifera*). Likewise, low A_{max} was found in species of various habitat moisture preferences. *Acer saccharum*, the most shade tolerant species, had lower A_{max} than other species regardless of moisture preference. Thus, A_{max} and seasonal mean A, even under chronic intermittent drought, appears to be determined more by a species' adaptation to light availability than by its habitat moisture preference. However, species distributions along moisture and light gradients (Table 6) suggest that under light-limited conditions, trees are less able to withstand extreme moisture conditions. Shade tolerant species are generally found only in less extreme moisture environments with the exception of *Acer saccharinum*, which is a streamside species. A similar pattern was found in a survey of the distributions of 116 eastern North American hardwood and conifer tree species along light and soil moisture gradients (N. Ives, unpublished ms).

Photosynthetic capacity (A_{max}) reflected leaf investment in both nitrogen and carbon. Across species, there was a strong trend of increasing A_{max} with concurrent increases in N_{area} and SLM, suggesting an underlying design for species-to-species variation in these three parameters, at least for deciduous broadleaved trees. Field and Mooney (1986) first brought attention to the A_{max}: N relationship, showing A_{max} to increase with increasing leaf N across species from various environments. Positive relationships between A_{max} and N have also been found within a tree canopy (DeJong & Doyle 1985), in *Acer saccharum* growing in contrasting light environments (Ellsworth & Reich 1992b), among 40 species of wetland herbs (Shipley & Lechowicz *in review*) and across a wide number of species from diverse ecosystems and biomes (Reich, Walters & Ellsworth 1992). The relationship appears to be particularly strong when both parameters are measured on a mass basis (Reich, Walters & Ellsworth 1992), but is also often found when measurements are made on an areal basis, such as in this study. Walters & Reich (1989) found no correlation between N_{area} and A_{max} in *Ulmus americana* seedlings subjected to short-term drought. A strong relationship would not be expected under imposed short-term drought when the plants were raised with adequate water and, thus, would have a capacity for greater A than could be achieved under stressed conditions. The correlation found under the long-term conditions of this study indicates that over the long-term, investment is adjusted to match potential under the conditions of growth.

The correlation between A_{max} and SLM was particularly strong. On theoretical grounds, A_{max} is expected to increase with increasing SLM (Gutschick 1987, Gutschick & Wiegel 1988). In a study of six hardwood tree species, Jurik (1986) found higher A_{max} in species with higher SLM. Shipley and Lechowicz (*in review*) have also found SLM to be highly correlated with photosynthetic capacity in 40 wetland herbs, while Ellsworth & Reich (1992b) found SLM to be an equally good predictor of A_{max} as N_{area} in young *A. saccharum* grown in habitats of different light availability. They also found a similar relationship within a canopy of *A. saccharum*

(Ellsworth & Reich 1993). This relationship holds in spite of the fact that SLM is comprised of density and thickness, which can vary independently (Witkowski & Lamont 1991). This relationship between A_{max} and SLM is reversed when extended to comparisons of species greatly differing in leaf life span (Reich, Walters & Ellsworth 1991b), which show greater differences in investment in leaf protective mechanisms (which are often related to increases in SLM, *e.g.* herbivore defenses such as sclerophylly and leaf toughness (Chabot & Hicks 1982)), than is apparent among the species considered in the studies cited above.

The high A_{max} of shade intolerant species such as *Betula papyrifera, B. populifolia, Juglans nigra, Populus deltoides, P. balsamifera,* and *P. tremuloides* resulted from high leaf investments in carbon (SLM) and, generally, also N_{area}. Shade tolerant species such as *Acer saccharum, A. pensylvanicum, A. rubrum* and *Carya ovata* tended to have lower N_{area} and SLM values. *Acer saccharum* was rather unusual; it had the lowest A_{max} and low SLM, but moderate N_{area} and high N_{mass}. In this very shade tolerant species, a greater proportion of leaf N may be incorporated into the light harvesting apparatus allowing efficient light capture in the dense shade of the forest understory, but at the expense of carboxylation capacity (Evans 1989). *Ulmus americana* was also somewhat peculiar in having the lowest N_{area} and N_{mass} and very low SLM, yet attaining moderate A_{max}. Its high mean g and high mean c_i presumably account for its moderate mean A; its apparent relatively low concentration of Rubisco active sites (assumed from its low N, see Evans 1989) may be compensated for by its relatively high c_i, which was obtained by maintaining a high g. A noticeable outlier in the A_{max}-N_{area}-SLM relationship was *Populus deltoides*, which had the highest A_{max}, achieved at high N_{area}, but only moderate SLM. A possible explanation for its proportionally low SLM may be related to the species' habitat distribution: *P. deltoides* is a streamside species, which usually has ample water available in its natural habitat and generally has roots extending below the water table (Tyree *et al.* 1994). It, therefore, would not need leaves of high SLM to minimize excessive water loss (Gutschick & Wiegel 1988). Also, its flattened petioles and "trembling" leaves may help minimize the increase in leaf temperature during warm weather (Roden & Pearcy 1993) and, along with its high g, may preclude the need for higher SLM to minimize heat load (Gutschick & Wiegel 1988).

Wong, Cowan & Farquhar (1979) and numerous subsequent studies have demonstrated a close relationship between A and g within a species when photosynthetic capacity was altered by various means, indicating coordination between carboxylation rate and stomatal aperture over the short-term. This relationship is also quite strong across species as shown for 27 Japanese species (Yoshie 1986) and 40 species of wetland plants (Shipley & Lechowicz *in review*). The current study shows that the strong, linear relationship holds across a wide range of tree species and over the varying environmental conditions encountered over two growing seasons; species with high mean A also had high mean g. Thus, capacity for CO_2 assimilation is, in general, quite closely coupled with stomatal conductance both in terms of coordination of diurnal variation in A and g and also from an evolutionary perspective: species have evolved such that A and g across species form a fairly tight line. This reflects the fact that C_3 species share the same photosynthetic mechanisms and, in general, are similarly limited by CO_2 concentration under favourable conditions (Ting 1982).

Since the relationship between A and g is usually discussed from a mechanistic perspective (*e.g.* Wong, Cowan & Farquhar 1979, Farquhar & Sharkey 1982), there has been little attention paid to interspecific variation within the relationship. However, among the species studied, especially in the mid-range values of A, there was considerable variability in seasonal mean g. This variability in the relationship between seasonal mean A and g was related to differences in seasonal mean c_i. In the mid-range of A and g, species with higher g for a given A also had a higher mean c_i. Mean c_i, as determined here with repeated assays over two growing seasons, can be thought of as a "setpoint" for c_i, with each species having a particular setpoint depending on the species-specific relationship between A and g (Yoshie 1986, Schulze

& Hall 1982). Mean c_i ranged from 229 ppm in *Q. rubra* to 266 ppm in *U. americana*. These interspecific differences in c_i setpoint are likely to be important in terms of daily carbon gain because of the influence of c_i on quantum yield (the amount of CO_2 taken up for each mole of photons absorbed). In C_3 plants, quantum yield depends on c_i because of competition between oxygen and CO_2 for Rubisco enzyme sites. Thus, quantum yield at high c_i can be substantially greater than that at lower c_i (Tenhunen, Pearcy & Lange 1987).

In the median range of A and g, species with lower c_i for a given A had higher N_{area} and SLM than species with higher c_i. Overall, seasonal mean c_i was negatively correlated with N_{area} and SLM. Much of the N in a leaf is invested in photosynthetic enzymes, predominantly Rubisco (Evans 1989); hence, a high N_{area} suggests a large number of enzyme active sites which would allow efficient "capture" of CO_2 molecules and rapid drawdown of CO_2. Thus, species with a high N_{area} might be expected to have a lower c_i and be more limited by stomatal aperture than species with less N_{area}, which would be relatively less limited by stomatal aperture and more by biochemical factors and, therefore, operate at a higher c_i.

The relationship between c_i and leaf N concentration has been explored theoretically by Hilbert, Larigauderie & Reynolds (1991). Using a cost-benefit model, they predicted that the leaf N concentration (*i.e.* N_{mass}) optimal for maximum plant relative growth rate would decrease with an increase in c_i. The current study indicates that across species high c_i is associated with lower N_{area}, supporting their model predictions in general. However, I found no correlation between c_i and N_{mass} due to interspecific variability in SLM (which was not incorporated into Hilbert *et al.*'s model). Higher N_{area} could presumably compensate for the effects of lower c_i on quantum yield. The negative relationship between c_i and SLM was probably due primarily to the strong correlations between both c_i and SLM and N_{area}. Thicker leaves may present greater resistance to diffusion of CO_2 to carboxylation sites within the leaf (Parkhurst *et al.* 1988), although there are no clear conclusions as to the degree of resistance to CO_2 diffusion within the leaf (Sharkey *et al.* 1982, Mott & O'Leary 1984, Parkhurst *et al.* 1988, Parkhurst & Mott 1990). However, in the current study, c_i is calculated in the standard manner and, thus, reflects substomatal CO_2 concentration rather than CO_2 concentration at the actual carboxylation sites (Farquhar & Sharkey 1982). Therefore, the relationship between SLM and c_i cannot be due to differences in diffusive resistance to CO_2 within the leaf.

The negative relationship between c_i and N_{area} was reflected in a negative correlation between mean A and mean c_i across species. This contrasts with reports of a number of experiments showing A to increase with increasing c_i. However, such experiments usually involve a single species and varying the external CO_2 concentration both above and below ambient (*e.g.* von Caemmerer & Farquhar 1981, Ball & Farquhar 1984, Wong, Cowan & Farquhar 1985a) and, thus, a similar relationship is not necessarily expected in leaves studied under ambient conditions or in cross-species comparisons. A negative correlation between mean A and c_i under ambient conditions in single leaves of a mangrove (*Bruguiera parviflora*) was reported by Cheeseman *et al.* (1991), who concluded that photosynthesis was under direct photosynthetic, non-stomatal control under all light and conductance levels and was rapidly adjustable such that c_i varied inversely from a minimum when gas exchange rates were highest to ambient when gas exchange was at its lowest. Similar relationships have also been seen in non-woody species (Morison 1987, Ghashghaie & Saugier 1989, Wise *et al.* 1990). Across species, the negative correlation between seasonal mean A and c_i suggests that species with greater photosynthetic capacity have lower c_i setpoints and/or are subject to greater stomatal limitation of CO_2 assimilation under drought.

In addition to its role in determining leaf photosynthetic capacity, leaf N content also influences leaf WUE, estimated from $\delta^{13}C$ values. In this instance, it is appropriate to examine leaf N concentration (N_{mass}) as $\delta^{13}C$ is a mass-based variable. Across the 22 tree species, there was a significant positive relationship between N_{mass} and long-term WUE. Several other studies have found similar relationships. Reich, Walters & Tabone (1989), studying *Ulmus americana* grown under different water and soil nitrogen regimes, found that seedlings grown at high N levels always had higher WUE (A/E) compared to low N plants. Tall fescue plants grown at high N availability showed a greater increase in WUE (A/E) during drought than plants grown at low N availability (Ghashghaie & Saugier 1989).

N_{mass} appears to determine the upper limit of WUE a species can attain. Species with higher N_{mass} appear capable of greater WUE under chronic intermittent drought than species with lower N_{mass}. However, N_{mass} alone did not determine WUE because not all species with high N_{mass} had high WUE. The actual WUE attained also depended on gas exchange rates and c_i. These interrelationships can be examined by comparing species. For instance, in *Castanea dentata* and *A. saccharum* high N_{mass} was related to high WUE, but both species had low seasonal mean A and g and low c_i at A_{max}. In contrast, *Populus deltoides* had high N_{mass} along with high A_{max} and mean A, but higher c_i at A_{max} and low WUE. *Prunus serotina* and *Juglans nigra* had similar N_{mass} and A rates, but *P. serotina* attained higher WUE because of its lower mean g and c_i values. Thus, actual long-term WUE depended on investment in photosynthetic capacity, but also on the relationship between A and g and the resultant c_i over the conditions encountered. There were negative relationships between $\delta^{13}C$ and both A and g, which indicates that, in general, species with high gas exchange rates tend to have low WUE and that there is a trade-off between minimizing water loss and maximizing carbon gain.

A novel result of this study was the positive relationship between the extent that c_i varied over the two growing seasons and both short- and long-term WUE. Although most studies have reported c_i to remain fairly constant over the course of a day (Tenhunen, Pearcy & Lange 1987) or under different experimental conditions (Wong, Cowan & Farquhar 1979, 1985a,b,c, Friend 1991), c_i does vary considerably among species (Chapter 1, Yoshie 1986, Smedley *et al.* 1991), among plants of different life-history classes (Cui & Smith 1991, Donovan & Ehleringer 1992), under different environmental conditions (Chapter 1) and over time in response to changing environmental conditions (Smedley *et al.* 1991, Ehleringer, Phillips & Comstock 1992). Variability in c_i over repeated assays has not been much discussed, although it has been mentioned by Winter (1981), Briggs, Jurik & Gates (1986) and Kubiske & Abrams (1992). Authors of these studies have suggested that variability in c_i most likely results from errors in estimation of c_i at low g values (see Appendix V for further discussion). However, variability in c_i seems likely to be a character of considerable importance given the importance of c_i with regard to quantum yield (Tenhunen, Pearcy & Lange 1987). It also appears to be a factor in the way plants regulate their carbon and water relations to attain a given level of WUE. In Chapter 1, I showed that drought-stressed trees of four deciduous species had more variable c_i than their well-watered counterparts. Variability in c_i was closely correlated with A/E and δ^{13C} across species and treatments and, thus, was considered an indicator of WUE. The current study shows that across species, trees with more variable c_i over time had both higher short-term (A/E) and higher long-term ($\delta^{13}C$) WUE. These findings suggest that greater WUE can be attained if c_i varies over the season, *i.e.* if it deviates from the set-point at which maximum carboxylation efficiency is attained. Variability in c_i, thus, seems to be related to the trade-off between minimizing water loss and maximizing carbon gain, since species with more stable c_i based on repeated assays over a two-year period had higher mean A.

In contrast to photosynthetic capacity, which appears to be most closely related to habitat light availability, WUE is related to the habitat moisture availability which these species usually encounter in their natural environments, although the situation is complex. Earlier studies have presented conflicting evidence as to whether hardwood trees from more xeric sites tend to show higher or lower WUE than species from more mesic sites. Some studies have suggested that more xeric species tend to be more conservative in their water use patterns (*e.g.* Wuenscher & Kozlowski 1971, Davies & Kozlowski 1977, Field, Merino & Mooney 1983), while others have suggested that more xeric species tend to be more prolifigate in their use of water (*e.g.* Bunce, Miller & Chabot 1977, DeLucia & Schlesinger 1991). The current broad comparison of hardwood trees encompassing a wide range of habitat moisture preference indicates that, in general, species from more xeric habitats have more conservative water use patterns (*i.e.* higher WUE) than species from habitats with greater water availability. Under conditions of chronic intermittent drought, the wet to wet-mesic species *P. deltoides, P. tremuloides, J. cinerea, J. nigra, B. alleghaniensis, B. populifolia, C. occidentalis, A. saccharinum, C. cordiformis, F. pennsylvanica,* and *U. americana* had low WUE and maintained high or fairly high mean gas exchange rates over the two seasons assayed with low and/or stable c_i over time. Mesic to dry species, *C. dentata, A. saccharum, A. pensylvanicum, P. serotina, Q. rubra*, and *C. ovata* were more efficient in their water use and generally had lower gas exchange rates and higher and/or less stable c_i over time. An exception was the dry-mesic *B. papyrifera,* which had median WUE and high gas exchange rates. Most of the species of bimodal moisture distributions (three out of four) behaved as the wetter peak of their distribution would predict.

Exceptions to these general trends were *P. pensylvanica, Celtis occidentalis, A. rubrum, F. americana* and *P. balsamifera*. *Prunus pensylvanica* had low gas exchange rates (due to low N_{area} and SLM) compared to other very shade intolerant species; however, its rates were similar to those of several shade intolerant species. Similar gas exchange rates for *P. pensylvanica* have been reported by Bazzaz & Carlson (1982). *Celtis occidentalis* had high mean A and A_{max} and also high SLM compared to other species of intermediate shade tolerance. This species is found more commonly on moist sites (Preston 1976, Burns & Honkala 1990), but is said to be drought tolerant, although it may be stunted and scraggly on dry sites (Fowells

1965, Preston 1976). *Acer rubrum*, a species classed as bimodal in its distribution, but with somewhat greater prevalence on more moist sites, had relatively high WUE. This may reflect the fact that it is known to have a wide range of environmental tolerance (Hosie 1979, Fowells 1965, Burns & Honkala 1990) and, thus, classification is difficult and, to a certain extent, arbitrary. *Populus balsamifera* and *F. americana* had high WUE for wet habitat species. *Populus balsamifera* appeared to accomplish fairly high WUE as well as high gas exchange rates by having a fairly low c_i at A_{max} and among the highest SLM and N_{area} values, indicating a leaf structure that would tend to have lower transpiration rates. *Fraxinus americana* seems little able to tolerate drought conditions. It maintains high WUE by having very low g and A under dry conditions compared to under well-watered conditions (Chapter 1). Tobiessen & Kana (1974) have also noted the "hypersensitivity" of its stomata to drought stress and concluded that this trait may restrict *F. americana* to moist sites.

There was considerable variation among species in all of the traits studied. There were no clear-cut groupings of species in terms of traditional classifications by shade tolerance or habitat moisture preference, rather the complex relationships among leaf levels traits resulted in species aligned along a continuum in any of the relationships discussed. Several general trends were seen: 1) there was a strong correlation between A and g across species, 2) variation in the A:g relationship was related to c_i, 3) photosynthetic capacity (A_{max}) was, in general, determined by concurrent investment in N_{area} and SLM, 4) higher N_{mass} allowed higher potential WUE, however the WUE actually achieved also depended on the pattern of gas exchange, 5) variability in c_i over time was related to the degree of WUE attained, and 6) there was a trade-off across species between maximizing photosynthesis and minimizing water loss. Among hardwood trees, there seems to be a general trend of higher WUE in species from mesic to dry habitats compared to species from more moist habitats. The responses of gas exchange traits to drought is likely to reflect their relationships to other physiological, morphological and phenological traits.

Before attempting to untangle all of these relationships, it is first necessary to examine gas exchange response and the interrelationships among gas exchange characteristics and related leaf traits as I have done here. In the following chapter, I relate these patterns of gas exchange response to relative growth rate attained over a five-year period under conditions of chronic intermittent drought.

CHAPTER 3

Traits underlying interspecific variation in growth of 22 deciduous tree species under conditions of chronic intermittent water shortage

Introduction

The purpose of the present chapter is to consider traits correlated with interspecific variation in relative growth rate (RGR) among 22 species of hardwood trees grown under conditions of chronic intermittent water shortage. In Chapter 1, I examined the relationships among physiological, phenological and morphological traits in four species (*Acer saccharum, Betula papyrifera, Fraxinus americana* and *Quercus rubra*) and how these relationships related to growth under well-watered conditions *versus* conditions of chronic intermittent drought. Leaf physiological traits were found to be the most responsive to water shortage, but other traits were also involved in whole plant performance as indicated by RGR over a five-year period. All species showed reduced seasonal mean stomatal conductance (g), lower and/or less stable internal CO_2 concentration (c_i) and increased water use efficiency (WUE), both on the short term (A/E) and over the long term ($\delta^{13}C$), under non-irrigated *versus* irrigated conditions. In addition to these universal responses, there were species-specific responses, most notable being the greater physiological and morphological plasticity of the early successional *B. papyrifera* relative to the mid- and late-successional species. Chapter 2 focussed on the leaf physiological traits which were found to be the traits most responsive to soil water availability. I examined patterns in gas exchange characteristics and related leaf traits across 22 species grown under chronic intermittent drought. Linkages among traits were seen: 1) photosynthetic capacity (A_{max}) was positively related to specific leaf mass (SLM) and leaf N per unit area (N_{area}), 2) variation in the relationship between seasonal mean A and g was related to species differences in seasonal mean c_i, 3) high A_{max}, SLM and N_{area} were associated with lower c_i, and 4) leaf N content (N_{mass}) set an upper limit on the long-term WUE ($\delta^{13}C$) a species could attain. A trade-off between maximizing seasonal carbon gain and minimizing water loss was indicated by a negative relationship between seasonal mean A and long-term integrated WUE ($\delta^{13}C$). This was further emphasized by the fact that variability in c_i over the season was positively related to WUE (both A/E and $\delta^{13}C$), but negatively related to A. Indications were that photosynthetic capacity is related more to habitat light availability (shade tolerance classification), while WUE was related more to species habitat moisture preference.

In this chapter, I summarize and combine the findings of the first two chapters by examining a whole suite of traits as they relate to RGR (as in Chapter 1) in the 22 species that were the focus of Chapter 2. External factors, both abiotic (*e.g.* availability of resources including light, water, CO_2 and mineral nutrients) and biotic (*e.g.* competition for available resources, herbivory and pathogens) can greatly affect growth rate in a natural environment (Loehle 1988, Herms & Mattson 1992, Pacala *et al.* 1994, Kobe *et al.* 1994). There is also inherent variation in RGR across species resulting from endogenous regulation of growth (Grime & Hunt 1975, Poorter & Remkes 1990, Shipley & Peters 1990, Shipley & Parent 1991). The actual growth attained will be related to a tree's inherent growth characteristics, the environment in which it is growing and the interactions between the two. The focus of the present study is on the endogenous differences in growth rate across species growing in only a single resource environment, one of the many in which these species may be found naturally.

Although trees require the same basic resources (light, water, CO_2 and mineral nutrients) and share the same basic growth form, different "strategies" of resource exploitation have evolved and can explain species distribution and community composition (*e.g.* Grime 1979, Tilman 1990). The successful competitor in a resource-limited environment will be the species that is able to deplete the limiting resource to the lowest possible level at which it can survive, but its competitors cannot (Tilman 1990). In the current study, soil water availability is the limiting resource and high relative growth rate (RGR) is the indication of competitive ability and success appropriate to trees (Pacala *et al.* 1994, Kobe *et al.* 1994). Thus, this study identifies which species are most "successful" in Tilman's terms (Tilman 1990) under conditions of chronic drought during the early years of seedling growth which are critical to establishment and survival (Pacala *et al.* 1994, Kobe *et al.* 1994). However, I am not directly comparing competitive ability (*i.e.* species were not grown in combination). Instead, my focus is on mechanisms underlying potential competitive ability (Keddy 1992), that is, the functional design of trees that result in differences in RGR and, hence, competitive ability under chronic drought. I have done this by measuring a wide number of traits across many species, exploring the relationships among these traits and how these traits and the interactions among them relate to performance (RGR) in a water-limited environment.

At present there is no comprehensive theory organizing the functional relationships among traits at the whole plant level for either herbaceous or woody species. Although linkages among certain variables have been established in the literature theoretically and supported by empirical evidence, we have only preliminary ideas how the whole tree is put together functionally (Küppers 1989, Ceulemans 1990). There is currently great interest in scaling up from leaf level processes to those concerning the canopy and whole tree (*e.g.* Jarvis & McNaughton 1986, Kramer 1988, Körner 1991) as the limited ability of leaf-level traits to explain interspecific variation in response to environment has become widely recognized (Körner 1991). Recently attention has also turned to individual plant traits and, especially, the linkages among traits across species as a means of building our understanding of whole plant function or design (Lei & Lechowicz 1990, Poorter, Remkes & Lambers 1990, Lambers & Poorter 1992, Reich, Walters & Ellsworth 1992, Reich 1993, Walters, Kruger & Reich 1993, Shipley & Lechowicz 1994).

In the current study, I examine above-ground traits generally recognized to be important in carbon uptake and/or water use. The traits included are listed in Table 1. I chose to examine tree performance under a regime of chronic intermittent water shortage because of the importance of soil water availability in determining tree growth (Fraser 1962, Zahner 1968, Sands & Mulligan 1990) and species distributions (Transeau 1905, Curtis 1959, Peet & Loucks 1977). Limited soil moisture availability will highlight interspecific variation in growth response to scarcity of water (Tilman 1990). No single environment is likely to be "seen" as equally stressful by all species. My objective was not to impose conditions of extreme unmitigating drought stress, but to represent one of the range of environments these species encounter naturally, that of episodic drought over the growing season. Examination of performance under other regimes would further increase our understanding of the causes of interspecific variation in growth in hardwood trees.

Table 1. Traits included in Chapter 3: acronyms, definitions and units.

Acronym	Definition	Units
RGR	relative growth rate (5 yr.)	cm $cm^{-1}yr^{-1}$
A	seasonal mean photosynthesis (2-yr. mean)	μmol $m^{-2}s^{-1}$
g	seasonal mean conductance (2-yr. mean)	mmol $m^{-1}s^{-1}$
c_i	seasonal mean internal CO_2 concentration (2-yr. mean)	ppm
sd_c_i	seasonal variability in c_i (std. dev.)	ppm
A/E	seasonal mean instantaneous WUE (2-yr. mean)	(μmol $m^{-2}s^{-1}$ CO_2)/ (mmol $m^{-2}s^{-1}$ H_2O)
$\delta^{13}C$	carbon isotope ratio	‰
N_{mass}	foliar N concentration (2-yr. mean)	% dry wt.
N_{area}	area-based leaf N content (2-yr. mean)	mg cm^{-2}
SLM	specific leaf mass (2-yr. mean)	mg cm^{-2}
la_totbr	leaf area/total stem and branch length	cm^2 leaf area/cm length
ldi	leaf display index; leaf area/branch length	cm^2 leaf area/cm length
canopy/ht	canopy area/height (2-yr. mean)	cm^2 leaf area/cm height
LSC	leaf specific conductivity	[(kg $MPa^{-1}m^{-1}s^{-1}$)/m^2 leaf area supplied]
MSC	maximum hydraulic conductivity/branch x-sect. area	[(kg $MPa^{-1}m^{-1}s^{-1}$)/m^2 x-sect. area]
LCE	loss of conductivity due to embolism	%
density	wood density	g cm^{-3}
bud	date of budbreak (2-yr. mean)	day of year
sen	date of leaf senescence (2-yr. mean)	day of year
candur	canopy duration (2-yr. mean)	days

Materials and Methods

The experimental protocols used to collect the data presented in this chapter are described in Chapters 1 and 2. This chapter is based on the gas exchange and leaf data for 22 species that is presented in Chapter 2, with the addition of data on relative growth rate, canopy architecture, leaf phenology and hydraulic conductivity, obtained by the same methods described in Chapter 1. Below, I briefly describe the materials and methods used, noting any deviations from the protocols described in the earlier chapters.

1. Experimental tree nursery.

Twenty-two species in the Mont St. Hilaire experimental nursery were chosen for a broad study of whole tree function and growth under conditions of chronic intermittent water shortage (see Chapters 1 and 2 for description of nursery and study plots, irrigation and fertilization protocols, and Chapter 2 for environmental conditions during the study). One non-irrigated m^2 plot of each species was used (the same plots as in the gas exchange study presented in Chapter 2). Three trees were individually tagged and these same individuals were used for all measurements when possible. Efforts were made to use the same individuals as used for the gas exchange assays. However, when this was not possible (due to tree mortality over the five years of the study), other tree(s) in the same plot were sampled in order to maintain n=3 at the species level. Studies have indicated that small numbers of individuals are sufficient to characterize species-level differences in physiological (Abrams 1988, Bahari, Pallardy & Parker 1985, Hinckley *et al.* 1978) and other traits. There were a few cases where it was not possible to obtain three values for one or more variables; these cases are noted below.

2. *Experimental protocols.*

a) Relative growth rate (RGR) and canopy architecture. An index of relative growth rate (RGR) based on growth in height, stem basal diameter and total length of lateral branches over five years was calculated as described in Chapter 1 and Appendix III. Total leaf counts of each tree were carried out in August 1987 and August 1988. In 1987, mean leaf area for each species was calculated from random samples of 30 leaves per plot collected in early September (due to the small size of the saplings, leaf samples were not taken from the individuals used in the gas exchange assays). In early September 1988, 11 leaves were sampled randomly from each tagged tree and mean leaf area determined for each tree. Total canopy area for each tree was calculated from total leaf number and species mean leaf area in 1987 and from total leaf number and tree mean leaf area in 1988. Total canopy area/height was calculated as a measure of whole tree leaf display and canopy architecture. The mean of the 1987 and 1988 values are presented. In August 1987, total stem and branch length was measured to calculate canopy area/total stem and branch length (LA_TOTBR). Architecture at the branch level was estimated by a leaf display index (LDI), calculated as the total leaf area of the branches sampled for hydraulic conductivity measurements (see below) divided by total branch length (August 1990).

b) Leaf traits. The gas exchange, leaf nitrogen, specific leaf mass and carbon isotope data are the same data presented in Chapter 2, with the exception of carbon isotope ratio ($\delta^{13}C$) for *Prunus pensylvanica*. In Chapter 2, the $\delta^{13}C$ value for *P. pensylvanica* (-27.80‰) was the single available value for trees used in the gas exchange measurements. To better estimate a species mean $\delta^{13}C$ value, in this chapter an additional value (-26.33‰; from a tree in the same plot but not used for gas exchange measurements) was included to provide a mean of -27.07‰ based on n=2. The correlations among leaf traits presented here differ somewhat from those presented in Chapter 2 because the former are based on species mean values (n=22), while the latter are based on values for individual trees (n=64).

c) Leaf phenology. Timing of leaf budbreak and fall senescence was recorded in 1987 and 1988 as described in Chapter 1. In 1987, budbreak was early and all species broke bud over a 15-day period, from day 105 (April 15) to day 120 (April 30). In 1988, budbreak took place over 27 days with *Prunus pensylvanica* breaking bud on day 105 (April 14), 13 days ahead of the next species. The ranking of species by date of budbreak was similar in both years. There were no 1987 budbreak data for the *Populus deltoides* study plot since the original trees had died and the replacements tagged only after budbreak. Therefore, the mean date of budbreak in two other, adjacent, non-irrigated *P. deltoides* plots (otherwise not included in the study) was substituted for the species mean value. The two-year mean date of budbreak and date of senescence (1987 and 1988) are entered into analyses. Canopy duration (days) was calculated as (date of senescence - date of budbreak) for each year; the two-year mean canopy duration is presented. The two-year means were calculated from the values for individual trees, except in the case of *P. deltoides* where budbreak 1987, canopy duration 1987 and two-year mean canopy duration were based on species mean values.

d) Hydraulic conductivity and wood density. Branch sampling protocols and hydraulic conductivity technique are described in Chapter 1. In summary, in late August 1990, branches of 1 cm diameter (often the main stem) were marked for winter harvest for hydraulic conductivity measurements (one to two branches per tree; total number of branches = 81). All leaves beyond the marked segment were removed and total leaf area measured in order to calculate leaf specific conductivity (LSC), the maximum conductivity (kg MPa^{-1} m^{-1} s^{-1}) per m^2 leaf area supplied. In March 1991, the marked branches were harvested, wrapped in plastic and kept frozen in a lab freezer. The samples were prepared and assayed for hydraulic conductivity as described in Chapter 1. Assays were conducted using degassed water, filtered through a micropore filter and acidified to 1.2 - 1.9 pH with oxalic and hydrochloric acid. Initial conductivity (pre-flush) and maximum conductivity (after flushing with demineralized water passed through a micropore filter for 30 min. at 172 kPa pressure) were calculated as the slope of the regression of 10 consecutive water mass measurements (recorded manually at exactly 60 s intervals) on time. Percent loss in conductivity due to embolism (LCE) was calculated as [1-(preflush conductivity/postflush conductivity)]*100. In 11 branches, conductivity was reduced after flushing, most likely due to the plugging of xylem vessels by small particles or microorganisms already in the branch that were not flushed out. In these cases, the percent reduction in conductivity due to embolism was set to zero. Maximum conductivity was divided by mean cross-sectional area of the branch segment and is reported as maximum specific conductivity (MSC). Only two unreliable measurements were obtained for *Carya ovata*; therefore, no hydraulic conductivity values are reported for this species. The branch segment assayed and the rest of the branch were then dried and dry wood density was determined by displacement in water (as described in Chapter 1).

3. Statistical analysis. Bivariate relationships were determined using Spearman non-parametric correlations (Proc CORR, SAS, 1985b). Regressions were done using Proc REG (SAS, 1985a). Wilcoxon non-parametric t-tests (Proc NPAR1WAY, SAS, 1985a) were used to test differences in leaf phenology and hydraulic architecture between species classed as diffuse-porous (n=11) or ring- and semi-ring-porous (n=11) in wood anatomy.

Results and Discussion

1. Traits directly correlated with RGR.

In an initial exploration of traits related to interspecific variation in relative growth rate (RGR), I ran Spearman correlations among the traits listed in Table 1. There were no direct correlations between RGR and traits related to water use efficiency (WUE) or hydraulic conductivity, even under the non-irrigated conditions of the study. Nor was RGR correlated with wood density across these 22 species. However, RGR was directly correlated with aspects of leaf gas exchange, tree architecture and leaf phenology (Figure 1*a-h*). These relationships are discussed below.

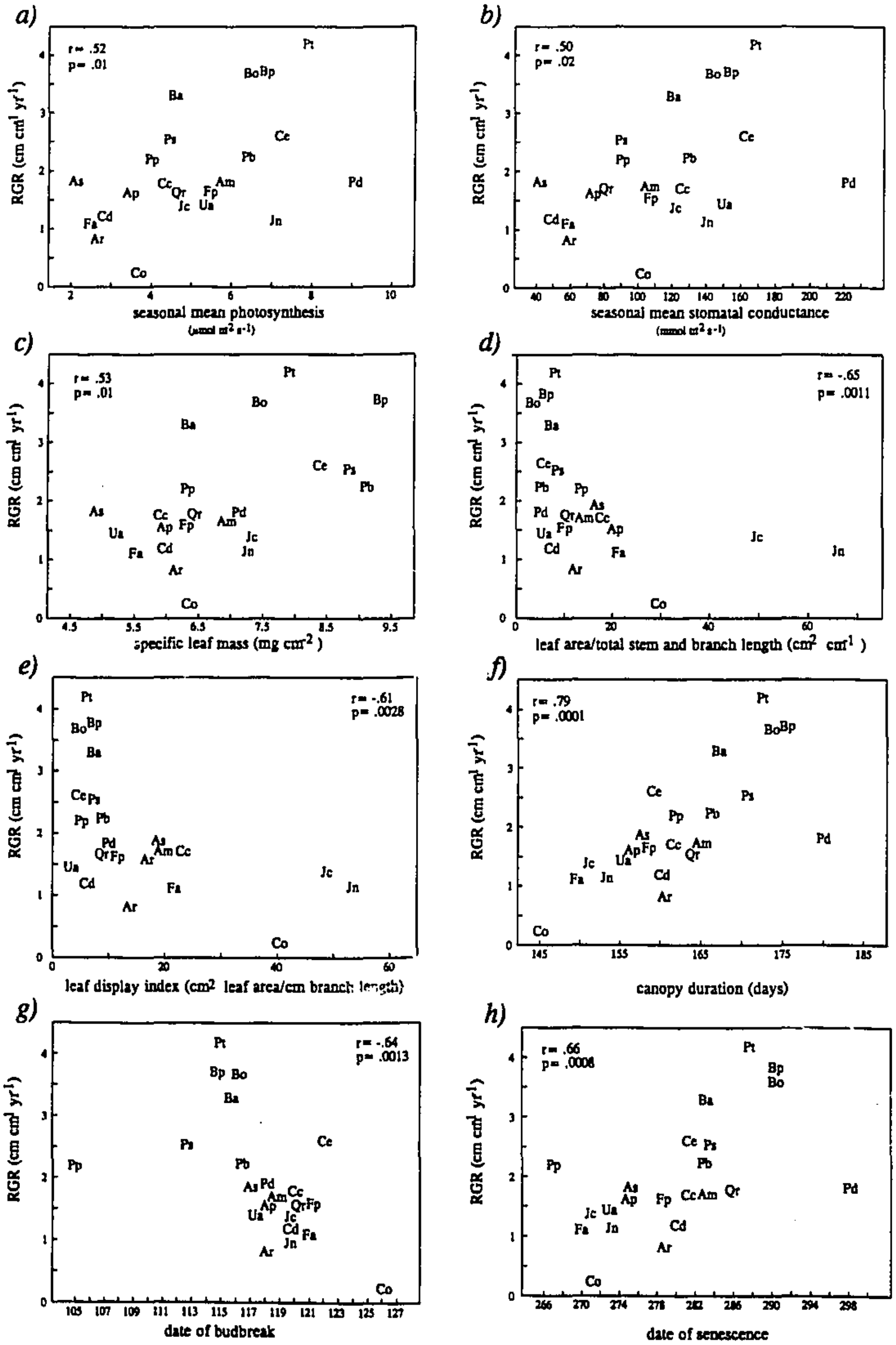
Leaf physiology

RGR was related to seasonal mean A, seasonal mean g (also to A_{max} and g_{max}; data not shown) and specific leaf mass (SLM) (Figure 1*a,b,c*). These three leaf variables are themselves closely correlated, as discussed in Chapter 2. Thus, species with high A, g and SLM tended to have higher RGR than species with lower A, g and SLM. Although, trees may not be able to operate at their maximum photosynthetic capacity in the field due to limiting environmental conditions, the current study shows that trees do tend to operate in line with their photosynthetic capacity: species with higher A_{max} also had higher seasonal mean A ($r= .93$, $p= .0001$). The correlation between RGR and seasonal mean A was slightly greater than that between RGR and A_{max} (mean A: $r= .52$, $p= .01$; A_{max}: $r= .49$, $p= .02$), indicating the importance of actual performance *versus* potential capacity.

Canopy architecture

Leaf display (Ceulemans 1990, Wu 1993) and proportional allocation of

Figure 1. Traits related to relative growth rate (RGR) in 22 species of decidous trees.



biomass to leaves have been shown to be important determinants of RGR in herbaceous species (Poorter & Remkes 1990, Lambers & Poorter 1992) and also in trees (Walters, Kruger & Reich 1993b). In the current study, negative relationships were found between RGR and LDI (leaf area/branch length) (Figure 1*d*) and LA_TOTBR (leaf area/total stem and branch length), a whole tree index of leaf display and estimate of proportional allocation to leaf tissue *versus* woody biomass (Figure 1*e*). Species with greater investment in leaf area per unit woody length tended to have lower RGR than species with proportional less investment in leaf area. This was due to the proportionally higher investment in leaves relative to branches in compound-leaved species (*Carya* spp., *Fraxinus* spp. and *Juglans* spp.). Compound leaves have been described as an inexpensive way to support a large leaf area, the rachis serving as a cheap, "throw-away" branch (Givnish 1987). When the six compound-leaved species were omitted from the analyses, there was no relationship between RGR and branch or tree architecture (data not shown). This is in contrast to other studies that have shown proportionally greater allocation to leaves *versus* stems and roots to result in higher RGR (Poorter & Remkes 1990, Lambers & Poorter 1992, Walters, Kruger & Reich 1993b). This discrepancy most likely arises from the different units of measurement used in this study. Leaf area, branch length and a non-massed based RGR were used here; a relationship may have been found if allocation of biomass to leaves and stem were related to a mass-based RGR as in the other studies.

Canopy duration

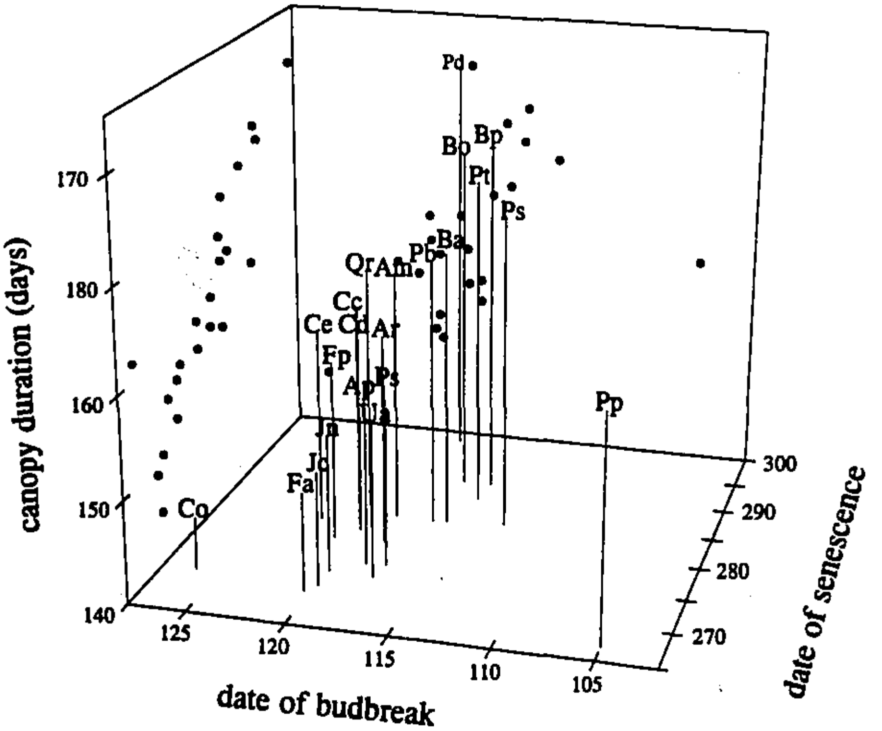
In the temperate forest, productivity of hardwood trees is ultimately limited by the seasonal duration of the leaf canopy (Chabot & Hicks 1982). Seasonal carbon gain will be determined by photosynthetic rate and also by the duration of photosynthetic activity. Thus, canopy duration might be expected to be of primary importance, setting an upper limit on productivity. The importance of canopy duration is affirmed by the strong correlation between RGR and canopy duration among these 22 species growing under chronic drought conditions. In fact, RGR was more closely related to canopy duration than to any other single variable (Figure 1*f*). RGR was also directly related to the timing of budbreak and senescence individually (Figure 1*g*,*h*).

Leaf phenology has been little studied in relation to tree productivity. The most developed theory relating aspects of leaf phenology to the productivity of individual leaves is that of Kikuzawa (1991). Kikuzawa has related the longevity of individual leaves to their total net gain (total photosynthetic gain minus leaf construction and maintenance costs). At a given latitude with a fixed favourable period for photosynthesis within the annual cycle, different tree species have different leaf longevities that are related to their total net gain. Using a cost-benefit analysis, Kikuzawa (1991) predicts whether a tree will be evergreen (maintaining leaves over the unfavourable period) or deciduous (shedding leaves at the end of one favourable period and replacing them at the beginning of the next). The same analysis could be done for species growing within a single locality. Across the 22 species studied here, canopy duration ranged from 145 days in *Carya ovata* to 176 days in *Betula papyrifera*. This broad range of canopy duration under conditions of chronic drought suggests that some species (*e.g. Carya ovata*) may drop their leaves with the onset of summer drought, while others (*e.g. Betula papyrifera*) maintain leaves through the dry season and are, thus, able to capitalize on the climatically more favourable period in early fall. Whether a species shows drought-induced leaf abscission or not may, thus, be related to the total net gain of its leaves in addition to being a means of reducing transpirational water loss (Parker 1969, Parker & Pallardy 1985, Zimmermann 1983, Tyree & Sperry 1988). The direct correlation between RGR and both date of budbreak and date of senescence suggests that both the ability to capitalize on favourable water availability early in the season and the the ability to retain leaves through drought episodes and into the more favourable fall period benefits growth.

Species mean date of budbreak spread over a 21 day period, while mean date of senescence had a range of 18 days across species. Longer canopy duration was related to both earlier budbreak ($r = -.65$, $p = .0010$) and later senescence ($r = .89$, $p = .0001$) (Figure 2). Consistent with other studies (Chapter 1, Lechowicz 1984, Wang, Ives & Lechowicz 1992), when grouped by wood anatomy, diffuse-porous species leafed out earlier than species with ring-porous and semi-ring-porous anatomy (day 115.3 ± 3.8 *versus* day 120.5 ± 2.3, respectively; $p = .002$) and had longer canopy duration (166.3 ± 6.6 *versus* 158.1 ± 9.2 days, respectively; $p = .026$). Although the proximate control of budbreak in temperate trees is known to be the cumulative heat sum to which the buds are exposed after a prerequisite cold period (Ahlgren 1957, Kramer & Kozlowski 1979, Hunter & Lechowicz 1992) and also, in some cases, daylength (Bell & Johnson 1975, Heide 1993), little is known about the causes of interspecific variation in timing of leaf senescence. Some species appear to senesce in response to summer drought (*e.g. Prunus pensylvanica, Fraxinus americana* and *Carya ovata*), but even this phenomenon is not well understood.

While canopy duration describes the total period during which a tree is in leaf, it does not necessarily indicate the life spans of individual leaves. Species with similar canopy durations may have leaves that turnover at different rates (Kikuzawa 1983, 1988). Leaf turnover rate is related to the pattern of shoot growth: trees producing only one cohort of leaves will have no leaf turnover during the growing season, while species with indeterminate growth may replace early leaves with new leaves as the season progresses (Kikuzawa 1989). In a comparison of three Japanese species, Koike (1987) found the early successional *Betula platyphylla* to have high A rates in short-lived leaves, the late successional *Acer mono* to have low A in longer-lived leaves, while the intermediate species *Fraxinus mandshurica* had leaves of intermediate A and longevity. Leaf lifespan has been linked to a number of traits including leaf N content, A, SLM and leaf area ratio (LAR) (Reich, Walters & Ellsworth 1992) across diverse ecosystems, although the relationships may be weak

Figure 2. Relationships among date of budbreak, date of senescence and canopy duration in 22 hardwood tree species.



among temperate trees (Koike 1988, Reich 1993). Thus, although canopy duration explains a large proportion of the interspecific variation in RGR across the species studied here, interspecific variation in leaf longevity may be related to the variation seen within the relationship. Leaf turnover rates have not been studied in North American deciduous trees, but may provide insight into the relationships between canopy duration, leaf traits including A, N, SLM, and RGR.

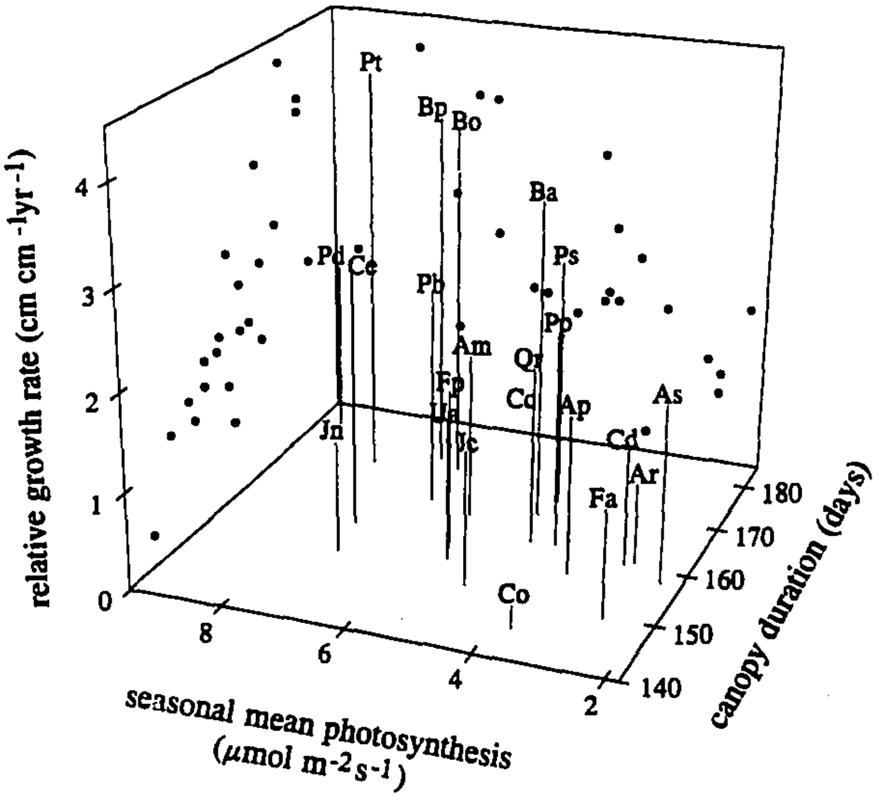
2. *Combinations of traits.*

Although variation in canopy duration accounted for almost 80% of the interspecific variation in RGR and RGR was also directly correlated with several additional individual traits, there was considerable variation within the relationships indicating that RGR is not entirely determined by simple bivariate relationships. Thus, it is useful to examine the combined influence of two or more traits on RGR.

While canopy duration sets the temporal limit to seasonal productivity in a temperate climate, photosynthetic capacity determines the potential rate of carbon gain during the photosynthetically active season. High seasonal carbon gain, leading to high RGR, could be the result of photosynthetic activity over a long period of time, a high photosynthetic rate or a combination of a high photosynthetic rate over a long time period. The current study indicates that both factors generally contribute to high RGR (Figure 3). Tree species with the highest RGRs had both high seasonal mean A and long canopy duration (*e.g. Populus tremuloides, Betula papyrifera, B. populifolia*). Species with either low A and/or short canopy duration had lower RGR under conditions of chronic intermittent drought (*e.g. Carya ovata, Fraxinus americana, Acer rubrum, Castanea dentata* and *Juglans nigra*).

In a resource-limited environment, the efficiency with which a plant uses the

Figure 3. Relationships among relative growth rate, seasonal mean photosynthesis rate and canopy duration in 22 hardwood tree species.



limiting resource may have important impacts on RGR (Cohen 1970, Bloom, Chapin & Mooney 1985). A logical hypothesis is that under chronic intermittent drought conditions high WUE will have a negative impact on potential productivity (RGR). This seems reasonable based on the fact that stomatal closure to reduce transpirational water loss generally also reduces A and, hence, carbon gain (Wong, Cowan & Farquhar 1979, Sands & Mulligan 1990). The negative relationship found between WUE and seasonal mean A in both Chapters 1 and 2 lends support to this idea.

Stomatal regulation of water loss has been suggested to be a necessary constraint on gas exchange in species that are vulnerable to drought-induced xylem cavitation (Tyree & Sperry 1988, 1989). On the other hand, under certain circumstances, high stomatal conductance, in spite of the resulting loss of a proportion of the conducting xylem due to embolism, may be beneficial in terms of maximizing short-term productivity (Jones & Sutherland 1991). In a competitive environment, high WUE will be of no benefit if the water "saved" is taken up by neighbouring trees (Cohen 1970, Bunce, Miller & Chabot 1977). Thus, either WUE or absolute water use might be expected to be related to RGR depending on the species' hydraulic vulnerability, the presence of competitors and on the degree of water shortage. I will discuss both possibilities starting with WUE.

In general, one might expect trees with high maximum hydraulic conductivity to have high leaf-level WUE under drought conditions. However, across the 22 species, there was no correlation between long-term integrated WUE (δ^{13}C) and either maximum specific conductivity (MSC) or leaf specific conductivity (LSC). Moreover, when species were grouped by wood anatomy, there were no differences between the diffuse-porous species and the ring- and semi-ring-porous species in WUE, MSC, LSC or loss of conductivity due to embolism (LCE) (Wilcoxon non-parametric t-test significance values from 0.13 to 0.70). Therefore, the relationships between hydraulic architecture and leaf-level WUE are complex and are likely to be influenced by other traits. As such, these relationships are worthy of further study.

Although there was no simple correlation between RGR and WUE, species with the highest RGRs (*e.g. Populus tremuloides, Betula* spp. and *Celtis occidentalis*) had low WUE (Figure 4). However, other species had low WUE and low RGR (*e.g. Carya ovata, Juglans* spp.). WUE appears to set a limit on the RGR a species may achieve, at least under drought stress conditions: none of the species with high WUE attained RGRs as high as some of the less water use efficient species (Figure 4). The low RGR of some of the species with low WUE may be related to their wood anatomy. *Juglans cinerea, J. nigra, Ulmus americana,* and *Populus deltoides* are all either ring-porous or semi-ring-porous. Furthermore, they are typical of wet to wet-mesic habitats with *P. deltoides* and *U. americana* being riparian species (Burns & Honkala 1990). The low RGRs and low WUE of these species under drought conditions suggests that these species were not able to control water loss, to the detriment of productivity.

The second possibility is that water use *per se* rather than WUE may explain some of the residual scatter in the relationship between RGR and canopy duration (Figure 1f). Seasonal mean g gives an estimate of total water use since it is based on repeated point-in-time measurements, *i.e.* species with high mean g had high rates of conductance (and, hence, water loss) over the many times it was assayed. To test whether seasonal mean g and other traits would explain the scatter in the RGR-canopy duration relationship, RGR was regressed on canopy duration and the residuals screened for correlations with the traits listed in Table 1. Seasonal mean g (and, hence, water loss) was found to explain part of the variation in the relationship between RGR and canopy duration (Figure 5). The correlation is not significant when all 22 species are included (r= .31, p= .15); however, when the outlier, *Populus deltoides*, is removed the correlation becomes .50 (p= .02). The plot of the residuals on seasonal mean g is shown in Figure 5. The same correlation was obtained when g_{max} was used instead of mean g (data not shown).

Figure 4. Relationships among relative growth rate, carbon isotope ratio and canopy duration in 22 hardwood tree species.

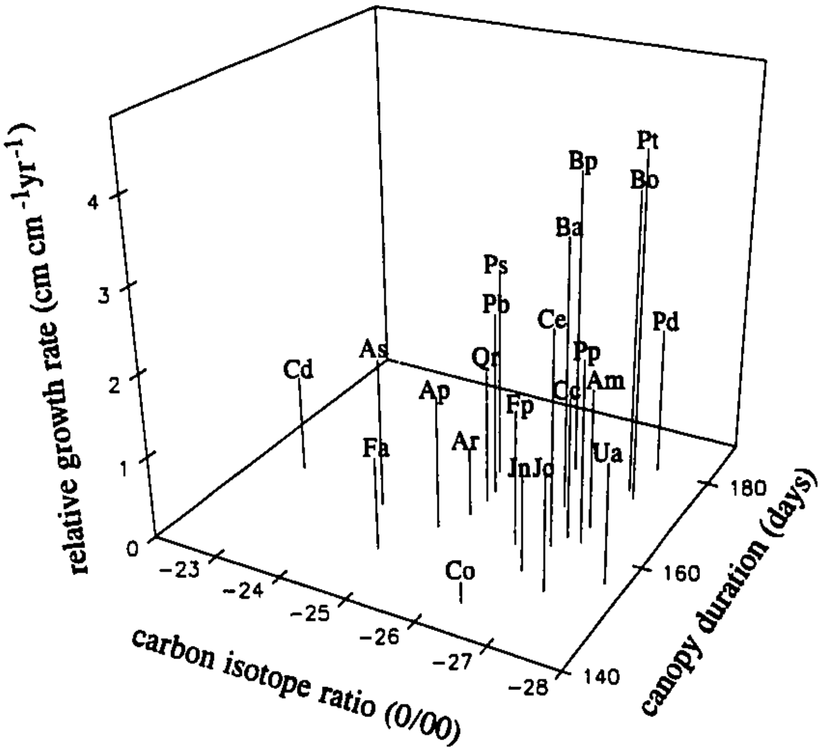


Figure 5. Graph of the residuals from a regression of relative growth rate (RGR) on canopy duration plotted against the mean stomatal conductance for each of 22 tree species grown under chronic drought. Refer to Table 1 for units and Figure 1f for the original regression.

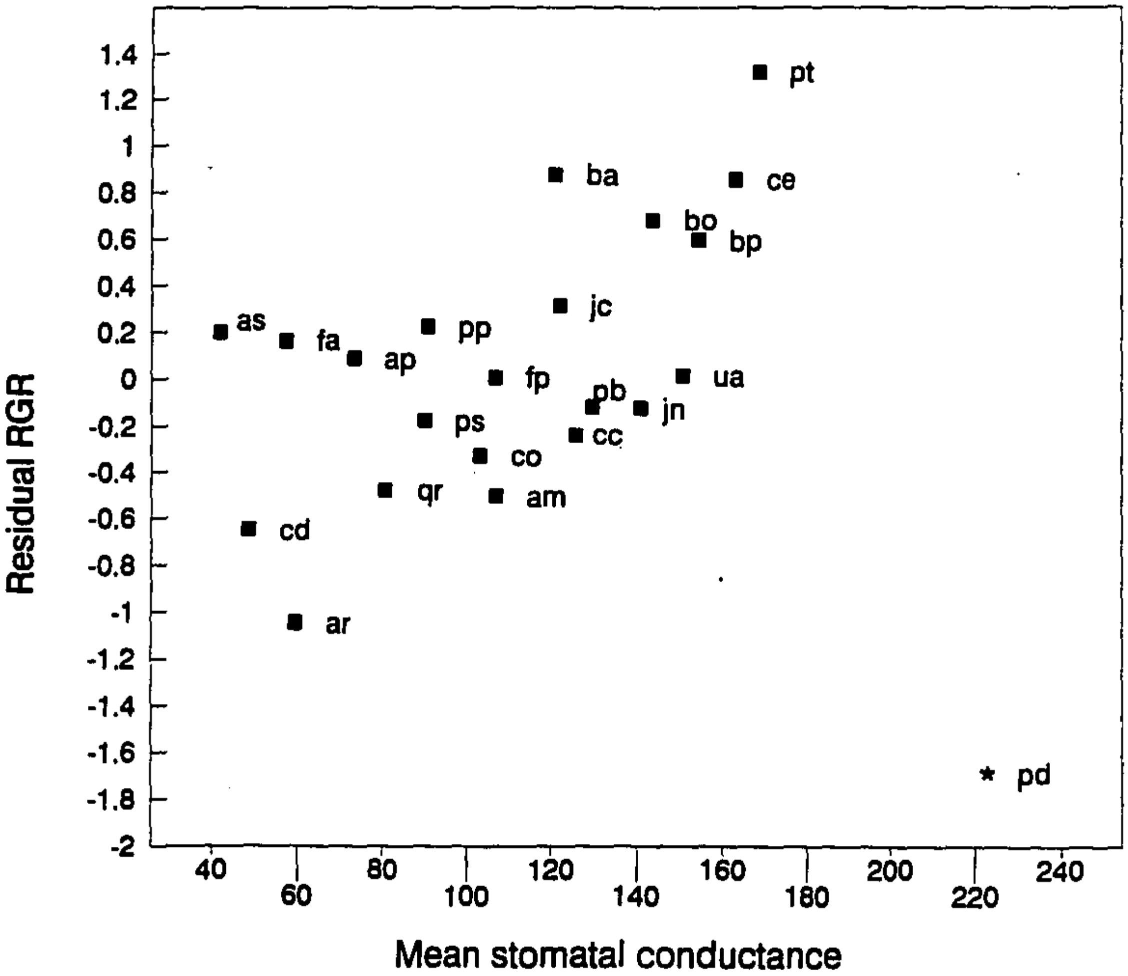


Figure 5 indicates that for a given canopy duration, species with higher seasonal mean g (*i.e.* higher water use) had higher RGR. Thus, species such as *Populus tremuloides, Betula* spp. and *Celtis occidentalis* are "water spenders". Even under conditions of chronic intermittent drought, these species appear able to take up enough water to allow high photosynthesis rates (Figure 1*a*), which, in turn, leads to a high RGR over a five-year period. On the other hand, species with lower seasonal mean g fall below the regression line of RGR on canopy duration and have lower RGR than species of similar canopy duration but higher water use. For example, *P. tremuloides* and *Prunus serotina* differed in canopy duration by only two days (Figure 1, Table 2); however, *P. tremuloides* had nearly double the seasonal mean g of *P. serotina* and also close to double the RGR (Figure 1*b*, Table 2). *Populus deltoides* was a marked outlier in the relationship, having the longest canopy duration and highest mean g of all species, but attaining rather low growth (Figure 5). This species was spending water and maintaining high gas exchange rates, but was unable to take up enough water to meet its growth needs. This species is dependent on an ample water supply and also appears to be especially vulnerable to drought-induced xylem cavitation (Tyree *et al.* 1994). The inability of *P. deltoides* to regulate water loss, thus appears to limit this phreatophytic species to riparian environments (Tyree *et al.* 1994).

In summary, although several traits were directly correlated with RGR (Figure 1), by far the most important trait was canopy duration, which explained 79% of the interspecific variation in growth rate in these 22 species of northern hardwoods growing under conditions of chronic intermittent drought. Variation in the relationship was related to absolute water use: among species of similar canopy duration, those with higher seasonal mean g had higher growth rates. Water use, but not WUE, was related to the ability to maintain high rates of growth under chronic intermittent drought.

Table 2. Mean values for traits studied in 22 deciduous tree species growing under chronic drought, excluding the gas exchange and leaf traits listed in Table 4, Chapter 2. The acronyms for each trait appear in Table 1 (this chapter) and those for the tree species in Figure 3 of Chapter 2.

SP	RGR	LA_TOTBR	LDI	canopy area/ht	LSC	MSC	LCE	wood density	BUD	SEN	CANDUR
Am	1.717	14.4192	19.9968	51.870	1.22624	0.03472	8.0905	0.63013	118.5	283.3	164.8
Ap	1.632	18.7847	17.4708	39.828	0.59950	0.02063	57.9325	0.65727	118.3	275.0	156.7
Ar	0.831	12.4086	13.9817	32.080	0.41947	0.01358	79.8435	0.68064	118.2	278.8	160.7
As	1.833	17.6225	19.0648	36.850	0.40237	0.01896	26.9015	0.71596	117.3	275.2	157.8
Ba	3.306	7.5196	7.3513	69.066	1.32686	0.04988	71.0383	0.71991	115.8	283.2	167.3
Bo	3.690	3.5487	4.8897	35.892	1.50645	0.05582	83.4990	0.72708	116.3	290.5	174.2
Bp	3.729	4.2630	6.6563	84.624	1.32965	0.05821	81.2373	0.66362	114.8	290.5	175.7
Cc	1.718	18.2086	23.0350	43.642	2.34633	0.08470	52.8107	0.83322	120.2	281.8	161.7
Cd	1.196	7.5911	6.2383	68.304	3.98658	0.13934	93.1865	0.77219	119.8	280.2	160.3
Ce	2.615	6.3142	4.6356	187.807	1.20285	0.03665	92.3622	1.05344	122.2	281.5	159.3
Co	0.250	29.6447	40.6296	42.418	.	.	.	0.89087	126.2	271.3	145.2
Fa	1.120	21.4482	21.8760	56.540	1.98668	0.07001	66.1553	0.76691	120.3	270.0	149.7
Fp	1.640	10.0618	11.0457	56.476	1.92627	0.05197	73.1845	0.78867	120.8	278.7	157.8
Jc	1.392	49.7487	48.9539	89.898	0.04374	0.00280	36.8375	0.60470	119.8	271.0	151.2
Jn	1.150	66.2845	53.4876	169.501	0.09540	0.00438	50.3045	0.73979	119.8	273.3	153.5
Pb	2.245	5.5952	9.0367	16.011	2.37150	0.07438	29.3201	0.61688	116.5	283.0	166.5
Pd	1.818	5.4207	10.1865	35.601	1.81922	0.08348	71.4977	0.58236	118.1	298.2	180.1
Pp	2.211	13.7232	5.1846	35.404	1.45126	0.07391	57.4528	0.68567	105.0	267.0	162.0
Ps	2.549	8.0817	7.4779	114.676	2.24196	0.06986	15.1935	0.74852	112.8	283.7	170.8
Pt	4.202	8.2403	6.1639	42.667	2.61049	0.05903	21.3433	0.67265	115.0	287.7	172.7
Qr	1.701	10.7739	9.3441	48.286	2.53898	0.10821	59.9142	0.82558	120.3	284.7	164.3
Ua	1.456	5.9426	3.3957	23.340	1.31855	0.02787	87.3392	0.75568	117.5	273.0	155.5

GENERAL CONCLUSIONS AND ORIGINAL CONTRIBUTIONS

- Perhaps the most original contribution of this thesis lies in its approach to investigating tree seedling response to water shortage. Unlike most previous studies, I focus neither on one or a few traits across many species nor on many interacting traits in one or a few species. Instead I consider many traits affecting the growth of diverse hardwood trees under water shortage, and I do this for even-aged seedlings subject to intermittent drought over five years under reasonably natural and uniform outdoor conditions. The lack of such comprehensive data for a broad range of species growing under the same experimental conditions has hampered interspecific comparisons in the past (Keddy 1992).

- A related original contribution is the introduction of a novel approach to the study of leaf gas exchange. Repeated assays over two summers allowed comparison of average physiological activity under the varying edaphic and atmospheric conditions young trees naturally encounter. This approach differs considerably from the standard ecophysiological approach of measuring gas exchange only a few times and generally under optimal, controlled or semi-controlled conditions. This is, thus, an original contribution in providing the most comprehensive data set on gas exchange in hardwood trees growing in a common outdoor environment.

- While past research has focussed primarily on gas exchange and other leaf level responses to water shortage (*e.g.* foliar nitrogen, specific leaf mass), I have attempted to integrate these responses with other above-ground traits relevant to carbon and water relations. These include aspects of foliar phenology, hydraulic architecture, canopy architecture and wood density. In turn, I have related the diverse responses to water shortage in this assemblage of traits to interspecific variation in relative growth rate over the five-year experiment.

● All the tree species show plastic adjustments to water shortage in at least some traits. Although it has been generally assumed that leaf traits are the relevant traits to study vis-à-vis drought stress, no one has examined response in the broad range of other traits studied here. Leaf traits are indeed the most plastic in response to contrasting soil water regimes (original contribution). Canopy architecture, foliar phenology, wood anatomy and hydraulic conductivity show relatively little plasticity in response to soil water availability. Interspecific differences in growth rate under drought, however, arise from interactions among both plastic and invariant traits.

● Interspecific variation in relative growth rate under conditions of chronic intermittent drought was most closely related to canopy duration: species with longer canopy duration had higher relative growth rate (original contribution). In addition, species with higher rates of stomatal conductance had enhanced relative growth rate, even under drought conditions (original contribution).

● There is a close relationship between stomatal conductance and photosynthesis, but there is variability within the relationship that is related to the internal CO_2 concentration (c_i) maintained in the leaf. This in turn is related to leaf nitrogen concentration and specific leaf mass. In addition to interspecific variation in seasonal mean c_i, species differed in the extent to which c_i was stable from assay to assay over the season. This is the first study to examine variability in c_i over time and to identify a relationship between variability in c_i over the growing season and water use efficiency: species that allow their c_i to vary had higher water use efficiency, but generally lower photosynthesis, than species that maintained a more stable c_i (original contribution).

● Finally, this thesis has approached interspecific variation among the traits affecting growth as intrinsically continuous rather than categorical. Species do not fall into neat categories characterized by dichotomous contrasts in one or another trait. My data suggest that traditional categorical classifications of forest tree species by shade tolerance or successional status have only limited value in predicting response to water shortage or relative growth rate under conditions of chronic intermittent drought.

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APPENDIX I

Tree species included in the study: seed provenances, nursery plots and planting dates

Species	data set[1]	nursery plot	seed lot	date planted	provenance
Acer pensylvanicum	2	2.3	3	Nov. 1984	Montréal, Qué. (Morgan Arboretum)
A. rubrum	2	6.3	95	Nov. 1984	Gravenhurst, Ont. (PNFI[2])
A. saccharinum	2	4.9	112	May 1985	Mont St. Hilaire, Qué. (Otterburn Park)
A. saccharum	1(w)	5.11	7	Nov. 1984	Ithaca, New York (Ellis Hollow)
A. saccharum	1(d)	6.11	7	Nov. 1984	Ithaca, New York (Ellis Hollow)
A. saccharum	1(w)	9.14	98	Nov. 1984	Algonquin Park, Ont. (PNFI)
A. saccharum	1(d), 2	10.14	98	Nov. 1984	Algonquin Park, Ont. (PNFI)
Betula alleghaniensis	2	4.6	20	Nov. 1984	unknown
B. papyrifera	1(w)	5.6	24	Nov. 1984	Algonquin Park, Ont. (PNFI)
B. papyrifera	1(d), 2	6.6	24	Nov. 1984	Algonquin Park, Ont. (PNFI)
B. papyrifera	1(w)	7.9	29	Nov. 1984	Ithaca, New York
B. papyrifera	1(d)	8.9	29	Nov. 1984	Ithaca, New York
B. populifolia	2	4.14	33	Nov. 1984	unknown (Schumacher's[3])
Carya cordiformis	2	10.7	42	Nov. 1984	Montréal, Qué. (Morgan Arboretum)
C. ovata	2	10.6	44	Nov. 1984	Ithaca, New York (Airport Woods)
Castanea dentata	2	8.16	46	Nov. 1984	Montréal, Qué. (Morgan Arboretum)
Celtis occidentalis	2	8.12	48	Nov. 1984	unknown (Schumacher's)
Fraxinus americana	1(w)	5.15	56	Nov. 1984	Tara, Ont. (PNFI)
Fraxinus americana	1(d)	6.15	56	Nov. 1984	Tara, Ont. (PNFI)
Fraxinus americana	1(w)	7.13	58	Nov. 1984	unknown (Schumacher's)
Fraxinus americana	1(d),2	8.13	58	Nov. 1984	unknown (Schumacher's)
F. pennsylvanica	2	4.12	63	Nov. 1984	Rondeau Prov. Park, Ont. (PNFI)
Juglans cinerea	2	10.3	64	Nov. 1984	Ithaca, New York (Ellis Hollow)
J. nigra	2	2.10	67	Nov. 1984	Montréal, Qué. (Morgan Arboretum)
Populus balsamifera	2	10.13	121	May 1985	Mont St. Hilaire, Qué. (Gault Estate)
P. deltoides	2	6.4	115	June 1985	Ithaca, New York (Stewart Park)
P. tremuloides	2	4.10	108	May 1985	Mont St. Hilaire, Qué. (Gault Estate)
Prunus pensylvanica	2	10.15	102	Nov. 1984	Petawawa, Ont. (PNFI)
P. serotina	2	6.13	81	Nov. 1984	Ithaca, New York (Ellis Hollow)
Quercus rubra	1(w)	5.8	86	Nov. 1984	Mont St. Hilaire (Gault Estate)
Quercus rubra	1(d)	6.8	86	Nov. 1984	Mont St. Hilaire (Gault Estate)
Quercus rubra	1(w)	7.11	83	Nov. 1984	unknown (Schumacher's)
Quercus rubra	1(d),2	8.11	83	Nov. 1984	unknown (Schumacher's)
Ulmus americana	2	2.12	111	June 1985	Mont St. Hilaire, Qué. (Otterburn Park)

[1] data set(s) in which species/plot is included:

1 = non-irrigated plot (d) or irrigated plot (w) in comparison of 4 species (Chapter 1).
2 = 22 species grown under chronic drought conditions (Chapters 2 and 3).

[2] seed obtained from Petawawa National Forestry Institute, Chalk River, Ontario.

[3] seed obtained from F.W. Schmacher Co. Inc., 36 Spring Hill Road, Sandwich, Mass. 02563-1023 USA.

Appendix II

Soil Psychrometer Calibration

A. Calibration set-up

Ceramic cap soil psychrometers (model PCT55, Wescor, Logan, Utah, USA) were individually calibrated in solutions of known water potential as described below. Readings were taken with a Wescor psychrometric microvoltmeter (model HR-33T).

1. Before calibration, the soil psychrometers were soaked in distilled, deionized water for one day and then set to air dry thoroughly for one day. They were individually labelled.

2. Calibrations were conducted at 20°C in a dark growth chamber in the McGill University Phytotron (June 1988). The psychrometers were taped together and immersed in a beaker of saline solution in such a manner that the probes were all at the same depth (with the ceramic cap fully immersed, but the lead wire above the solution) and not touching either each other or the glass sides of the beaker. Inside the growth chamber, the beaker with the probes was placed on a styrofoam pad in a large box surrounded by styrofoam squiggles to make the temperature of the solution and the probes as stable as possible. A ring stand was used to secure the bunch of probes in place, hanging into the solution. The beaker was sealed with parafilm. The lead wires were taped in place along the floor of the growth chamber and laid flat near the door so they could be passed through the door and the door closed. The ends of the wires were left extending out of the door.

B. Saline solutions.

1. A series of NaCl solutions was prepared: 0.00 (pure water), 0.05, 0.10, 0.20, 0.40, 0.50 and 0.60 M NaCl, corresponding to water potentials of 0.00, -.230, -.454,

-.900, -1.791, -2.241 and -2.694 MPa, respectively, at 20°C (Wiebe *et al.*, 1971).

2. The probes were taken through the calibration series from low to high NaCl concentrations. After the final solution, they were soaked and rinsed in pure water and allowed to dry thoroughly in air before installation in the field.

3. After placement in a solution, the probes were allowed to equilibrate for 2 hours before the first readings were taken. Three sets of readings were taken with 15 minutes between sets (offsets and readings were no different with 15 minutes between sets than with 1 hour between sets, so the shorter interval was used for economy of time). Each set of readings took 30 minutes. The individual psychrometers were tested in random order and the order re-randomized for each set of measurements.

4. The measured plateau in microvolt (μv) output was recorded; for psychrometers that did not show a true plateau, the μv value at which the falling needle was moving most slowly was recorded. A cooling time of 5 seconds was used for 0.00, 0.05, 0.10. and 0.20 M NaCl; 10 seconds was used for 0.40, 0.50, and 0.60 M NaCl.

5. In between solutions, the psychrometers were rinsed in pure water for approximately 1-2 hours with 3 water changes during that time.

C. Calculations.

1. Microvolt readings were corrected for temperature:

$$\text{corrected reading} = \frac{\text{reading in } \mu\text{v}}{(0.325 + 0.027\ T)},$$

where T = temperature (°C).

2. The corrected readings were regressed on solution molality individually for each probe, using the three sets of readings (r^2 values ranged from 0.87 to 0.98).

3. The individual regressions obtained for each psychrometer were used to convert μv readings obtained in the field (corrected for temperature) to soil water potential (MPa):

$$\Psi_{soil} = \text{intercept} + (\text{slope} * \text{reading}).$$

APPENDIX III

Construction of the Index of Relative Growth Rate

In order to compare relative growth rates among tree species differing in canopy architecture, I calculated an index of relative growth rate which incorporates growth in height, stem basal diameter and total branch length. Measurement protocols are described in Chapter 1. Five-year relative growth rates were calculated as follows (Evans 1972):

stem basal diameter: RGR(di)=(ln diameter 1990/ln diameter 1985)/5
height: RGR(ht)=(ln height 1990/ln height 1985)/5
total branch length: RGR(br)=(ln branch length 1990/5)

Note that total branch length in 1985 was 0.0 cm since it was the seedlings' first growing season. Units are cm cm^{-1} yr^{-1}.

The three RGR values for each tree (four species data set, Chapter 1) or each species (22 species, Chapters 2 and 3) were submitted to a Principal Components Analysis (Proc Factor, SAS Institute, Inc. 1985a) to obtain an RGR index based on diameter, height and branch growth: RGRINDEX = factor 1 + 2.0 (to make all values positive).

Below I give the correlations among the RGR components for both data sets and present the results of the Principal Components Analyses.

A. Four species data set.

RGR(di), RGR(ht) and RGR(br) were calculated for each tree in the study (n=42). For one *Acer saccharum* tree in the non-irrigated treatment, RGR(di) and RGR(ht) were calculated on four, rather than five, years' growth (mortality necessitated the replacement of one original tree after the first year of growth).

All three RGR component variables were significantly correlated. RGR(di) was closely correlated with both RGR(ht) (Spearman r= .73, p= .0001) and RGR(br) (r= .72, p= .0001), while the correlation between RGR(ht) and RGR(br) was .62 (p= .0001). Figure 1 shows the relationships among the three variables for the 42 trees in the data set. In the Principal Components Analysis, standardized scores for factor 1 were 0.37 for RGR(di), 0.36 for RGR(br) and 0.35 for RGR(ht). Factor 1 accounted for 85% of the total variance and, thus, the RGR index is a good indicator of overall relative growth rate.

B. Twenty-two species data set.

Due to sapling mortality over the course of the study, it was not possible to obtain five-year relative growth rates in diameter, height and total branch length for all trees. In some cases, it was necessary to base species means on two rather than three trees. For *Fraxinus pennsylvanica*, RGR(di) and RGR(ht) were based on a single tree. For *Castanea dentata*, RGR(di) and RGR(ht) were based on five-year values for one tree and four-year values for another (the five- and four-year values were similar). For *Populus balsamifera* and *P. deltoides*, RGR(di) and RGR(ht) were based on four years' growth (two trees for *P. balsamifera*, three trees for *P. deltoides*). Species mean values were entered into the correlation and Principal Components analyses.

RGR(di) was closely correlated with both RGR(ht) (Spearman r= .76, p= .0001, n= 22) and RGR(br) (r= .65, p= .0010). There was no correlation between RGR(ht) and RGR(br). The relationships among the three component RGR values are shown in Figure 2. In the Principal Components Analysis, standardized scores for factor 1 were 0.44 for RGR(di), 0.39 for RGR(ht) and 0.33 for RGR(br). Factor 1 accounted for 75% of the total variance and, thus, the RGR index is appropriate for use as an index of overall relative growth rate.

Figure 1. Relationships among RGRs in stem basal diameter, total branch length and height in four deciduous hardwood species grown under irrigated and non-irrigated conditions. Capital letters denote irrigated trees; small letters denote non-irrigated trees. *Acer saccharum* - A, a; *Betula papyrifera* - B, b; *Fraxinus americana* - F, f; *Quercus rubra* - Q, q. Units: cm cm^{-1} yr^{-1}. $n = 42$ trees.

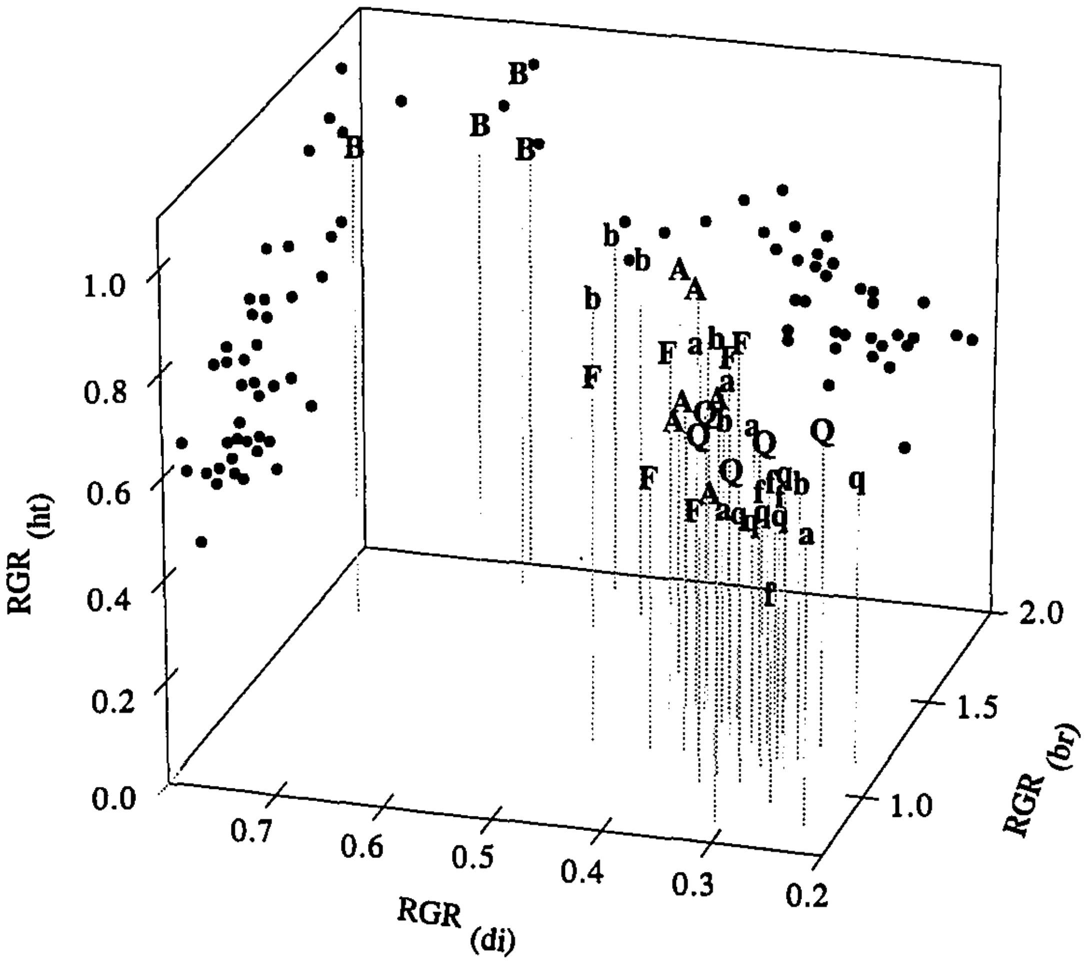
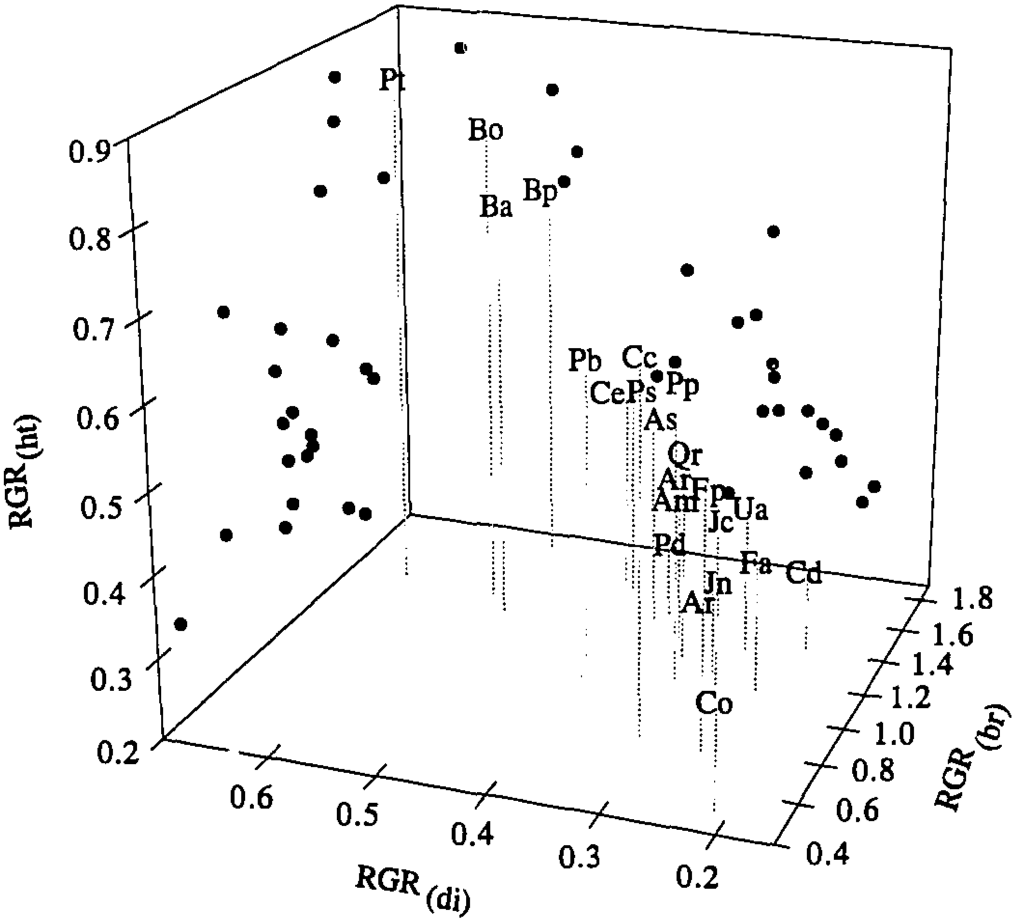


Figure 2. Relationships among RGRs in stem basal diameter, total branch length and height in 22 deciduous hardwood tree species. Units: cm $cm^{-1}yr^{-1}$.



Species:

Ap - *Acer pensylvanicum*
Ar - *A. rubrum*
Am - *A. saccharinum*
As - *A. saccharum*
Ba - *Betula alleghaniensis*
Bp - *B. papyrifera*
Bo - *B. populifolia*
Cc - *Carya cordiformis*
Co - *C. ovata*
Cd - *Castanea dentata*
Ce - *Celtis occidentalis*

Fa - *Fraxinus americana*
Fp - *F. pennsylvanica*
Jc - *Juglans cinerea*
Jn - *J. nigra*
Pb - *Populus balsamifera*
Pd - *P. deltoides*
Pt - *P. tremuloides*
Pp - *Prunus pensylvanica*
Ps - *P. serotina*
Qr - *Quercus rubra*
Ua - *Ulmus americana*

APPENDIX IV

Summary of gas exchange data

The gas exchange data obtained during 1988 for four species grown with and without irrigation (Chapter 1) and during 1987 and 1988 for 22 species grown without irrigation (Chapters 2 and 3) are presented in the following box plot figures. The data were screened for outliers and measurements made under non-ambient conditions; the boxplots shown contain all data retained after screening. Photosynthesis (A), stomatal conductance (g) and internal CO_2 (c_i) data are shown.

The box plots consist of a box indicating the range between the 25th and 75th percentiles of the data. A solid line marks the 50th percentile; a dashed line marks the average value. Capped bars extend to the 10th and 90th percentiles. The 5th and 95th percentiles are shown with dots. The 95th percentiles of photosynthesis (A) and stomatal conductance (g) values are the maximum photosynthesis rate (A_{max}) and maximum stomatal conductance rate (g_{max}) discussed in the text.

Explanation of box plots:

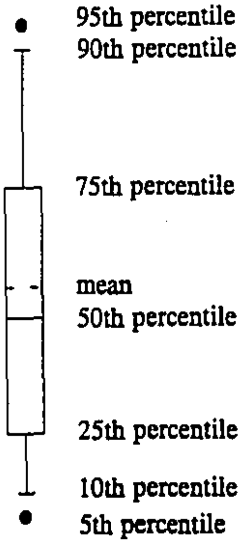


Figure 1 (caption). Gas exchange data for *Acer saccharum, Betula papyrifera, Fraxinus americana,* and *Quercus rubra* grown under irrigated and non-irrigated conditions. Measurements are based on 17 assays taken in 1988.

Number of observations for each species treatment combination:

Species	irrigated	non-irrigated
Acer saccharum	92	73
Betula papyrifera	79	86
Fraxinus americana	89	57
Quercus rubra	74	92

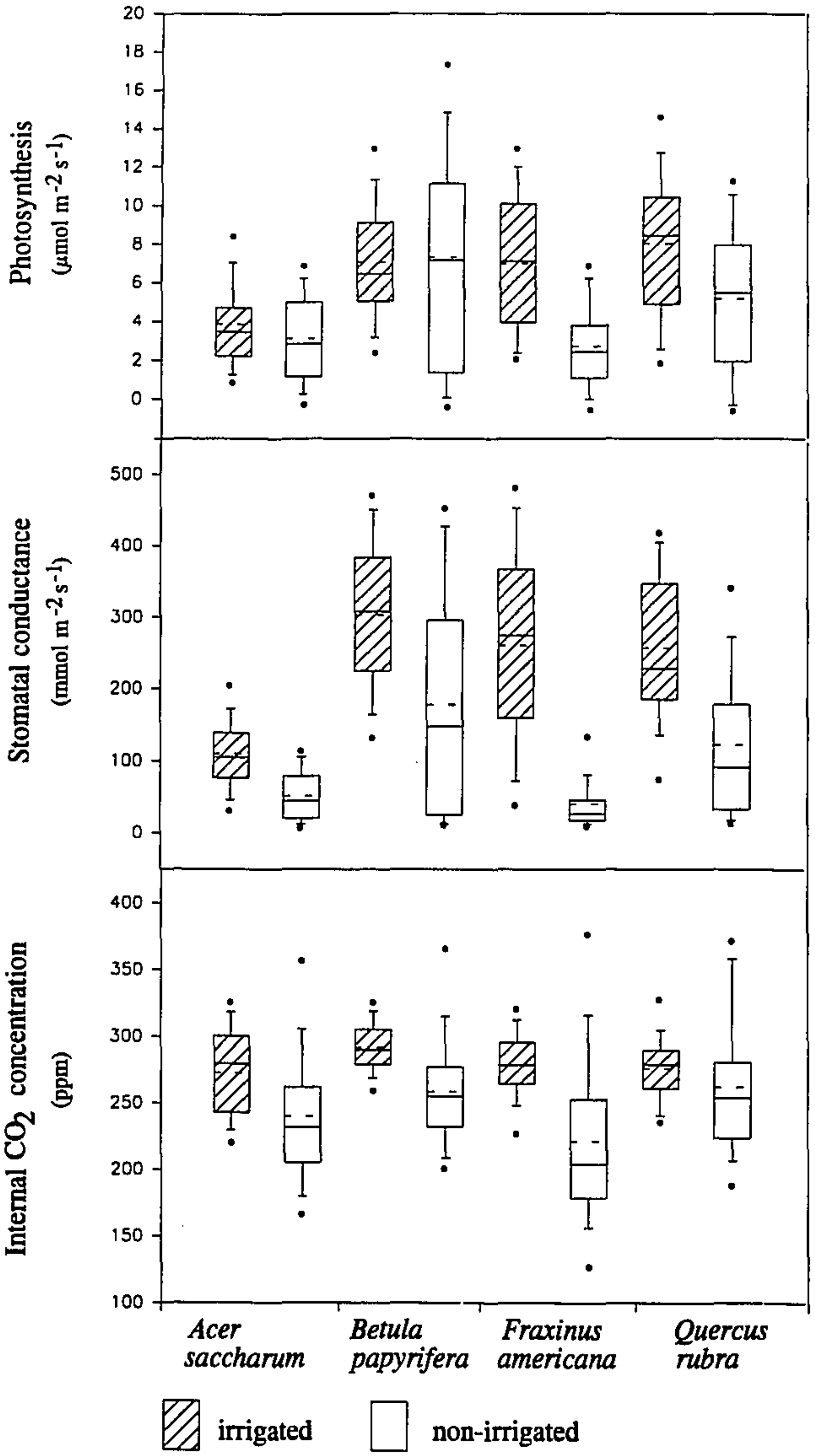
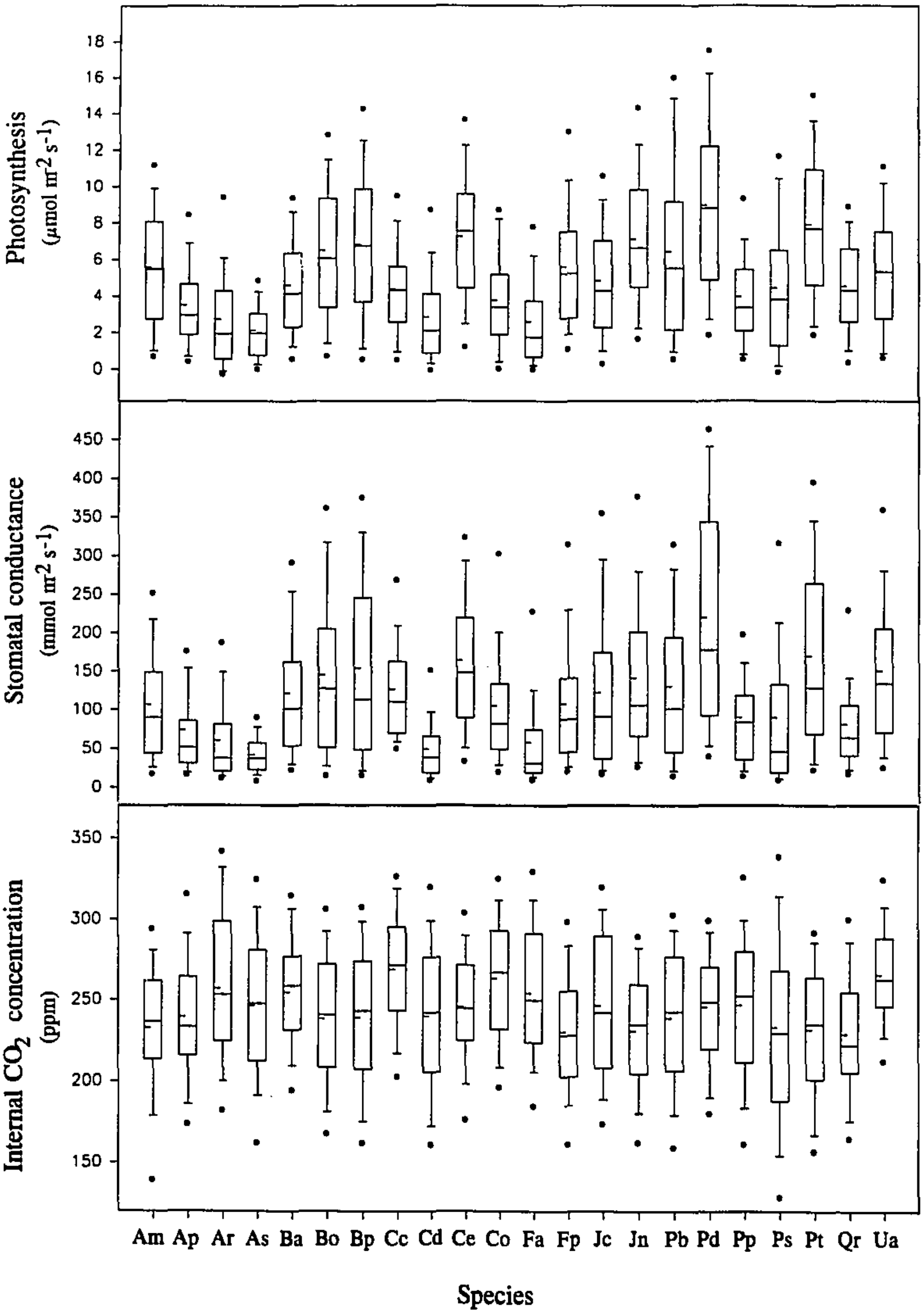

Photosynthesis (μmol m^{-2} s^{-1})
20
18
16
14
12
10
8
6
4
2
0
Stomatal conductance (mmol m^{-2} s^{-1})
500
400
300
200
100
0
Internal CO$_2$ concentration (ppm)
400
350
300
250
200
150
100
Acer saccharum
Betula papyrifera
Fraxinus americana
Quercus rubra
irrigated
non-irrigated

Figure 2 (caption). Gas exchange data for 22 tree species grown under non-irrigated conditions. Measurements are based on 47 assays taken in 1987 and 1988. The number of observations for each species is given in parentheses.

List of species abbreviations:

As, *Acer pensylvanicum* (120)
Ar, *A. rubrum* (116)
Am, *A. saccharinum* (124)
As, *A. saccharum* (107)
Ba, *Betula alleghaniensis* (125)
Bp, *B. papyrifera* (128)
Bo, *B. populifolia* (125)
Cc, *Carya cordiformis* (93)
Co, *C. ovata* (113)
Cd, *Castanea dentata* (121)
Ce, *Celtis occidentalis* (135)
Fa, *Fraxinus americana* (82)
Fp, *F. pennsylvanica* (122)
Jc, *Juglans cinerea* (129)
Jn, *J. nigra* (131)
Pb, *Populus balsamifera* (119)
Pd, *P. deltoides* (104)
Pt, *P. tremuloides* (130)
Pp, *Prunus pensylvanica* (92)
Ps, *P. serotina* (127)
Qr, *Q. rubra* (125)
Ua, *Ulmus americana* (89)


Photosynthesis
(μmol m-2 s-1)
0
2
4
6
8
10
12
14
16
18
Stomatal conductance
(mmol m-2 s-1)
0
50
100
150
200
250
300
350
400
450
Internal CO2 concentration
(ppm)
150
200
250
300
350
Am Ap Ar As Ba Bo Bp Cc Cd Ce Co Fa Fp Jc Jn Pb Pd Pp Ps Pt Qr Ua
Species

APPENDIX V

Interpretation of carbon isotope and gas exchange data

Introduction

In this appendix, I address two areas of concern with regards to the data presented in this thesis: the interpretation of differences in carbon isotope ratios as differences in long-term integrated water use efficiency (WUE) and the validity of calculations of internal CO_2 concentrations (c_i) based on gas exchange data, particularly when stomatal conductance (g) is low. The discussion is based on aspects of these topics that concern the study of plants with C_3 metabolism; additional aspects involving C_4 and Crassulacean acid (CAM) metabolism are not covered.

I. Interpretation of carbon isotope ratios

The interpretation of carbon isotope ratios ($\delta^{13}C$ values) as a measure of relative long-term WUE depends on two assumptions: that the species and/or plants being compared do not differ in vapour pressure deficit (vpd) experienced or in the proportion of carbon gain lost through respiration (Farquhar & Richards 1984). Neither of these assumptions are likely to be entirely met in field studies comparing several species (Smedley *et al.* 1991). The proportion of carbon gain respired does show both phenotypic and genotype variation, but is difficult to predict in the field (Farquhar, Ehleringer & Hubick 1989). Although it is represented in equations describing whole plant WUE (the number of moles of carbon in the plant divided the number of moles of water transpired during growth) (*e.g.* Farquhar & Richards 1984, Farquhar, Ehleringer & Hubick 1989), the proportion of carbon respired is usually ignored in studies of leaf-level WUE, where variation among species with leaves of similar age and morphology is less likely to be of considerable magnitude. However, differences in leaf temperature (and, hence, vpd) may be substantial and have been shown to be quite important in a comparative study of 15 aridland species (Ehleringer, Phillips & Comstock 1992). Using *Acamptopappus sphaerocephalus* as an example, the authors calculated that, although carbon isotope values remained approximately constant, WUE (A/E) varied from 3.0 to 1.7 mmol $m^{-2}s^{-1}$ between early winter and late spring due solely to seasonal differences in vpd. Thus, generally carbon isotope ratios can be interpreted as an indication of comparative water use efficiency only with caution when differences in leaf temperature or vpd are found among the plants being compared.

In the four species comparison presented in Chapter 1, analysis of variance (ANOVA) on ranked data showed no species or species x treatment interaction effects in vpd, leaf temperature (t_{leaf}) or relative humidity (RH) experienced during the gas exchange assays. However, there were treatment effects, with vpd and t_{leaf} higher and RH lower in the non-irrigated treatment compared to the irrigated treatment ($p= .0001$ in all cases, $n=42$). Within species, Wilcoxon t-test approximations showed significant treatment differences in vpd for *Betula papyrifera* ($p= .0366$) and *Quercus rubra* ($p= .0456$) and a marginal difference in *Fraxinus americana* ($p= .0520$). *Betula papyrifera* also showed marginally higher t_{leaf} under non-irrigated conditions ($p= .0520$). There were no other significant treatment differences within species.

The treatment differences in vpd, t_{leaf} and RH raise the question of potential bias in the carbon isotope ratios measured for trees experiencing different soil water availability. Significant treatment differences in vpd can, in some circumstances, preclude interpretation of treatment differences in $\delta^{13}C$ as differences in relative WUE (Ehleringer, Phillips & Comstock 1992, Donovan & Ehleringer 1992, L.A. Donovan *pers. comm.*). In the current data set, however, this is not the case. This is shown by the following calculations:

$$A/E = (c_a - c_i)/1.6\ (\Delta w),$$

where A/E is instantaneous WUE (μmol CO_2/mmol H_2O), c_a and c_i are ambient and internal CO_2 concentrations, respectively, 1.6 is the ratio of gaseous diffusivities of CO_2 and water vapour in air, and Δw is the leaf to air water vapour concentration gradient (Ehleringer & Osmond 1989). Using the mean Δw values for irrigated and non-irrigated *B. papyrifera* (17.8 and 23.4 mPa Pa^{-1}, respectively) and, for simplicity, assuming c_a equals 350 ppm and c_i equals 250 ppm, A/E is calculated as follows:

$$\text{Irrigated:} \quad A/E = 100/1.6\,(17.8) = 3.51$$

$$\text{Non-irrigated:} \quad A/E = 100/1.6\,(23.4) = 2.67$$

From the above, based on differences in vpd or Δw alone (the two are essentially equivalent), the higher vpd values experienced by non-irrigated plants would be expected to result in lower WUE for those plants compared to irrigated plants. In fact, the converse was found: non-irrigated *B. papyrifera* had higher A/E than their irrigated counterparts (2.71 *versus* 1.55 μmol CO_2/mmol H_2O for irrigated plants). If the non-irrigated plants had experienced the lower vpd experienced by the irrigated trees, the WUE values of the former would be even higher than those presented in Chapter 1, Table 4. Thus, in the four species data set, treatment differences in vpd served to dampen, rather than accentuate, the estimated differences in WUE and the $\delta^{13}C$ values can indeed be interpreted conservative estimates of relative WUE.

In the 22 species data set presented in Chapters 2 and 3, analysis of variance (ANOVA) on ranked data showed species differences in vpd and t_{leaf} ($p < .0001$). However, Tukey's Studentized Range Tests (Proc GLM) showed a considerable overlap in vpd and t_{leaf} among species (Table 1). Thus, the $\delta^{13}C$ values of the species represent a general trend of differences in WUE, but care must be taken when comparisons are being made between specific species.

Table 1. Tukey's Studentized Range Tests for differences in vpd and t_{leaf} among 22 tree species. Species are listed in order of descending mean vpd and t_{leaf}. Species followed by the same letter do not differ significantly in the variable tested (n=2557 observations). Mean vpd ranged from 2.23 kPa in *Q.rubra* to 1.71 kPa in *P. pensylvanica*; mean t_{leaf} ranged from 26.8°C in *Q. rubra* to 24.0°C in *P. pensylvanica*.

Species	vpd	t_{leaf}	
Q. rubra	a	*Q. rubra*	a
C. dentata	a	*C. dentata*	a
A. saccharum	a	*A. saccharum*	ab
B. alleghaniensis	ab	*A. rubrum*	ab
A. rubrum	ab	*B. alleghaniensis*	ab
P. balsamifera	abc	*C. ovata*	ab
F. americana	abc	*F. pennsylvanica*	ab
F. pennsylvanica	abc	*P. serotina*	ab
P. serotina	abc	*A. pensylvanicum*	ab
A. pensylvanicum	abc	*P. balsamifera*	ab
C. ovata	abc	*F. americana*	ab
A. saccharinum	abc	*A. saccharinum*	ab
J. nigra	abc	*J. nigra*	ab
P. tremuloides	abc	*P. tremuloides*	ab
P. deltoides	abc	*P. deltoides*	ab
C. occidentalis	abc	*C. occidentalis*	ab
J. nigra	abc	*J. cinerea*	ab
B. populifolia	abc	*B. populifolia*	ab
B. papyrifera	abc	*B. papyrifera*	ab
U. americana	abc	*U. americana*	ab
C. cordiformis	bc	*C. cordiformis*	ab
P. pensylvanica	c	*P. pensylvanica*	b

II. Calculation of c_i from gas exchange data

Internal CO_2 concentration (c_i) is generally calculated from the CO_2 assimilation rate (A) and stomatal conductance (g) measured by an infrared gas analyser (IRGA) (LI-COR, Inc. 1987, von Caemmerer & Farquhar 1981, Sharkey *et al.* 1982). While c_i is generally considered a conservative parameter, *i.e.* remaining relatively constant under varying plant and environmental conditions (Wong, Cowan & Farquhar 1979, Schulze *et al.* 1987, Friend 1992), the data presented in this thesis show substantial variation in the extent to which c_i varied over time (days to months). These differences in variability were seen both within species grown under different irrigation regimes (Chapter 1) and among species (Chapter 2). In both data sets, greater variability in c_i was related to increased WUE (Chapters 1 & 2). Thus, it appears to be a character of considerable biological interest. However, some researchers have suggested that variability in c_i may result from errors of estimation when g is low (Winter 1981, Briggs, Jurik & Gates 1986, Kubiske & Abrams 1992).

Winter (1981) found greater diurnal variability in c_i in water-stressed chickpea plants (*Cicer arietinum*) than in non-stressed plants. He suggested that this variability may have resulted from errors of estimation when g is low (<100 mmol $m^{-2}s^{-1}$). Briggs, Jurik & Gates (1986) also pointed out that calculation of c_i at low g is very sensitive to errors in the estimation of g. In their study, low g values were on the order of 5 to 50 mmol $m^{-2}s^{-1}$. Neither of these studies specifically addressed this potential problem, but mentioned it as a possible explanation of unexpected variation in the data. Other studies have also indicated greater variability in c_i under drought-stressed conditions (*e.g.* Reich, Walters & Tabone 1989).

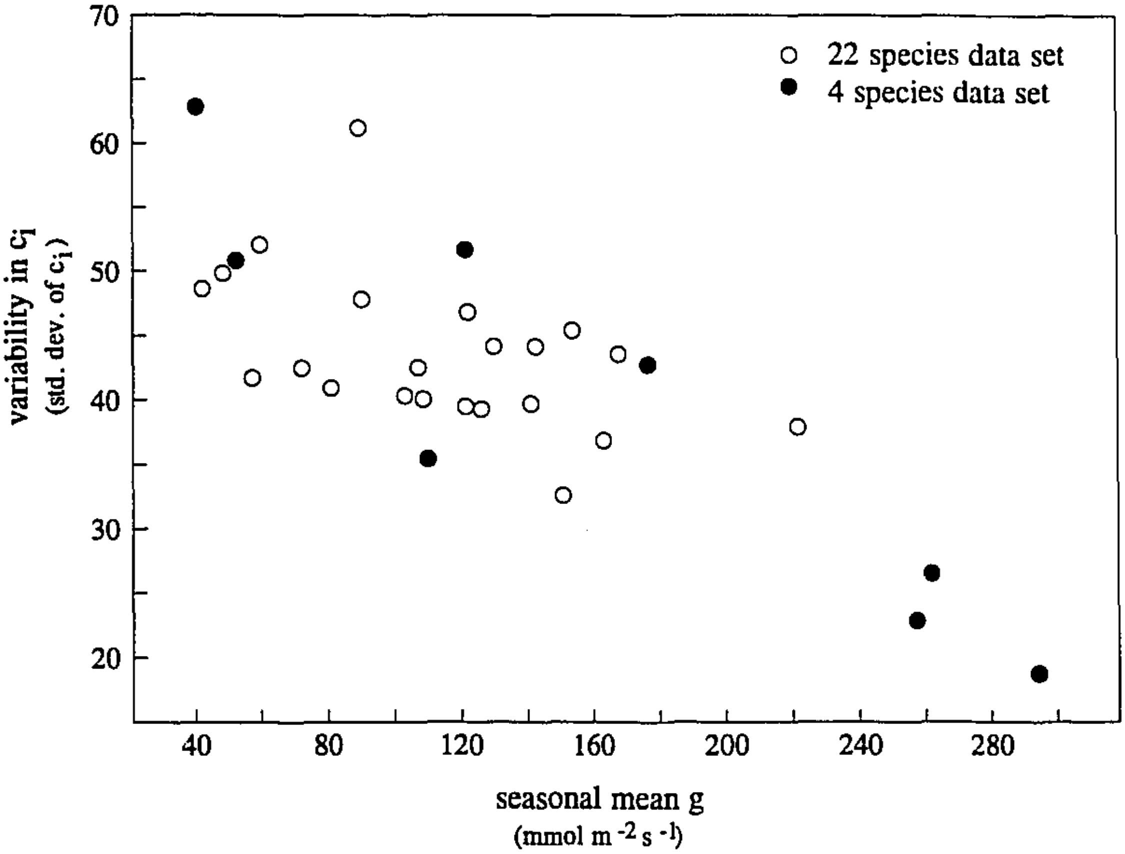
To investigate whether the c_i values obtained in my research were sound, I examined the relationship between variability in c_i and seasonal mean g. I then examined chamber conditions during measurement and ran simulations to test the effects of varying A and transpiration (E) on the calculation of c_i at different values of g. Finally, I examined the results in a biological context.

In both of the data sets in this thesis, plants with more variable c_i over time (measured as the standard deviation of the c_i values obtained during repeated assays) tended to have lower seasonal mean g (Spearman r= -.81, p= .0001 for four species grown irrigated and non-irrigated; r= -.44, p= .0003 for the 22 species). This suggests errors of estimation at low g may be, at least in part, responsible for the observed variability in c_i. There are several points, however, that indicate that the observed variability reflects the biology of the trees and is not due solely to estimation and calculation errors.

First, although there was a negative correlation between variability in c_i and seasonal mean g, there was also considerable variability in c_i in species with moderate to high seasonal mean g, as well as considerable differences in c_i variability among species with similar mean g (Figure 1). This would not be expected if variability in c_i resulted primarily from errors in the estimation of g when g was low.

Second, chamber conditions during measurements do not suggest substantial errors in the estimation of g. The LI-6200 can be operated in a steady state or transient mode, or a combination of the two (LI-COR, Inc. 1987, McDermitt 1990). The calculation of g is based on both a steady state and transient term. In the steady state mode (with chamber RH kept constant), resolution may be difficult when the flow rate is very low (McDermitt 1990, J.M. Welles *pers. comm.*). Under such conditions, the transient term predominates over the steady state term (*i.e.* chamber RH changes). When estimation of g is based primarily on the transient component, water sorption may be a problem. Both water adsorption (if RH is increasing) and desorption (if RH is decreasing) will dampen the change in chamber RH and lead to an underestimate of g (McDermitt 1990). If changes in RH lead to water sorption in some measurements but not others, random bias could enter into the measurements of

Figure 1. The relationship between stomatal conductance and variability in internal CO_2 concentration in hardwood trees. Spearman r= -.44 (p= .0003) for the 22 species; r= -.81 (p= .0001) for four species grown irrigated and non-irrigated.



g and, hence, into the calculated values of c_i. Under the conditions of the study, the transient term was likely to predominate (flow rates were on average approximately 12% of the maximum, *i.e.* about 12% of the air passing through the chamber was diverted through the desiccant). To test whether change in RH during measurements may have introduced random error, I calculated the mean change in RH during measurement for each tree in the 22 species data set and the four species data set. The overall mean change in RH during a measurement was 1.1 ± 1.3% for the four species data set and 1.2 ± 1.3% for the 22 species data set, far less than the 7-17% changes that were shown to result in errors in estimation of c_i by Leuning and Sands (1989). Furthermore, there was no correlation between the mean change in RH and seasonal variability in c_i (Spearman $r= -.15$, $p= .34$ for the four species; $r = .10$, $p= .44$ for the 22 species): trees that over the season had more variable c_i did not have greater changes in RH, on average, during a measurement. In addition, there was no correlation between seasonal variability in c_i and the standard deviation of change in RH values; therefore, it is unlikely that greater variability in c_i was caused by random error due to changes in RH and water sorption effects in some measurements, but not in others. Fresh desiccant was used for each assay, chamber temperature was kept close to ambient, the flow meter zero offset was frequently adjusted during the assays, the chamber was cleaned regularly, overall mean RH was not extreme (50.7 ± 10.1% for the four species set, 43.5 ± 11.0% for the 22 species set), and leaf temperature was greater than air temperature in approximately 90% of all measurements in the 22 species set and in over 35% of all measurements in the four species set. Under these operating conditions, substantial error due to difficulty in estimation of g is less likely (McDermitt 1990, Leuning & Sands 1989).

Third, it is also possible that the equation used by the LI-6200 to calculate c_i gives incorrect c_i values at extreme values of g, *i.e.* when the denominator is very small. The equation used is:

$$c_i = \frac{((g - E/2) * c_a - A),}{(g + E/2)}$$

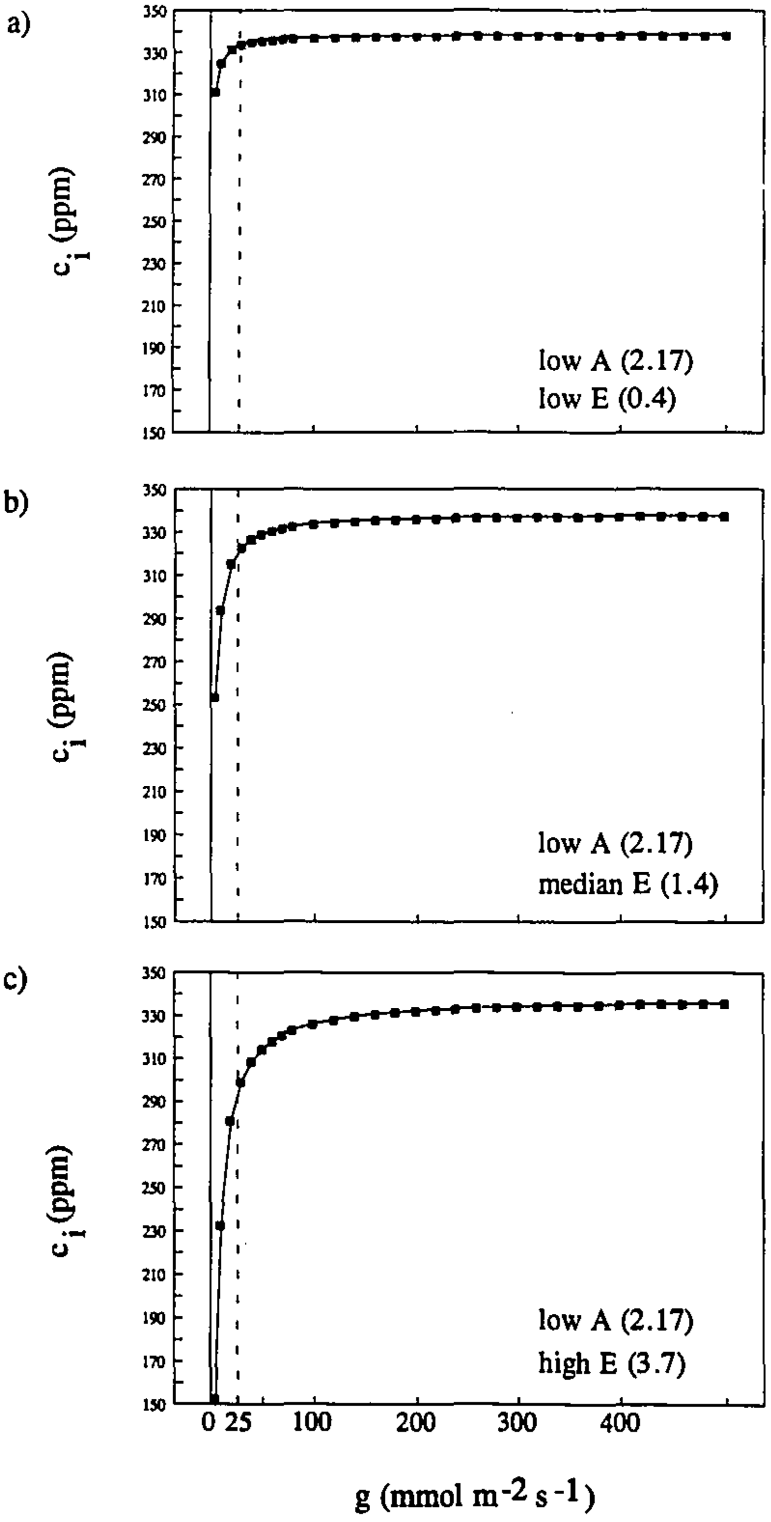
where c_i and c_a are internal and ambient CO_2 concentrations (ppm), respectively, g is total conductance to CO_2 (stomatal conductance plus boundary layer conductance), E is transpiration rate (mmol $m^{-2}s^{-1}$), and A is photosynthesis rate (μmol $m^{-2}s^{-1}$) (LI-COR, Inc. 1987). To examine the behaviour of the equation, I ran simulations in Lotus 123 Release 2.2 (Lotus Development Corporation) using values taken from the 22 species data set, varying A and E to test the effects on the relationship between g and c_i. C_a was held constant at the overall mean of 338.7 ppm. For simplicity, stomatal conductance was used in place of total conductance; g was increased through the range of values encountered from 4.9 to 500 mmol $m^{-2}s^{-1}$. The E values calculated by the LI-6200 were used; although these probably do not reflect true E (McDermitt 1990), they are reasonable estimates for the purpose of these simulations. The values of A and E used are given in Table 2.

Table 2. Parameter values used in simulations.

Level	A (μmol $m^{-2}s^{-1}$)	E (mmol $m^{-2}s^{-1}$)
low (10th percentile)	2.17	0.40
median	4.44	1.40
high (90th percentile)	-	3.70

The results are shown in Figure 2. The curves were identical for low and median A, so only those for low A are presented. As can be seen in Figure 2, slight changes in g result in large changes in c_i only at g values less than about 25 mmol $m^{-2}s^{-1}$ when either both A and E are low (Figure 2a) or when A is low and the median value for E is used (Figure 2b). In the 22 species data set, while 14% of the measurements were <25 mmol $m^{-2}s^{-1}$, only 5% were <15 mmol $m^{-2}s^{-1}$ (the region of the steepest drop-off in Figures 2a and b). The only situation when g values >25 mmol $m^{-2}s^{-1}$ might result in significant errors in estimation of c_i is shown in Figure 2c, when A is low and E is high. Given the close correlation between A and E

Figure 2. Relationship between internal CO_2 concentration (c_i) and stomatal conductance (g) at various combinations of photosynthesis (A) and transpiration (E) rates. See text for explanation.



(Spearman $r = .81$, $p < .0001$), such conditions were unlikely to have occurred in this study. Low values of A were most likely to have been accompanied by low E and, thus, calculation of c_i when g is low is unlikely to be a major source of error.

Finally, the relationships between A, g and c_i are what one might expect biologically. In Table 3, these relationships are presented for the 22 species data set as a whole and for subsets of observations with $g \leq 25$ mmol $m^{-2}s^{-1}$ and with $g > 25$ mmol $m^{-2}s^{-1}$. In all cases, seasonal mean A was positively correlated with seasonal mean g and negatively correlated with seasonal mean c_i. For the whole data set and the subset of observations with moderate to high g, c_i was positively correlated with g: larger stomatal aperture allows greater influx of CO_2 and internal CO_2 concentrations closer to ambient. However, at low g values, c_i was negatively correlated with g. As g declined below 25 mmol $m^{-2}s^{-1}$, CO_2 fixation would also most likely be decreasing. As A declined, c_i would be expected to rise towards ambient, hence the negative correlation between c_i and g (a similar negative correlation was found when a subset of g values ≤ 50, rather than ≤ 25, mmol $m^{-2}s^{-1}$ was used). One might also expect conditions resulting in low g values would also result in greater variability in c_i over time because under these conditions replenishment of CO_2 will necessarily be slower. Moment to moment changes in CO_2 uptake due to, for example, passing clouds (Knapp & Smith 1987, Tenhunen, Pearcy & Lange 1987) would not so quickly be met by changes CO_2 supply, resulting in variable c_i. This might result in greater seasonal variation in c_i as well.

In summary, on the basis of the analyses described, I conclude that the differences in seasonal variability in c_i among species or within species between treatments, reflects true differences in the regulation of A and g. At least in the data sets presented here, variability in c_i does not appear to be solely the result of errors in estimation and/or calculation as has been suggested in earlier studies. The relationship found between seasonal variability in c_i and WUE makes this phenomenon worthy of further study.

Table 3. Spearman correlations among photosynthesis (A), stomatal conductance (g) and internal CO_2concentration (c_i) in 22 hardwood tree species. Correlations are given for the data set as a whole and for subsets with $g > 25$ mmol m^{-2} s^{-1} and $g \leq 25$ mmol m^{-2} s^{-1}; for all correlations, $p \leq 0.0001$.

Data set:	A * g	A * c_i	c_i * g
All observations (n=2557)	0.84	-0.21	0.25
$g > 25$ mmol m^{-2} s^{-1} (n=2204)	0.78	-0.15	0.43
$g \leq 25$ mmol m^{-2} s^{-1} (n=353)	0.52	-0.94	-0.29

Appendix VI

Information on Archival Data Files

Archival data diskettes are deposited with Dr. M.J. Lechowicz, to whom inquiries regarding the data files may be sent. Mailing address: Department of Biology, McGill University, 1205 avenue Docteur Penfield, Montréal, Québec, H3A 1B1, Canada. Electronic mail: EH39@MUSICA.MCGILL.CA. FAX: (514) 398-5069.

I. Major data files. All major data files are written in SAS programming language and are fully anotated.

Chapter 1: Four species of hardwood trees grown under irrigated and non-irrigated conditions.

1. **WDLI88.PRG** reads in **WDLICOR.DAT**. These files contain the complete set of gas exchange data (17 assays) obtained in 1988 for the four species. Each measurement (leaf) is included.

2. **WDFINAL!.NEW**. This file contains all the data presented for the 42 trees included in this study. See Chapter 1 for variables and units.

Chapter 2: Gas exchange characteristics of 22 hardwood tree species.

1. **LI2YRALL.PRG** reads in **LI2YRALL.DAT**. Complete set of gas exchange data taken in 1987 (34 assays) and 1988 (13 assays). Each measurement (leaf) is included.

2. **23SP_GE.PRG** reads in **23ALL.DAT**. These files contain the gas exchange, leaf nitrogen, specific leaf mass and carbon isotope ratio data for the 64 trees in

the 22 species data set presented in Chapter 2.

Chapter 3: All data presented for 22 hardwood tree species.

1. **22SPP_PA.DAT**. This file contains species mean values for the variables in **23SP_GE.PRG/23ALL.DAT** and the rest of the variables presented in Chapter 3.

II. Ancillary Data. The files listed below contain the raw data entering into the major data files listed above and also ancillary data gathered in the experimental tree nursery (including data on trees not included in the studies presented in this thesis). Files are written in SAS programming language or consist of LOTUS worksheets (*.WK1).

Growth data:

DIAMHT86.DAT, DIAMHT87.DAT, DIAMHT88.DAT, DIAMHT89.DAT, DIAMHT90.DAT: stem basal diameter and height measurements for all tagged trees in the nursery for the years 1986 to 1990.

DIHT8590.DAT: diameter and height measurements for 1985 and 1990 for all tagged trees in nursery (for RGR calculations).

23DIHTBR.DAT: diameter and height measurements for 1985 and 1990 plus 1990 branch measurements for the 22 species data set.

WDDIHTBR.DAT: diameter and height measurements for 1985 and 1990 plus 1990 branch measurements for the 4 species "wet/dry" set.

BRANCH90.WK1: 1990 whole tree branch measurements for the 22 species and wet/dry data sets.

22BRAN90.DAT: 22 species subset of **BRANCH90.WK1** data.
WDBRAN90.DAT: wet/dry species subset of **BRANCH90.WK1** data.

23BRAN87.DAT: total tree branch lengths for the 22 species set in 1987.

23TREE87.DAT: merged 1987 branch, leaf, diameter and height data for the 22 species set (includes calculation of canopy/height and other variables).

23TREE88.DAT: merged 1988 whole tree leaf counts, budbreak, spring and fall diameter and height data for the 22 species set (includes calculation of canopy/height and other variables).

22PA_RGR.DAT, WD_RGR.DAT: calculation of relative growth rate (RGR) variables for the 22 species and wet/dry data sets, respectively.

RGR3-4YR.DAT, RGR4_4YR.DAT, DIHTCDFP.DAT: calculation of 3- and 4-year RGR's for trees for which 5 years' data were not available.

HTDA20.WK1: 1986 weekly height growth data for whole nursery (20 weeks).

MEAN86.PRG and **SASALL86.PRG**, which both read in **SASALL.PRN**: data and programs to analyse weekly height growth measurements taken in 1986 for the *Acer saccharum, Fraxinus americana* and *Quercus rubra* seedlings used in the 1986 gas exchange assays (subset of **HTDA20.WK1**).

SEEDWGT.WK1: seed weights for seed from most nursery provenances.

Hydraulic conductivity and related data:

DENSITY.DAT: wood density, measured on branches collected for hydraulic conductivity measurements.

23DENSTY.DAT: subset for 22 species data set.
WDDENSTY.DAT: subset for wet/dry data set.

NEICOND.WK1: raw data for hydraulic conductivity measurements.

NEICOND.PRG reads in **ALLHCRAW.DAT, 23HCRAW.DAT** or **WDHCRAW.DAT** (all data, 22 species, wet/dry set, respectively): calculates hydraulic conductivity.

ALLCOND.DAT, 22COND.DAT, WDCOND.DAT: hydraulic conductivity files to be used in analysis for all data, 22 species and wet/dry sets, respectively.

HCBRANCH.WK1: length and diameter measurements for all branches collected for hydraulic conductivity measurements.

HCLEAF.WK1: leaf counts and leaf area measurements for all hydraulic conductivity branches.

22HC_ALL.DAT: merged leaf, branch length and conductivity data for the 22 species hydraulic conductivity branches.

WDHCBR.PRG reads in **WDHCBR.DAT**: merged leaf, branch length, density and conductivity data for the wet/dry data set.

Leaf data:

DELTA13C.DAT: carbon isotope data for the 22 species data set (1988 & 1989) and wet/dry data set (1989).

23DELTA.DAT: subset for the 22 species set.
WDDELTA.DAT: subset for the wet/dry set.

N_NEI8-9.SAS: nitrogen data (1988 & 1989), to be used for analysis, both data sets.

23_N8-9.DAT: subset for the 22 species set.
WD_N8-9.DAT: subset for the wet/dry set.

LEAF87.DAT: 1987 leaf samples for area & weight for the 22 species set (leaves taken from plot, not tagged trees).

23LF87.DAT: 22 species set, number of leaves and total leaf area for each tree (1987).

LEAF88.WK1: 1988 leaf samples for both data sets (measurements for individual leaves).

23LEAF88.DAT: 22 species subset (tree level mean leaf area & weight).
WDLF88.DAT: wet/dry subset (values for individual leaves).

LEAF89.WK1: 1989 leaf samples for both data sets (mean values for each tree).

23LEAF89.DAT: 22 species subset (tree level means).
WDLEAF89.DAT: wet/dry subset (tree level means).

WDLF89.WK1: 1989 wet/dry set whole tree leaf counts.

STOMAT86.PRG: stomatal counts and dimensions for *Acer saccharum, Fraxinus americana* and *Quercus rubra* seedlings assayed for gas exchange in 1986.

Phenology data:

PHEN87.WK1, PHEN88.WK1, PHEN89.WK1, PHEN90.WK1: spring phenology for the whole nursery for 1987 to 1990, respectively.

SUMMPH87.WK1, SUMMPH88.WK1: 1987 & 1988 records of "bud status" (*i.e.* cessation of growth, new flushes) for the whole nursery. See **SUMMPH88.WK1** for key to rankings.

SEN87.WK1, SEN88.WK1: 1987 & 1988 fall senescence data for the whole nursery.

23PH_NEW.DAT: 22 species set; budbreak, fall senescence and canopy duration for 1987 & 1988.

WD88PH87.DAT, WD88PH88.DAT: wet/dry set; 1987 & 1988 budbreak, respectively.

Psychrometer and neutron probe data:

PSICAL87.DAT, PSICAL88.NEW: December 1987 and June 1988 psychrometer calibrations, respectively.

PSYCH87.NEW, PSYCH88.NEW: 1987 & 1988 nursery reference plot psychrometer data.

NPROBE86.DAT: 1986 neutron probe data.

NROBE87.NEW: 1987 neutron probe data to go along with 22 species LICOR assays.

NPRB2388.NEW: 1988 neutron probe data to go along with 22 species LICOR assays.

NPRBWD88.DAT: 1988 neutron probe data to go along with wet/dry LICOR assays.

PSI_NP87.DAT: merged psychrometer and neutron probe data for the reference plot, 1987.

WS_ALL.NEW: merged psychrometer and neutron probe data for the reference plot, 1988.