Ecology, 74(3), 1993, pp. 798–815

GENDER-SPECIFIC PHYSIOLOGY, CARBON ISOTOPE DISCRIMINATION, AND HABITAT DISTRIBUTION IN BOXELDER, *ACER NEGUNDO*[1]

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Abstract. In the semiarid Intermountain West, boxelder, *Acer negundo* var. *interior*, a deciduous, dioecious tree, exhibits significant habitat-specific sex ratio biases. Although the overall sex ratio (male/female) does not deviate significantly from one, the sex ratio is significantly male biased (1.62) in drought-prone habitats, while it is significantly female biased (0.65) in moist, streamside habitats. The causes underlying gender-specific habitat associations in this species are not known. We hypothesized that spatial segregation of the sexes is maintained by differences in gender-specific photosynthetic behavior, water relations characteristics, and both instantaneous and integrated water-use efficiency. Gender-specific physiological characteristics were measured and related to growth, reproduction, population age structure, and habitat distribution of male and female trees.

Under both field and controlled-environment conditions, males and females differed significantly in a number of physiological traits. Males maintained lower stomatal conductance to water vapor (g), transpiration (E), net carbon assimilation (A), leaf internal CO_2 concentration (c_i), carbon isotope discrimination (Δ; an index of time-integrated c_i and water-use efficiency), and higher instantaneous (A/E) and long-term (Δ) water-use efficiency than females. Furthermore, male trees exhibited greater stomatal sensitivity to both declining soil water content and increasing leaf-to-air vapor pressure gradients, a measure of evaporative demand. Higher rates of carbon fixation in female trees were correlated with higher g, higher leaf nitrogen concentrations, and greater stomatal densities. For females growing in both wet and dry habitats, vegetative shoots had higher growth rates than reproductive shoots, while for males, growth rates of the two shoot types did not differ. In streamside habitats, female trees exhibited significantly greater vegetative shoot growth when compared to male trees. In contrast, males showed slightly greater vegetative and much greater reproductive shoot growth in non-streamside habitats. Regardless of habitat or growing conditions, females allocated proportionately more of their aboveground biomass to reproduction than did males.

These results suggest that (1) gender-specific physiological traits can help explain the maintenance of habitat-specific sex ratio biases in *A. negundo* along a soil moisture gradient, and (2) that the combination of the gender-specific physiology, growth, and allocation differences contribute to differences in the size (=age) structure of male and female plants within the population. Gender-specific physiological differences may have evolved as a product of selection to meet significantly different costs associated with reproduction in male and female plants.

Key words: Acer negundo; *allocation; carbon isotope discrimination; dioecious tree; growth; Intermountain West; net carbon assimilation; sex ratio; size structure; stomatal conductance; stress avoidance; stress tolerance; Utah; water relations; water-use efficiency.*

INTRODUCTION

Inscriptions on the ancient Egyptian tablets of King En-temena (≈3000 BC) document early knowledge of both the existence of, as well as an interest in, sexually dimorphic or dioecious plants within the plant kingdom (Dannemann 1928, Dzhaparidze 1969). Since that time, investigators have explored a broad range of topics in relation to the dioecious life history, focusing especially on its unique ecological characteristics and evolutionary origins. Many reports have documented ecological and morphological differences between genders in dioecious species and have shown that the differences may aid each gender in meeting different resource demands (Correns 1928, Putwain and Harper 1972, Opler and Bawa 1978, Wallace and Rundel 1979,

[1] Manuscript received 5 February 1992; revised 30 July 1992; accepted 31 August 1992.

Bullock and Bawa 1981, Gross and Soule 1981, Meagher and Antonovics 1982, Zimmerman and Lechowicz 1982, Hoffmann and Alliende 1984, Lovett Doust et al. 1987, Vitale et al. 1987, Ramp and Stephenson 1988, Iglesis and Bell 1989, Delph 1990, Jin and Coley 1990, Krischik and Denno 1990*a,b,* Carr 1991). It has been suggested therefore that gender-specific ecological and morphological traits may have evolved because of significantly different resource demands associated with male vs. female sexual reproduction (Darwin 1877, Cox 1981, Dawson and Bliss 1989). In contrast to ecological and morphological specialization, relatively little information has been gathered on gender specialization in physiology (but see Bourdeau 1958 and Dawson and Bliss 1989, 1993). Furthermore, little is known about how physiology may combine with other factors, such as allocation, to influence resource balance and overall performance (Dzhaparidze 1969, Cox 1981), and how it may ultimately affect population age structure and the habitat distribution of male and female plants in relation to environmental gradients (Lloyd and Webb 1977, Bierzychudek and Eckhart 1988).

Here, we report the results of an investigation on the physiological ecology of the dioecious tree *Acer negundo* L. var. *interior* (Britt.) Sarg. (Aceraceae), boxelder. This species is known to exhibit habitat-related sex ratio biases with males dominating xeric, non-streamside habitats and females dominating moist streamsides, along marked soil moisture gradients (Freeman et al. 1976). It is also known to be sensitive to water stress (Dina and Klikoff 1973). We were interested in knowing if the sexes differed in rates of net photosynthetic carbon assimilation, the use and regulation of water, and both instantaneous and long-term water-use efficiency (the molar ratio of carbon fixed via photosynthesis [A] to water lost via transpiration [E]; A/E). Moreover, if significant gender differences in physiology could be identified, we wanted to know if they could account for differences in not only habitat-specific sex ratio biases, but in growth, biomass allocation, and the size/age structure of trees in each of the two habitats.

We assumed that the costs of reproduction are higher for females relative to males and that streamside habitats are more favorable sites than drier, non-streamside habitats for growth, reproduction, and overall performance. We reasoned that, if there were no gender differences in physiology that affected the ability of plants to fix carbon for growth and reproduction, males would out-perform (e.g., grow more, die less) females in *both* habitat types because of their lower reproductive costs and that the differences in performance between the sexes would be most pronounced in the less favorable non-streamside habitats. Thus, in the absence of gender differences in physiology (and in other traits), we could account for male-biased sex ratios in dry sites, but could not explain female-biased sex ratios in wet sites. In order to explain spatial segregation of the sexes, we hypothesized (1) that gender-specific physiological differences exist, (2) that the sexes are physiologically specialized for different habitat types, and (3) that specialization to a particular habitat reduces performance in the contrasting habitat.

In dry habitats, physiological traits (specializations) that improve drought tolerance or drought avoidance will be favored. One way to avoid drought is through greater water-use efficiency and through relatively high stomatal sensitivity to soil or atmospheric water deficits (Cohen 1970, Cowan 1982, Passioura 1982, Geber and Dawson 1990, Johnson et al. 1990, DeLucia and Schlesinger 1991). On the other hand these same traits are likely to reduce net carbon assimilation and photosynthetic nitrogen-use efficiency (rate of carbon fixed per mole of leaf nitrogen; Field 1983, DeLucia and Schlesinger 1991), especially in mesic sites. Thus, trade-offs can and do occur between drought tolerance and/or avoidance (manifest as patterns of water-use efficiency) and carbon acquisition for growth and reproduction, and between performance in dry vs. wet habitats. In an ecological context, physiological trade-offs like these will influence the distribution of plants in space and time, and for perennial taxa, their population age structure (Harper 1977). For dioecious plants, such physiological trade-offs could influence the evolution of gender-specific traits. If the cost of reproduction is greater for a female than a male, females with high A/E (conservative water use) and hence low relative carbon assimilation may survive, but may not be able to reproduce very well in a drought-prone site. These same females would also be at a considerable disadvantage relative to females (and perhaps males) with lower A/E, in wet sites. Thus, natural selection may favor physiological traits in female plants that enhance carbon income at the expense of high A/E and drought avoidance, thereby restricting females to mesic habitat types in environments characterized by sharp soil moisture gradients. Males, on the other hand, are likely to meet their reproductive costs in both wet and dry sites. However, pollen dispersal, and hence male reproductive success, may even be greater in upland xeric sites (Freeman et al. 1976). Selection would therefore favor greater drought tolerance/avoidance in males compared to females. In sum, we expect males to exhibit greater stomatal responsiveness to soil and atmospheric water deficits, and higher water-use efficiency, but at the cost of lowered leaf-internal carbon dioxide concentrations and hence photosynthetic rates, lower carbon isotope discrimination, and reduced growth rates relative to females.

Methods and Materials

Description of the plant species

Acer negundo, the boxelder, is a common, deciduous tree usually found growing in riparian and floodplain habitats from Montreal, Canada to southern California

in the United States (Sargent 1965, Heywood 1978). Five varieties in North America are recognized and are distinguished primarily by the number (3, 5, or 7), shape, and size of the leaflets per leaf, several fruit characters, and geographic distribution. Our investigation focused on *A. negundo* var. *interior* (Britt.) Sarg., a form common throughout most of the semiarid Intermountain West (Welsh et al. 1987). *A. negundo* is unusual in that it is the only strictly dioecious North American species in the genus *Acer* (DeJong 1976). Sex expression in many other *Acer* species is known to be quite labile (DeJong 1976, Sakai 1990).

Sex ratio and size structure determinations

Sex ratio biases had previously been reported in boxelder (Lysova and Khizhnyak 1975, Freeman et al. 1976). We expanded upon these previous reports and surveyed the sex ratio of trees that were growing between 1550 and 2000 m along a wet-to-dry soil moisture gradient in Red Butte, Parley's, Little Cottonwood, Mill Creek, and Big Cottonwood canyons along the west slope of the Wasatch Mountains near Salt Lake City, Utah (40°46′ N, 11°55′ E). Between four and nine transects, 10m wide by 50m long that evenly bisected the wet and dry parts of the gradient were used in each canyon. The surveys were done in May when reproductively active trees could be sexed. Gravimetric soil moisture determinations showed that wet sites had, on average, 3–8 times higher soil moisture contents during the growing season than dry sites (averaged from −20, −35, and −50 cm deep; $n = 12$ per site, at four wet and four dry sites; t test, $P < .01$). In addition to gender, the diameter at breast height (dbh, measured at 1.4 m aboveground) of each tree was determined so that the size (=age) structure for each subpopulation as a function of both habitat type and sex ratio could be determined. A total of 1704 trees growing along 30 transects were sampled.

Physiological measurements: field observations

Physiological measurements conducted in the field were made on trees growing in a subpopulation (4.3 ha in area, 1820–1890 m elevation) within the Red Butte Canyon Research Natural Area, east of Salt Lake City, Utah. Approximately 30 trees of each sex (10 within each of three well-separated size classes) in both mesic (streamside) and xeric (non-streamside) habitats were used to monitor diurnal and seasonal gas exchange and water relations characteristics during the 1988 and 1989 growing seasons. Diurnal course measurements were made each hour between 0530 and 2030 Mountain Standard Time (MST). Seasonal course measurements were made biweekly from mid-May to late September (leaf senescence). Instantaneous measures of photosynthetic carbon assimilation (A), stomatal conductance to water vapor (g), and leaf internal CO_2 concentration (c_i) were determined on fully illuminated (1300–2100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of photosynthetically active radiation, PAR) and fully expanded leaves enclosed in a well-mixed cuvette attached to a portable photosynthesis system (LI-COR model LI-6200, Lincoln, Nebraska, USA). Approximately one-half of the terminal leaflet (≈ 30 cm^2) was enclosed in the cuvette during each measurement. The leaf boundary layer is essentially removed by the presence of a fan in the leaf cuvette so that the conductance measured is almost entirely stomatal conductance. During each measurement, the leaf reduced the CO_2 concentration by 20 μL per litre of air from 360 to 340 μL/L, 10 μL/L on either side of ambient (≈ 350 μL/L). Leaf-to-air water vapor pressure deficit (v) used in calculating transpiration (E; see next subsection) was determined from leaf temperature obtained with five thermocouples attached to the lower leaf surfaces next to the shoots on which gas exchange measurements were being made, and from measures of atmospheric relative humidity and ambient air temperature obtained with sensors positioned adjacent to these same leaves with a computerized data acquisition system (Campbell Scientific, model 21x, Logan, Utah, USA). Leaf water potentials (Ψ) were determined with a Scholander-type pressure chamber (PMS Instruments, Corvallis, Oregon, USA; Scholander et al. 1965). A fully expanded leaf on a terminal shoot was excised, removed from the light, and enclosed in plastic zip-lock bags to minimize changes in Ψ due to evaporative water loss. Water potential of these leaves was determined within 3 min of collection.

Physiological measurements: laboratory experiments

Gender-specific functional response characteristics were determined from 1.5-yr-old plants established from stem cuttings and grown in pot culture under ambient environmental conditions during the spring and summer growing seasons of 1988, 1989, and 1990. Five to seven replicate cuttings of eight male and nine female genotypes obtained from the Red Butte Canyon population were used in the experiments. Laboratory gas exchange experiments were conducted using a modified "open-flow system" described by Ehleringer (1983). Response curves of photosynthesis and stomatal conductance as a function of c_i (the A-c_i and g-c_i curves, respectively) were measured on fully mature leaves by holding PAR (1700 ± 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$), leaf temperature (28° ± 2.8°C), and v (10–12 mmol/mol air) constant and varying ambient CO_2 concentrations (c_a) in the leaf cuvette in steps of 75 μL/L from 50 to 575 μL/L. Measurements were first taken at a CO_2 concentration of 350 μL/L; the CO_2 concentration was then increased and then decreased, and finally returned to 350 μL/L. Response curves of stomatal conductance as a function of v were measured 1 wk later on leaves adjacent to those used for the A-c_i/g-c_i work, again by holding PAR, leaf temperature, and CO_2 (≈ 350 μL/L) constant and varying v in steps of 6–8 mmol/mol ranging from 10 to 50 mmol/mol.

Instantaneous water-use efficiency (A/E) was determined from the same gas exchange experiments by combining the maximum photosynthetic and transpiration rates using the equations for net photosynthesis:

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

and transpiration:

$$E = gv, \quad (2)$$

where v is defined as:

$$v = e_i - e_o/P, \quad (3)$$

where e_i and e_o are the vapor pressure of water in the air inside and outside of the leaf, respectively, and P is the atmospheric barometric pressure. Expressing A and E as a ratio yields:

$$A/E = [c_a(1 - c_i/c_a)]/1.6v, \quad (4)$$

where c_i and v are defined as before and 1.6 is the ratio of gaseous diffusivities of CO_2 and water vapor in air. This relationship implies that at similar c_a and v, instantaneous A/E is a function of c_i/c_a.

The percent stomatal limitation of photosynthesis (L_s) was determined from the A-c_i curves using the equation:

$$L_s = A_0 - A/A_0 \quad \text{or} \quad 1 - (A/A_0) \times 100, \quad (5)$$

where A is the assimilation rate at a c_a of 350μL/L and A_0 is the assimilation rate that would occur if there was no resistance to CO_2 diffusion (e.g., $c_i = 350$ μL/L; after Farquhar and Sharkey 1982). L_s approximates the proportion of limitation to net photosynthesis by stomata by calculating the difference between the actual assimilation rate measured at 350 μL/L (A) and what the assimilation rate would be if g were infinite and thus CO_2 never limiting (A_0).

Carbon isotope composition and leaf nitrogen determinations

Instantaneous measures of A/E provide one piece of comparative physiological information but are problematic if one is interested in obtaining a perspective on A/E in leaves over longer periods of time. The measurement of stable carbon isotopic composition (given as $\delta^{13}C$) of leaf tissue has recently emerged as an approach that provides a time-integrated index of physiological performance, including water-use efficiency (Farquhar et al. 1989). $\delta^{13}C$ is the difference in carbon isotope ratios between a sample and the PDB standard, in thousandths (‰) of the isotope ratio in the standard:

$$\delta^{13}C = \left[\frac{(^{13}C/^{12}C)_{sample} - (^{13}C/^{12}C)_{PDB}}{(^{13}C/^{12}C)_{PDB}}\right] \times 10^3.$$

(PDB refers to the belemnite carbonate standard from the Peedee Formation, South Carolina, USA.) The $\delta^{13}C$ of leaf tissue is determined by physical factors such as the diffusion of different carbon isotope species ($^{13}CO_2$ and $^{12}CO_2$) through the stomatal pore, the $\delta^{13}C$ of the source air (−8‰ under the well mixed conditions of our experiments), and by metabolic factors. Carbon isotope discrimination (Δ) in plants that possess the C_3 photosynthetic pathway is related to the leaf gas exchange properties at the time the leaf is being made and is a measure of this isotopic ratio. Δ can be expressed as:

$$\Delta = a + [(b - a)c_i/c_a], \quad (6)$$

where a is the fractionation that occurs due to differential diffusion of the two isotopes in air (4.4‰, where ‰ = parts per thousand), and b is the net fractionation caused by carboxylation (primarily discrimination by ribulose bisphosphate [RuBP] carboxylase; 27‰). The ratio c_i/c_a is determined by variation in the amount of stomatal opening (the supply of CO_2; g_{CO_2}) and the demand for CO_2 by the leaf chloroplasts. Since the carbon incorporated into leaf tissues is assimilated over a considerable period of time and under more than one set of environmental conditions, measurements of Δ provide an average estimate of c_i/c_a, and therefore, Δ is an index of time-integrated (and flux-weighted) plant metabolism. Because *both* Δ and A/E are a function of c_i/c_a (Eqs. 6 and 4, respectively), Δ can be used to estimate long-term A/E from the same foliage that gas exchange observations are made on. This is only true provided (1) that v is equivalent and known at each site, (2) that each sex experienced the same range of v during tissue synthesis, and (3) that the sexes do not differ in the fraction of their carbon that was fixed during photosynthesis but lost during respiratory processes (Farquhar and Richards 1984). Two final points should be noted. First, that it is unlikely that the assumptions (1–3) stated above will be strictly met, and Δ values of leaf tissue are thus unlikely to provide a direct, quantitative measure of long-term A/E. As such, we view Δ values as absolute indices of integrated c_i/c_a and a relative index of A/E. Secondly, the reader should note that Δ is inversely proportional to A/E (Farquhar and Richards 1984) so that high water-use efficiency in leaves leads to low Δ.

Foliage samples from three heights and the four cardinal compass points (n = 12 samples/tree) within each canopy were pooled. Twenty-five (25) mature trees (9–14 cm dbh) of each sex within both habitats were sampled. Leaves were dried to a constant mass at 70°C and homogenized in liquid nitrogen to a very fine powder. The carbon isotope composition is obtained from the cryogenically purified CO_2 produced by combustion of the dried sample in a sealed tube containing cupric oxide and a silver foil catalyst (see Ehleringer and Osmond 1989 and Smedley et al. 1991 for details) and then measured on either a Finnigan MAT delta E or delta S isotope mass spectrometer (San Jose, California, USA). Overall precision of the preparation and analysis is ±0.15‰. The measurement of carbon iso-

TABLE 1. Sex ratio (male/female) of *Acer negundo* as a function of habitat type within five canyons along the west slope of the Watsatch Mountains near Salt Lake City, Utah. n = number of trees.

	Streamside		Non-streamside		Total	
	Sex ratio	n	Sex ratio	n	Sex ratio	n
Red Butte Canyon	0.737**	356	1.724***	237	1.031[a]	593
Parley's Canyon	0.751	121	2.25***	156	1.367[c]	277
Little Cottonwood Canyon	0.509***	157	2.10***	152	1.020	309
Mill Creek Canyon	0.659*	146	0.741	148	0.699	294
Big Cottonwood Canyon	0.493***	100	1.911*	131	1.063[a]	231
Overall (n = 1704)	0.651***		1.624***		1.011	

* $P \leq .05$; ** $P \leq .01$; *** $P \leq .001$ (Statistically significant deviations from unity determined by chi-square analyses within a habitat).
[a] $P < .05$; [c] $P < .001$ (chi-square for heterogeneity between habitat types).

tope discrimination (Δ) determined from the isotopic composition of foliage samples is discussed fully in Farquhar et al. (1989) and Ehleringer (1991). Foliage nitrogen concentration was determined by micro-Kjeldahl technique (see Comstock et al. 1988) and is presented on both a mass and a leaf area basis (Evans 1989).

Growth and allocation determinations

Absolute growth rates (in millimetres per day) were determined during the 1989 growing season from 20 randomly selected vegetative and reproductive ramets on 40 trees of each sex in both habitat types. Ramets (i.e., branches) were measured weekly from bud break to leaf senescence. Aboveground biomass allocation to stem, leaf, and reproductive tissues was determined from five randomly selected reproductive ramets harvested from 75 trees of each sex in the streamside habitats and 45 trees of each sex in non-streamside habitats in both Red Butte and Mill Creek Canyons in 1989 and 1990. Allocation to reproduction in female trees is defined as biomass allocated to both flowers and mature seeds. Allocation to floral tissues was determined during peak anthesis (late May). Allocation to seed, stem, and leaf tissues was determined on ramets harvested when growth had essentially stopped for the season. First, area of a subsample of 50–70 leaves from 10 ramets (5 of each type) of each sex in both habitat types was determined. Samples were then divided into seeds, stems, and leaves, dried as before, and their dry mass determined.

Statistical analyses

All statistical analyses were performed with either SYSTAT or JMP (statistical packages for the Apple Macintosh Computer). Differences in daily and seasonal course of gas exchange and A/E were analyzed by an analysis of variance for repeated measures (ANOVAR) where multiple measurements on a given plant constitute the repeated variables (Potvin et al. 1990). Values of A/E were $\log_e$ transformed to conform to normality assumptions of the ANOVAR. In each analysis, the main effect of gender is tested as a between-subjects effect. Diurnal, seasonal, and between-habitat variation (e.g., time × gender or gender × habitat) were tested as both within-subjects effects (refer to Potvin et al. 1990 for a complete discussion of this analysis). Testing for differences in functional responses between sexes, sites, or times of the season was often made difficult because the assumption of compound symmetry in the covariance matrix was violated. In the absence of compound symmetry, we performed an Huynh–Feldt corrected analysis of variance for repeated measures. We chose this analysis because in some cases our sample sizes were small and testing for normality was difficult and because the compound symmetry of the covariance matrix showed mild violation of Mauchly's criterion (epsilon = 0.9874 to 0.9642). Our analysis of within-subjects effects is based on the Huynh–Feldt corrected significance levels. To test for overall differences in physiology, growth, and allocation, an analysis of covariance (ANCOVA) was performed on mean values for each gender (in each habitat type in the case of field data) with the covariate being plant size. Other statistical analyses used appear in the specific figure or table legends.

RESULTS

Field observations: sex ratio and physiology

1. *Sex ratio.*—Though the overall sex ratio (male/female) of *Acer negundo* did not deviate significantly from one (1.011), marked and significant habitat-specific sex ratio biases were observed (Table 1), leading to clear spatial segregation of the sexes (SSS; after Bierzychudek and Eckhart 1988). At the driest, non-streamside, half of the transect (4–11% soil water content), the sex ratio was significantly male biased (1.624), while at the wettest, streamside end (16–89% soil water content) the sex ratio was significantly female biased (0.651; Table 1).

2. *Seasonal and diurnal physiology.*—In the drier, non-streamside, habitats, mature female trees generally maintained higher rates of net photosynthesis (A) and stomatal conductance (g) (Fig. 1). Results from the ANOVAR indicated that no significant differences for A, g, or leaf water potential (Ψ) between the sexes or

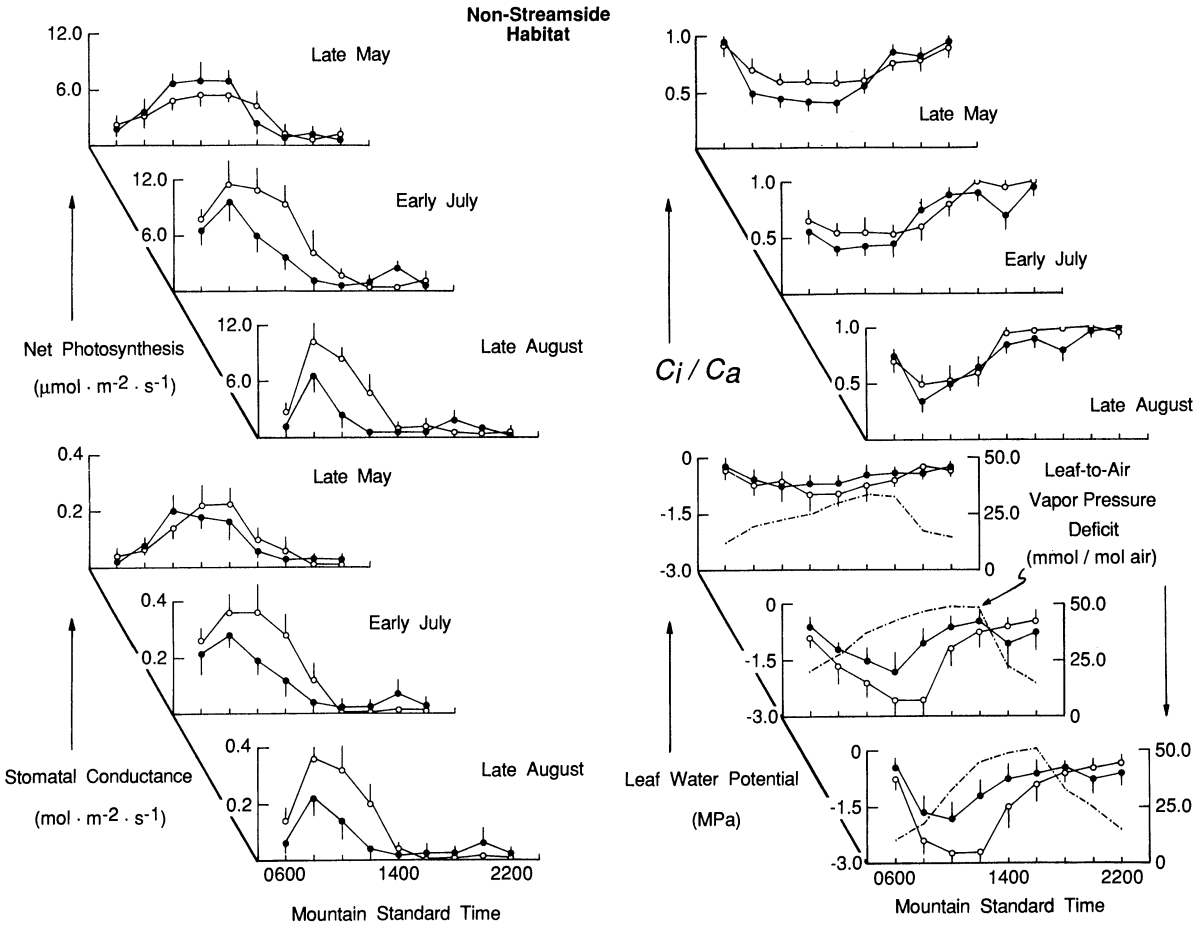

FIG. 1. Diurnal course of net photosynthesis, as CO_2 uptake (upper left), stomatal conductance, as H_2O flux rate (lower left), the ratio of the leaf internal (c_i) to ambient (c_a) CO_2 concentration (c_i/c_a; upper right), and leaf water potential (lower right) for three periods during the 1989 growing season in mature male (●) and female (○) trees of *Acer negundo* inhabiting a non-streamside (dry) site in Red Butte Canyon, Utah. —·— in the lower righthand plot is the average leaf-to-air vapor pressure deficit at this site. Measurements were made on fully illuminated canopy leaves. Values are means (error bars = 1 SD) of five leaves per tree and five trees per sex inhabiting each site. Results of the ANOVA for repeated measures using these data appear in Table 2.

habitat types could be detected in late May, a time when soils were still extremely moist from winter snowmelt, and leaves were still actively expanding (Table 2; Fig. 1). Significant differences in c_i/c_a (determined by stomatal aperture and the efficiency of carbon assimilation) were found, however, during this same time period (late May). As the season progressed and canopy leaves matured, and both soil moisture and atmospheric humidity declined, strong and significant differences in A, g, and Ψ developed (Table 2) between the sexes (Fig. 1). Interestingly, in early July, the shape of the daily c_i/c_a curve was found to be significantly different between the sexes, though the daily average c_i/c_a was not. No such differences were found in late August, at the peak of the drought (see Fig. 1). A pattern of early afternoon stomatal closure was present during the entire season and appeared to be most pronounced when leaf water potential was low (<-2.1 MPa) and the leaf-to-air vapor pressure deficits were greatest (>28 mmol/mol) (Fig. 1). When Ψ dropped below ≈ -2.1 MPa in female trees, both A and g dropped to near zero for the rest of the day despite the fact that Ψ recovered in the afternoon. Male plants never achieved the high rates of A or g observed in females during the morning, but were always able to reopen their stomates in the late afternoon, after Ψ increased to above ≈ -0.8 MPa. These data suggest that males demonstrate more conservative water use (e.g., greater water-use efficiency) than females as soil and atmospheric moisture deficits develop.

For the streamside habitats, both male and female trees maintained slightly higher, yet more variable, gas exchange (A and g) and c_i/c_a compared with plants inhabiting non-streamside habitats (Fig. 2). Again, no significant differences for A, g, c_i/c_a, or Ψ were found between the sexes during the late-May sampling period (Table 2; Fig. 2). Like plants in the non-streamside habitats, A, g, and Ψ were significantly different be-

TABLE 2. Analysis of variance for repeated measures (ANOVAR) of net photosynthesis (A), stomatal conductance (g), the ratio of leaf internal to ambient CO_2 concentration (c_i/c_a), and leaf water potential (Ψ) for mature (>8.5 cm dbh) male and female trees of *Acer negundo* in two habitat types and at three dates during the 1989 growing season (from Figs. 1 and 2).†

Sources of variation	df of F	F values and significance levels for: A	g	c_i/c_a	Ψ
Between subjects					
Gender	1, 8	32.6***	24.4***	3.3*	21.7***
Date	2, 2	9.6**	4.8*	1.1NS	19.5***
Contrasts					
Gender × habitat	1, 1	64.7***	32.3***	2.5*	10.2**
Within subjects‡					
Hour	8, 81	121.4***	78.7***	9.3***	244.5***
Hour × gender	80, 81	267.8***	156.7***	23.9***	444.8***
Hour × date	80, 4	15.5**	8.8*	1.4NS	98.7***
Contrasts					
Hour × habitat	8, 81	12.7**	6.3*	4.7**	22.4***
Date × habitat	8, 4	143.7***	87.7***	2.6*	107.9***

* $P < .05$; ** $P < .01$; *** $P < .001$; NS: nonsignificant.

† The criteria and assumptions used in the analyses follow Potvin et al. 1990 and Geber and Dawson 1990 (see *Methods and materials*).

‡ Significance levels of within-subject effects represent Huynh–Feldt corrected values.

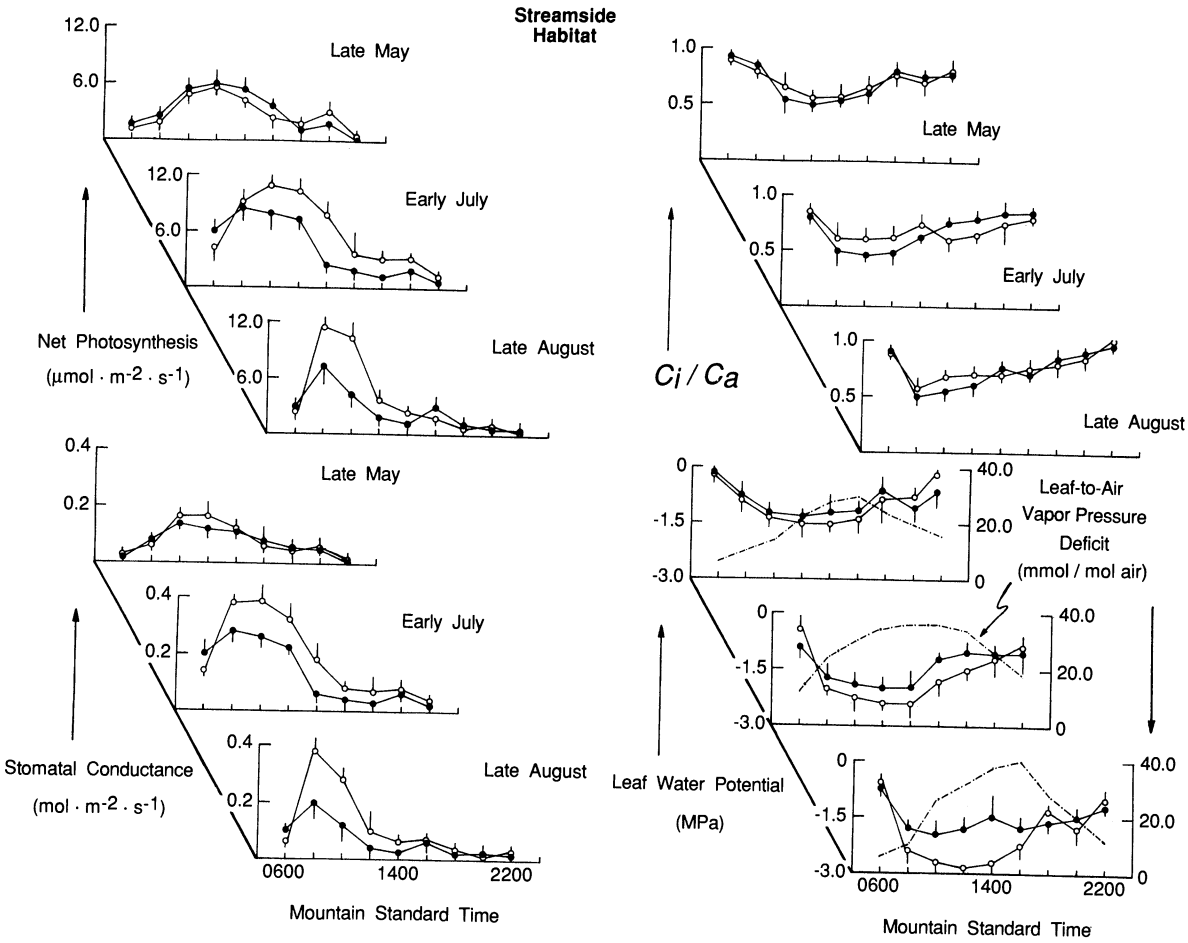

FIG. 2. Diurnal course of net photosynthesis (upper left), stomatal conductance (lower left), the ratio of the leaf internal (c_i) to ambient (c_a) CO_2 concentration (c_i/c_a; upper right), and leaf water potential (lower right) for three periods during the 1989 growing season in mature male (●) and female (○) trees of *Acer negundo* inhabiting a streamside (wet) site in Red Butte Canyon, Utah. Other symbols as in Fig. 1.

TABLE 3. Maximum rate of net photosynthesis (A) and stomatal conductance (g), the ratio of leaf internal to ambient CO_2 concentration (c_i/c_a) at maximal A and g, and minimum daily leaf water potential (Ψ) for male and female saplings (<8 cm dbh) and mature trees (10.5–16 cm dbh) of *Acer negundo* in two habitat types (all means ± 1 SD).† Measurements were made on 21–25 July (peak drought) during the 1989 growing season.

	A (μmol·m^{-2}·s^{-1})	g (mol·m^{-2}·s^{-1})	c_i/c_a	Ψ (MPa)
		Streamside habitat		
A) *Saplings*				
Male	$7.17 \pm 3.4^{*}_{1}{}^{a}$	$0.23 \pm 0.08^{**}_{1}{}^{a}$	$0.59 \pm 0.10^{*}_{1}{}^{a}$	$-1.57 \pm 0.48^{*}_{1}{}^{a}$
Female	$10.39 \pm 3.1^{*}_{1}{}^{c}$	$0.34 \pm 0.13^{**}_{1}{}^{c}$	$0.67 \pm 0.11^{*}_{2}{}^{c}$	$-1.78 \pm 0.24^{*}_{1}{}^{c}$
B) *Mature trees*				
Male	$8.92 \pm 3.1^{**}_{2}{}^{b}$	$0.27 \pm 0.07^{***}_{1}{}^{b}$	$0.56 \pm 0.09^{**}_{1}{}^{a,b}$	$-1.72 \pm 0.34^{**}_{1}{}^{a}$
Female	$14.89 \pm 2.2^{**}_{2}{}^{e}$	$0.46 \pm 0.11^{***}_{2}{}^{d}$	$0.70 \pm 0.08^{**}_{2}{}^{c}$	$-2.59 \pm 0.45^{**}_{2}{}^{d}$
		Non-streamside habitat		
C) *Saplings*				
Male	$6.64 \pm 2.7^{**}_{1}{}^{a}$	$0.21 \pm 0.12^{**}_{1}{}^{a}$	$0.53 \pm 0.07^{*}_{1}{}^{b}$	$-1.62 \pm 0.30^{**}_{1}{}^{a}$
Female	$8.26 \pm 2.1^{**}_{1}{}^{d}$	$0.37 \pm 0.14^{**}_{2}{}^{c}$	$0.64 \pm 0.09^{*}_{2}{}^{d}$	$-2.33 \pm 0.35^{**}_{2}{}^{d}$
D) *Mature trees*				
Male	$9.32 \pm 2.1^{*}_{2}{}^{b}$	$0.25 \pm 0.09^{*}_{1}{}^{a,b}$	$0.53 \pm 0.04^{**}_{1}{}^{b}$	$-1.66 \pm 0.22^{***}_{1}{}^{a}$
Female	$11.87 \pm 4.2^{*}_{2}{}^{c}$	$0.34 \pm 0.15^{*}_{2}{}^{c}$	$0.71 \pm 0.06^{**}_{3}{}^{c}$	$-2.79 \pm 0.41^{***}_{3}{}^{d}$

† Sample sizes: male saplings, $n = 11$; female saplings, $n = 10$, mature males, $n = 14$; mature females, $n = 10$. Asterisks (*P <.05; **P < .01; ***P < .001) indicate significant differences between male and female plants within a size class and habitat type, as shown by ANOVA. Different subscript numbers indicate significant (P < .01) differences between size classes within a habitat and sex (Bonferroni-adjusted t tests). Different superscript letters indicate significant differences between habitat types across size classes and sexes (Bonferroni-adjusted t tests). All gender × habitat interactions were significant at P < .01.

tween the sexes in July and August, and female trees always maintained higher rates of A and g and lower Ψ than males (Fig. 2), despite the fact that soil water content was never less than 25% in these sites at these times. As with non-streamside trees the shape of the daily c_i/c_a curve was found to be significantly different between the sexes, though the daily average c_i/c_a was not during the early July sampling period. No significant differences were seen between the sexes in the shape of the daily c_i/c_a curve in late August. The higher rates of water loss (higher g) from streamside females resulted in Ψ that were generally as low as those measured in trees inhabiting the non-streamside habitats (compare Figs. 1 and 2). We attribute the ability of trees in both habitats to recover daily leaf water deficits to the fact that once trees reached maturity (>8.5 cm dbh) they all were tapped into the groundwater (see Dawson and Ehleringer 1991). As such, marked habitat-induced differences in physiology between the sexes that were present in younger trees were significantly ameliorated in larger trees. This is evidenced by the fact that if young male and female trees in both habitat types are compared to mature trees (those measured in Figs. 1 and 2), there is a strong and significant effect of age on A, g, c_i/c_a, and Ψ, and all young trees in non-streamside habitats showed significantly lower gas exchange rates and leaf water potentials than young trees in streamside habitats (Table 3).

The importance of a seasonal effect on the manifestation of differences in gender-specific physiology is clear when leaf stomatal conductance is plotted against water potential (Ψ_{min}), for both expanding leaves (May) and fully mature leaves (July) in both habitat types (Fig. 3). No significant differences between the sexes in either habitat were seen in the g vs. Ψ_{min} relationship early in the season. Once leaves had matured, maximal g increased and while male trees demonstrated stomatal closure at essentially the same minimum water potential as early season leaves, female trees had shifted significantly and stomatal closure occurred at Ψ_{min} of 0.5–0.9 MPa lower than early season leaves (Fig. 3). In addition, female genotypes from non-streamside habitats maintained higher g at low Ψ when compared to streamside trees (Fig. 3; Table 4). This response was also observed in plants grown from cuttings and subjected to an experimental dry-down in pot culture (T. E. Dawson, *unpublished data*).

Laboratory observations and experiments

1. *Gas exchange physiology.*—Field observations of stomatal conductance in relation to both soil and atmospheric moisture deficits suggested that males never attained as high a rate of gas exchange and were considerably more conservative in their water use when compared with females (Figs. 1–3). To investigate the significance of this observation, gas exchange characteristics were measured on 1.5-yr-old saplings established from stem cuttings and then grown under identical conditions in pot culture. These young trees were established from a subset of the same male and female genotypes observed in the field (shown in Figs. 1–3). All trees were provided with ample water and fertilized weekly with half-strength Hoagland's solution.

Under controlled conditions (e.g., leaf temperature

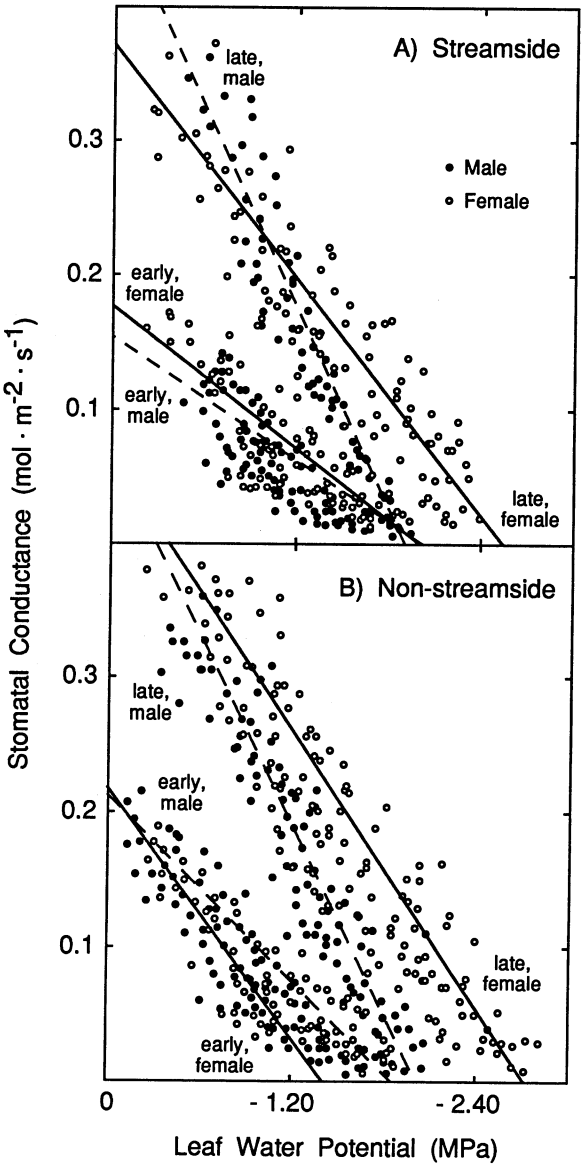

FIG. 3. The rate of stomatal conductance to water vapor as a function of the minimum leaf water potential in mature male (●, - - -) and female (○, ——) trees of *Acer negundo* inhabiting streamside (upper panel) and non-streamside (lower panel) sites in Red Butte Canyon, Utah. Measurements were made in the field, both early (May) and late (August) in the 1989 and 1990 growing seasons. No statistical differences were found between the sexes in either site in May. Late season responses were found to be different between the sexes in both sites (streamside, $P = .0489$; non-streamside, $P = .0501$). Significant differences between the sexes were also found (see Table 4).

28°C, photon flux density [PAR, 400–700 nm] 1250–1600 μmol·m^{-2}·s^{-1}, CO_2 concentration 348–356 μL/L) females attained higher maximal stomatal conductance (g_{max}), and as the leaf-to-air vapor pressure deficit (v) increased, stomatal closure began later when compared to males (Fig. 4; Table 4). At a v of 30 mmol/mol, males had essentially fully closed their stomata, while females were still at ≈50% of their maximal rate (Fig. 4). These results suggest that male trees are more sensitive to atmospheric moisture deficits, even under well-watered conditions. This leads to higher water-use efficiency in males relative to females.

Because male trees maintain lower stomatal conductance than females, they should differ in rates of net photosynthesis too. For both male and female trees, leaf photosynthesis was at its maximum at a v of 8–12 mmol/mol, at a leaf temperature of 26°–34°C, and at a PAR of 1175–1400 μmol·m^{-2}·s^{-1} (T. E. Dawson and J. R. Ehleringer, *unpublished data*). Under these conditions, the relationship between net photosynthesis (A) and the internal CO_2 concentration (c_i) (the A–c_i relationship) was investigated. The A–c_i relationship provides a graphical description of the photosynthetic capacity of a plant and can be analyzed to show differences that may occur in the degree of stomatal limitation to A (L_s; Eq. 5) and in the biochemical capacity of leaf carbon metabolism. Fig. 5 shows that average A–c_i relationship for male and female trees. Consistent with the field observations, female trees maintain higher overall rates of A and at the current ambient CO_2 concentration of ≈350 μL/L (c_a) operate at a c_i of 40–65 μL/L higher than male trees (Fig. 5). Although marked overlap between the sexes was observed, the A–c_i relationships were significantly different (ANOVA) between the sexes (Fig. 5). These laboratory data demonstrated that distinct differences in both the maximal rates of A and the average c_i, as well as other biochemical differences exist between the sexes (T. E. Dawson and J. R. Ehleringer, *unpublished manuscript*) and could be due to: (1) greater stomatal limitation of carbon assimilation in males relative to females; (2) higher carboxylation capacity and hence leaf nitrogen investment in the principal carboxylating enzyme, Rubisco, in females relative to males (indicated by a downward shift in the initial slope of the A–c_i curve in males [between 50 and 150 μL/L, c_i]); and/or (3) the sexes differ in their ability to regenerate RuBP via electron transport, indicated by a downward shift in the maximal rate of A at high c_i (>400 μL/L) (see Fig. 5).

Table 5 shows the average stomatal limitation of A (L_s), transpiration rate (E; from $E = gv$), leaf stomatal density, leaf nitrogen concentration, and instantaneous

TABLE 4. Analysis of covariance for the effect size, gender, leaf water potential (Ψ), and the leaf-to-air vapor pressure deficit (v) on stomatal conductance for mature male and female trees of *Acer negundo*.

Source	df	ss	F	P
Size	1	39.64	9.72	.002
Gender	1	245.37	122.34	.0001
Gender × size	5	47.81	11.35	.008
Gender × Ψ	8	73.06	13.44	.0237
Gender × v	8	467.19	122.34	.0005
Error	90	396.76		

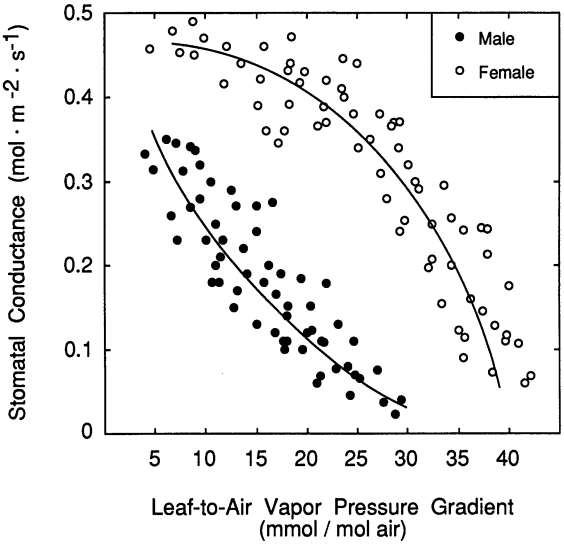

FIG. 4. The rate of stomatal conductance to water vapor as a function of the leaf-to-air vapor pressure deficit (v) in male (●) and female (○) saplings of *Acer negundo* grown out-of-doors in 60-L pots. All plants received identical growing conditions. Measurements were conducted with an "open" gas exchange system 2 h after plants were moved to the laboratory. Values were obtained from three replicates of nine female (total $n = 27$) and eight male (total $n = 24$) genotypes. Saplings were established from stem cuttings from randomly selected genotypes for which field data were collected. All other conditions were held constant and only v was varied. Results from statistical analyses are in Table 4.

water-use efficiency (A/E) for each gender. Males possess a greater L_s when compared to females, which is likely to explain their lower rates of carbon assimilation (Fig. 5), as well as their lower E (Table 5). The lower rates of both g (as shown above) and E and the higher L_s can in part be explained by significantly lower stomatal densities per unit of leaf area in males compared to females (Table 5). Despite lower A and E, males possessed significantly higher A/E than females. In addition, leaf nitrogen concentrations were higher in female leaves than in male leaves. These results suggest that males show greater stomatal limitation to A when compared to females. Data presented elsewhere (T. E. Dawson and J. R. Ehleringer, *unpublished manuscript*) on the biochemical control coefficient (after Ball et al. 1987 and Flanagan and Jefferies 1988), the carboxylation efficiency, the amount and activity of Rubisco, and results from modeling electron transport limitations confirm these interpretations.

Carbon isotope analysis

The flux-weighted and time-integrated c_i was compared to instantaneous measures using the carbon isotope composition of leaf cellulose (see Farquhar et al. 1989, Smedley et al. 1991). As shown in the methods section above, these data were also viewed as an index of time-integrated A/E.

1. *Field collections.*—Table 6A presents the average leaf carbon isotope discrimination (Δ) values for the leaves from which field gas exchange measurements were conducted (from Figs. 1 and 2). Overall, females demonstrated greater Δ than males and this was especially pronounced in trees growing in the drier, non-streamside habitats. In addition, males showed a 1.41‰ difference in Δ across habitat types, while females only differed by 0.16‰ (Table 6A). The strongest differences between the sexes were among trees inhabiting the non-streamside habitats, where Δ differed by twice as much as it did in the streamside habitats. The differences in Δ indicate that flux-weighted and time-integrated c_i for males and females was very different at the time their leaves were being made and suggest that strong gender-specific differences in integrated A/E may also exist.

2. *Common environment collections.*—Under common growing conditions male trees demonstrated lower Δ than females (Table 6B). Discrimination values and differences between the sexes of these smaller trees were quite comparable to the values obtained from the leaves collected from non-streamside trees (Table 6B). These data further suggest that males generally operate at lower c_i and greater A/E than females. Moreover, because the differences persisted when grown under

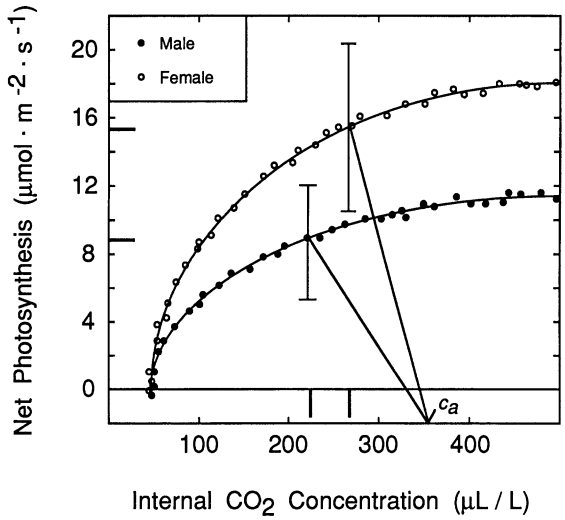

FIG. 5. The relationship between net photosynthesis and the internal CO_2 concentration of a leaf (c_i) in the same male (●) and female (○) saplings of *Acer negundo* measured in Fig. 4. Data points plotted on the curve represent means of raw data from all leaves measured for each gender. The shape of the curve was determined from fitting a second-order polynomial regression to the data. The vertical bar at the point of intersection between the curve and the linear (supply) line shows the range across all genotypes of each sex measured. Bars on the y axis and near the x axis show the average net photosynthetic rate and c_i, respectively, for each gender when measured at an ambient CO_2 concentration (c_a) of ≈ 350 μL/L of air. Significant differences between the sexes were detected ($P = .00379$; ANOVA). During these measurements [CO_2] was varied while all other conditions were held constant.

TABLE 5. Maximum rate of transpiration (E), instantaneous water-use efficiency (A/E), stomatal limitation coefficient (L_s), stomatal density, and leaf nitrogen concentration on the bases of leaf-tissue mass and on an area for mature male and female trees of *Acer negundo* (means ± 1 SD).†

	Male	Female
Transpiration ($mmol \cdot m^{-2} \cdot s^{-1}$) (at ν of 11–15 mmol/mol)‡	2.90 ± 0.71**	5.71 ± 0.57**
Water-use efficiency (mmol/mol)	3.97 ± 1.41*	2.71 ± 1.07*
Stomatal density (number/mm^2)		
Upper surface	64.8 ± 9.3	59.1 ± 12.6
Lower surface	189.4 ± 23.7**	255.1 ± 33.9**
Stomatal limitation coefficient (%)	21.2 ± 5.7**	13.3 ± 6.9**
Leaf nitrogen concentration		
Mass basis (mg/g)	26.8 ± 2.8*	32.2 ± 4.9*
Area basis (mmol/m)	126.9 ± 9.6**	162.7 ± 12.9**

* $P < .05$ or ** $P < .01$ (comparisons between the genders, Student's t test); $n = 35$ per sex.
† A, E, A/E, and L_s were determined from laboratory gas exchange experiments. Stomatal densities and leaf nitrogen concentrations were determined on leaves collected in the field during the 1989 growing season. Additional stomatal density information was obtained from plants grown in pot experiments under common growing conditions in 1989 and 1990.
‡ ν = leaf–air vapor pressure gradient; see Eq. 3.

common conditions, our data suggest that the gender-specific differences observed in both instantaneous and time-integrated measures of performance are genetically based. We cannot explain why the same genotypes sampled in the field but grown in containers had greater Δ. Plants were well watered and fertilized, were not root bound in their containers, but showed Δ values more like non-streamside plants growing in the field.

Field observations: growth and allocation determinations

1. *Growth.*—Growth rates of vegetative and reproductive ramets showed marked differences between the sexes, both within and between habitat types. In general, female trees grew more rapidly in streamside habitats, while male trees grew more rapidly in non-streamside habitats (Fig. 6). Vegetative ramet growth for trees of both sexes inhabiting streamside habitats was greater than in the drier, non-streamside habitats (Fig. 6), though the differences in males were not significant. Differences in vegetative vs. reproductive ramet growth were not significantly different for male trees in either habitat type. For female trees, however, the growth of reproductive ramets was less than half of that in vegetative ramets (Fig. 6). These data suggest that in female trees, ramets that bore fruit represent a significant carbon sink and reduce overall growth.

2. *Allocation.*—Allocation to stem tissues was equivalent for the sexes, regardless of habitat or gender, but male trees generally allocated a greater proportion of their biomass to leaves and less to reproduction than did female trees (Table 7). The results of a multivariate ANOVA (MANOVA) of allocation data show that both sexes allocated more to leaf and reproductive biomass in streamside habitats. Despite the fact that male trees do allocate a greater proportion of their biomass to leaves, the average leaf area was smaller in males and they generally had smaller canopies (T. E. Dawson and J. R. Ehleringer, *unpublished data*). The smaller canopies in male trees are due to their lower overall ramet growth (Fig. 6) and a greater allocation to a proliferation of basal trunks per tree (Table 7). This leads to shorter, broader, and more closed canopies in male trees, compared with the taller more open canopies of females that result in greater self-shading (T. E. Dawson, *unpublished data*) and perhaps a reduction in the

TABLE 6. Leaf carbon isotope discrimination for *Acer negundo* (Δ, in parts per thousand, ‰) as a function of gender from (A) field collections in two habitat types, and (B) from 1.5-yr-old saplings grown out-of-doors under common environmental conditions.† Values are means ± 1 SD for 25 separate individuals per sex within each habitat from the field and 12 separate individual saplings of each sex for plants grown in the common environment.

A) Field collections

	Habitat		Δ between habitats
	Streamside	Non-streamside	
Male	20.03 ± 0.35	18.62 ± 0.64	1.41*
Female	25.51 ± 0.11	21.67 ± 0.17	0.16NS
Δ between genders within a habitat	1.48*	3.05**	

B) Common environment collections

		Δ between genders
Male	17.44 ± 0.69	2.49**
Female	19.93 ± 0.51	

† Significant differences (ANOVA) either between habitats within a sex (values at the end of each row) or between sexes within a habitat (values at the bottom of each habitat column) were *$P < .05$; **$P < .01$; NS = not significant.

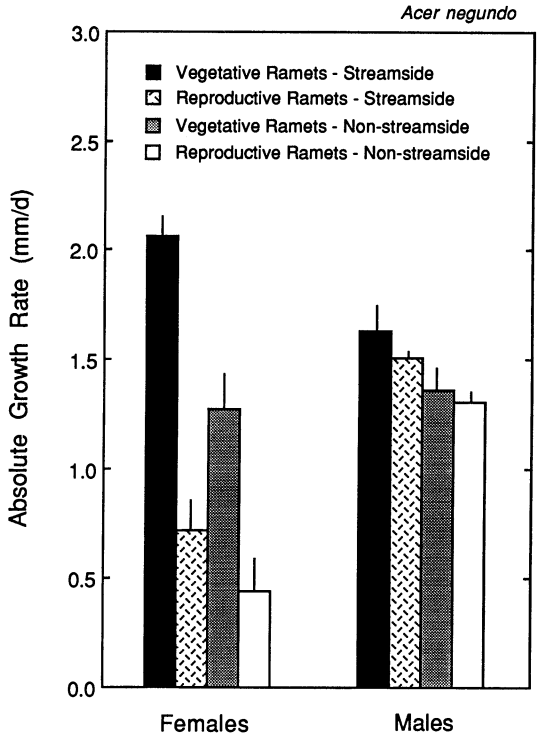

FIG. 6. The absolute growth rate (AGR) of vegetative and reproductive (leaves plus fruit) ramets measured on mature male and female trees, growing in both habitat types. No significant differences (ANOVA) in growth rate of vegetative and reproductive ramets were detected for male trees in either site. AGR of vegetative ramets in female trees was significantly greater than that of reproductive ramets in both streamside (P = .0134) and non-streamside (P = .0349) habitats. Both sexes have significantly higher AGR in streamside habitats (P = .0107, female; P = .0433, male). Average canopy AGR (vegetative + reproductive growth) was higher for female trees in streamside habitats (P = .0471) and higher for males in non-non-streamside habitats (P = .0377). Values are means (bar = 1 SD) of 20 randomly selected ramets of each type on each of 40 trees of each sex in each habitat type.

total canopy carbon fixation in male trees relative to females.

Field observations: size class × sex ratio determinations

When trees are young (<4 cm dbh), the sex ratio is only slightly and nonsignificantly biased towards females in streamside habitats, while non-streamside habitats show a slight, but nonsignificant, male bias (Table 8). In larger tree size classes, however, the sex ratio is significantly female biased in streamside habitats. Moreover, in non-streamside habitats, there is a strong tendency towards an ever increasing male-biased sex ratio (Table 8) and female trees that are present in the non-streamside habitats tend to be large (>8.5 cm dbh) rather than small. These data suggest that male trees suffer greater mortality in wet, streamside habitats while female trees die more often in the drier, non-streamside habitats. Once female trees reach a large size, however, they appear to be less vulnerable to mortality in drier habitats, and this is likely to be due to the fact that all large trees, regardless of gender or habitat type, use groundwater once they reach maturity (see Dawson and Ehleringer 1991).

DISCUSSION

Overview and the ecophysiological interpretation

We observed large and significant differences between the sexes of *Acer negundo* for an array of gas exchange traits, as well as for many of the growth and allocation parameters. In general, males maintained lower g, E, A, c_i, and Δ values, and higher A/E, as determined from both gas exchange and carbon isotopes, when compared to females (Figs. 3–5; Tables 5 and 6). In addition, males exhibited greater stomatal sensitivity to both declining soil water content (a long-term stress) and increasing leaf-to-air vapor pressure gradients (a short-term stress) (Figs. 3 and 4). Lower rates of carbon fixation in males were correlated with lower g, lower stomatal densities, and lower leaf nitrogen concentrations as well as a greater degree of stomatal limitation (larger L_s) to net photosynthesis (Table 5). The more conservative water-use patterns and lower rates of carbon assimilation in males resulted in significantly lower vegetative growth rates in streamside habitats but similar growth rates in non-streamside habitats when compared to females (Fig. 6).

1. *Temporal influences on gender-specific responses.*—The midday decline in g and A while c_i/c_a remained essentially constant (Figs. 1 and 2) indicates that both diffusional barriers to water loss and CO_2 uptake and changes in the biochemical capacity for photosynthesis may have occurred during the course of the day (Schulze 1986). The relatively stable c_i/c_a observed in *A. negundo* over a range of environmental conditions (as well as during the course of the day) has been observed in other plants (Wong et al. 1985, Moldau and Sober 1988) and may reflect a certain degree of coupling between the photosynthetic apparatus and the stomata (Küppers et al. 1988, Woodrow and Berry 1988). This apparent coupling is known to have a marked influence on carbohydrate accumulation and growth in plants (Moldau and Sober 1988) and may help explain some of the growth and allocation differences observed here for *A. negundo*.

Because A and E change in concert and c_i/c_a remains relatively unchanged, the relative rankings of A/E and Δ between the sexes would be predicted *not* to change as new leaves are formed under progressively drier soils (during the growing season; Toft et al. 1989). During the course of the growth period, as plants are exposed to periodic soil water deficits and an increase in the average v (which directly influences E; see Eq. 2), A/E for all trees does change because E increases proportionately more than does A. This change is also

TABLE 7. Aboveground biomass allocation subsampled from whole-tree canopies, the average number of basal trunks, and the mean leaf area in male and female trees of *Acer negundo* growing in streamside and non-streamside habitats within the Red Butte Research Natural Area, near Salt Lake City, Utah in 1989. Values are means ± 1SD.†

	Aboveground dry biomass (g)			Number of basal trunks	Leaf area (cm^2)
	Stems	Leaves	Reproduction		
Streamside					
Female	$32 \pm 4^{a, NS}$	$44 \pm 6^{c, NS}$	$24 \pm 3^{g, *}$	$2.60 \pm 2.17^{k, NS}$	$27.63 \pm 15.33^{n, **}$
Male	$34 \pm 5^{a, NS}$	$59 \pm 7^{d, NS}$	$7 \pm 2^{h, NS}$	$4.12 \pm 2.91^{l, NS}$	$21.37 \pm 8.62^{o, **}$
Non-streamside					
Female	$33 \pm 5^{b, NS}$	$48 \pm 6^{e, NS}$	$19 \pm 4^{i, *}$	$2.46 \pm 2.07^{m, NS}$	$22.89 \pm 9.34^{p, *}$
Male	$39 \pm 3^{b, NS}$	$55 \pm 3^{f, NS}$	$6 \pm 2^{k, NS}$	$3.71 \pm 2.90^{m, NS}$	$17.67 \pm 7.39^{p, *}$

† The data were analyzed by multivariate ANOVA (MANOVA). Statistically significant differences between the sexes within a habitat type are noted with different lettered superscripts ($P < .01$). Differences between habitat types within a sex were significant at $P = .05$*; or nonsignificant (NS). For aboveground biomass data, sample sizes were: $n = 70$ trees per sex per habitat for stems and reproduction; $n = 50$–70 leaves per tree, 75 trees per sex for leaves in streamside habitats; $n = 50$–70 leaves per tree, 45 trees per sex for leaves in non-streamside habitats. The number of basal trunks was determined from $n = 75$ trees of each sex in the streamside habitat and $n = 45$ trees of each sex in the non-streamside habitats. Leaf area data are averages of 50–70 leaves from five trunks of each type harvested from 10 trees of each sex in each habitat type.

reflected in a decline in the average c_i/c_a over the course of the growing season (Table 2). Since the flux-weighted/time-integrated c_i/c_a is recorded in Δ (Farquhar et al. 1989), and Δ differs between males and females, it appears that the degree of stomatal limitation to carbon assimilation is not only greater in males than females in the short term (L_s), but also in the long term (Δ). Together, this leads to an overall decline in the average A/E and Δ for both male and female trees, but the ranking of the sexes remained unchanged.

2. *Environmental influences on gender-specific responses.*—Our experimental design does not allow us to partition the importance of Ψ or v in reducing the overall gas exchange rates. However, our data indicate that the impact of Ψ and v on g is important (Table 4), depending on soil moisture availability, and that this response differs between the sexes. The increased stomatal sensitivity of males to atmospheric or soil water deficits may be due (1) to either gender-specific differences in the hydraulic conductivity and the vulnerability each sex shows to xylem embolism and cavitation (Tyree and Sperry 1988; J. Sperry, *personal communication*), (2) to gender-related differences in root-to-shoot communication, hormonally driven responses that have been shown to affect plant response to water deficit (Davies and Zhang 1991), or (3) to differences in root allocation.

The physiological differences we observed between the sexes were correlated with significantly different growth rates. Females showed (1) higher vegetative shoot growth than males in mesic habitats, (2) higher vegetative shoot growth when compared with reproductive shoot growth, regardless of habitat type, (3) but similar vegetative shoot growth to males in xeric habitats. These findings are consistent with what would have been anticipated to occur based on patterns of carbon fixation. We believe that the lowered growth of reproductive shoots relative to vegetative shoots in females but not in males represents a trade-off in carbon allocation and that the growth reduction reflects a greater carbon "cost" associated with reproduction in females not found in males (Fig. 6; Table 7; but see Willson 1986). Regardless of habitat or growing conditions, females allocated proportionately more of their aboveground biomass to reproduction relative to male trees. A greater proportion of biomass in leaves for males is consistent with the observations reported by Ramp and Stephenson (1988).

Physiological, ecological, and evolutionary implications

Gender-specific ecological and morphological traits in dioecious and subdioecious plants are well documented for a wide variety of taxa and growth forms. Differences in growth and resource allocation patterns between the sexes have been documented in grasses (Fox and Harrison 1981; but see Quinn 1991), her-

TABLE 8. Sex ratio (male/female) of *Acer negundo* in the Red Butte Canyon Research Natural Area, Utah, as a function of size class within two habitat types. Size is based on the diameter of the largest trunk at breast height (dbh, measured at ~1.4 m).†

Size class‡	Habitat type	Sex ratio
<3.5 cm dbh ($n = 254$)	Streamside	0.796^{NS}
	Non-streamside	1.231^{NS}
4–7 cm dbh ($n = 587$)	Streamside	0.473***
	Non-streamside	1.443**
8–11 cm dbh ($n = 649$)	Streamside	0.604**
	Non-streamside	1.892***
>12 cm dbh ($n = 354$)	Streamside	0.648**
	Non-streamside	2.211***

† Statistically significant deviations from unity were determined by chi-square analyses within a habitat or size class and chi-square for heterogeneity between habitat types or among size classes; significance levels are * $P \leq .05$; ** $P \leq .01$; *** $P \leq .001$; NS = not significant.

‡ 18% of the trees <3.5 cm dbh could not be sexed; for the other size classes <3% could not be sexed.

baceous annuals (Zimmerman and Lechowicz 1982, Lovett Doust and Lovett Doust 1985), perennial herbs and forbs, shrubs and sub-shrubs (Cook 1914, Wallace and Rundel 1979, Gross and Soule 1981, Hoffmann and Alliende 1984, Flanagan and Moser 1985, Ågren 1988, Dawson and Bliss 1989, Iglesis and Bell 1989, Delph 1990), and trees (Grant and Mitton 1979, Sakai and Burris 1985, Sakai and Sharik 1988, Carr 1991), including *Acer negundo* (Willson 1986, Ramp and Stephenson 1988). There are also a growing number of studies demonstrating gender-specific differences in defense and sensitivity to damage by pathogens and herbivores (Dannell et al. 1985, Lovett Doust and Lovett Doust 1985, Ågren 1987, Elmqvist et al. 1988, 1991, Polhemus 1988, Alliende 1989, Krischik and Denno 1990*b*), including a recent study by Jin and Coley (1990) on some of the same trees of *A. negundo* investigated in this study.

Spatial segregation of the sexes (SSS) and sex ratio biases by habitat are also well documented for many different species of vascular (see recent review by Bierzychudek and Eckhart 1988) and nonvascular (Cameron and Wyatt 1990) plants. For *A. negundo,* sex ratio bias is habitat specific and becomes more biased in the older age classes (Tables 1 and 8). This suggests that the patterns of SSS we observed may have resulted from increased mortality of male trees in streamside habitats and female trees in non-streamside habitats. Curiously, we found that in the drier, non-streamside habitats, there were a greater number of large female trees (>12 cm dbh) compared to smaller female saplings (4–11 cm dbh; Table 8). From our previous work we know that all larger trees use groundwater (Dawson and Ehleringer 1991), a water source that is not available to young trees during establishment. Access to groundwater ameliorates soil moisture deficits for large trees growing in non-streamside habitats, and in effect lessens the habitat differences between trees as they age. Thus, although there are fewer trees of both genders in the larger (older) size classes (>8.5 cm dbh) in non-streamside compared with streamside habitats, our data suggest that once trees reach groundwater (sizes >7.5 cm dbh and 20–25 yr old; see Dawson and Ehleringer 1991) more survive, especially females.

Gender-specific physiology in dioecious plants, by comparison to the other sorts of specializations cited above, has been poorly documented. This is surprising given that most studies that have looked for ecological differences, as well as differences in growth and allocation between the sexes, have found them and such differences are likely to be a result of gender-specific physiological behavior at the cellular, leaf, or whole-canopy level. Dzhaparidze (1969) refers to a number of early Soviet studies where differences in photosynthesis and transpiration were observed between the sexes, though the nature and magnitude of these differences are difficult to ascertain. Bourdeau (1958) documented higher respiratory metabolism in the leaves of female trees of *Populus tremuloides* when compared to males. Similar differences in respiration and also photosynthesis were found in females of the arctic-alpine willow, *Salix arctica* (Dawson and Bliss 1993), and of course in the present study of *A. negundo.* In contrast, Melampy (1981) reports no photosynthetic differences between the sexes of *Thalictrum.*

Gender-specific differences in aspects of water use, water stress, and water relations are the best studied and documented physiological parameters in dioecious plants. An early investigation by Sivstev and Sizov (1972) showed that among a variety of dioecious species, male plants were more drought resistant than females. Freeman and McArthur (1982) reported that males of six dioecious desert shrub species demonstrated lower Ψ and thus greater water stress than females. Dawson and Bliss (1989) documented differences in tissue elasticity and/or the ability to osmotically adjust in response to drought and showed that it was this physiological difference that allowed male plants of *Salix arctica* to maintain higher rates of stomatal conductance and carbon fixation in drier sites. In contrast, females of *S. arctica* had greater low-temperature tolerance and out-performed males in sites with cool soil temperatures. These physiological differences lead to marked differences in carbon balance (growth and reproductive allocation) and contribute to the dominance of males in dry habitats and females in wet habitats along extremely sharp soil moisture gradients.

Taken together, the gender-specific physiological and distributional differences of male and female *A. negundo* suggest that females are less frequent on dry and more open non-streamside sites because of a drought-induced mortality. Conversely, lower male abundance in wet and closed-canopy streamside sites is consistent with the notion that females out-compete males (Cox 1981) through a higher rate of carbon gain. The size class distributions of sexes in both habitat types are consistent with these hypotheses.

The occurrence of male plants in poor (dry) habitats and female plants in rich (wet) habitats is now well documented in dioecious plants (Bierzychudek and Eckhart 1988), though the role that physiology may play in helping to explain this pattern is not. For *A. negundo,* although sex ratio varies along a soil moisture gradient, neither sex demonstrated tolerance to water deficits; males closed their stomates and effectively avoided water deficits and females essentially avoided xeric sites. By comparison, in the study of *Salix arctica,* an arctic-alpine dioecious shrub, Dawson and Bliss (1989) showed that females had superior tolerance to cold soils in the mesic sites they dominated, while males demonstrated superior drought tolerance in xeric habitats. We would like to suggest that these two physiological studies indicate two very different sex-specific strategies in response to site quality and resource deficits: *stress tolerance* in the case of *S. arctica* (Dawson and Bliss 1989) and *stress avoidance* in *A. negundo*

(this study). Both of these strategies appear to result in males being able to persist in the poorest quality sites. If such a dichotomy can be drawn, then we must ask, under what circumstances during growth would we expect physiological stress tolerance vs. stress avoidance to evolve, and at what costs might such strategies come? We propose that *stress tolerance* should be favored in environments with short growing season lengths (e.g., arctic, alpine, deserts), while *stress avoidance* should be favored if resource levels are spatially or temporally heterogeneous but the growing season is predictable and sufficiently long for plants to capture the resources needed for their growth and reproduction (e.g., many temperate communities, including riparian zones). As stated above, either strategy resulted in males dominating the most stress-prone habitats. Differences between stress avoidance and stress tolerance in plants are well substantiated at the interspecific level (Alscher and Cumming 1990, Mooney et al. 1991), and there is no reason to expect that intraspecific, or with dioecious taxa, intersexual, difference would not also exhibit divergence in the degree of gender-related tolerance or avoidance, particularly because each gender has such different resource requirements.

We believe that dioecious plants provide an opportunity not available in other plant groups to explore how variation in the degree of physiological tolerance or avoidance can influence plant growth and distribution. Because comparisons are made at the intersexual (intraspecific) level in dioecious plants, traits that appear to confer some survival or fitness value for a particular gender in a particular habitat might more easily be used to establish whether traits are products of adaptive evolution or by-products of phylogenetic heritage. Investigating the possible adaptive value of traits within a single taxon and not across taxa should be a powerful approach because unlike most comparative studies, problems of phyletic origin do not hamper our ability to argue for or against an adaptive role for a particular trait or suite of traits (Harvey and Pagel 1991). Could the intersexual variation in physiology and growth have arisen as a product of selection acting on gender-specific demands to meet different costs associated with reproduction? Strong selection to meet the higher cost of reproduction may have influenced gender-specific physiology in such a way as to also directly influence growth, reproduction, and fitness. Because fitness is a function of a plant's reproductive success and reproductive success, especially for females, is in large part determined by their ability to capture resources, the more costly reproduction of females restricts them to habitats where they can best meet those costs. Higher net photosynthesis, at the expense of lowered A/E allows these costs to be more easily met or deferred, especially in sites where water is not limiting. Higher carbon gain and growth could potentially provide females with a competitive advantage over males and prevent sex ratios from ever approaching one. In contrast, the greater stress avoidance (higher A/E and lower Δ) in males comes at the expense of lowered overall carbon acquisition while at the same time allowing them to exploit dry habitats. The improved drought avoidance may come at the cost of reduced competitive ability for males in mesic sites, however. The cost of not avoiding stress for females appears to come at the expense of lowered survivorship in the drier, stress-prone habitats. The stress avoidance characteristics of males come at the expense of lowered gas exchange, but higher survivorship in drought-prone habitats. Males may in fact benefit from paying the cost of being stress avoidant by actually siring more females. That is, because males are in close proximity to females (within 10m), pollen flow between the sexes is not likely to be the primary determinant of reproductive success in either sex. Furthermore, it has been argued that males may actually gain higher fitness in the drier sites because pollen can move much greater distances; thus the potential to sire more offspring can occur (see Freeman et al. 1976, 1980 and Dawson and Bliss 1989 for similar arguments). We do know that pollen movement from dry site males is nearly 4 times farther than that from wet-site males (24.6 m in dry vs. 6.3 m in wet; $P < .01$; t test). It is not known, however, if dry-site males in fact sire more females than males inhabiting wet sites.

Selection to meet significantly different costs associated with reproduction in male and female plants as well as enhancing fitness for males in dry sites and females in wet sites could have been a powerful force in shaping other characteristics in *A. negundo,* particularly physiological traits associated with carbon acquisition and water use. Our investigation demonstrates that the gender-specific physiological traits can help explain what maintains habitat-specific sex ratio biases and thus the spatial segregation of male and female trees of *A. negundo.* Gender-specific physiological differences likely contribute to differences in the size (=age) structure we observed in these populations as well. Though it is not known what initially generates patterns of SSS in dioecious plants, it appears that gender specializations may help to maintain them. Such specializations in turn appear to confer growth and perhaps even fitness benefits for each gender within a particular habitat type and may be the reason why SSS in dioecious plants is so commonly observed.

Acknowledgments

This research was supported by grant BSR-8717583 from the National Science Foundation. Discussions with numerous people during various phases of this research were all very helpful; we would especially like to thank M. Aide, E. Charnov, J. Comstock, L. Delph, L. Donovan, V. Eckhart, L. Flanagan, A. Fu, C. Galen, M. Geber, J. Gregg, T. Hinckley, S. Jin, S. Klassen, J. Kohn, M. Lechowicz, J. Marshall, S. Philips, D. Sandquist, A. Sakai, J. Seger, M. Smedley, M. Stanton, S. Weller, J. Zimmerman, and Bear. We also thank C. Cook, S. Klassen, B. Sherrill, C. Kitty, and W. Ike for help with carbon isotope and leaf nitrogen analyses. Our deepest

thanks to M.A. Kobler and S. Noel for helping to grow and culture our plants. Our special thanks to Jonathan Comstock for his assistance with gas exchange experiments and equipment. Chris Field, Josh Kohn, Steve Mulkey, an anonymous reviewer, and especially Monica Geber provided comments that improved the manuscript.

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