Leaf size in three generations of a dioecious tropical tree, *Ocotea tenera* (Lauraceae): Sexual dimorphism and changes with age[1]

Nathaniel T. Wheelwright[2,6], Jordan P. Sinclair[3], Cris Hochwender[4], and Fredric J. Janzen[5]

[2]Department of Biology, Bowdoin College, Brunswick, Maine 04011 USA; [3]Department of Biology, Wayne State University, Detroit, Michigan 48202 USA; [4]Department of Biology, University of Evansville, Evansville, Indiana 47722 USA; and [5]Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, Iowa 50011 USA

- *Premise of the study:* In dioecious species, selection should favor different leaf sizes in males and females whenever the sexes experience distinct environments or constraints such as different costs of reproduction. We took advantage of a long-term experimental study of *Ocotea tenera* (Lauraceae), a dioecious understory tree in Monteverde, Costa Rica, to explore leaf size differences between genders and age classes across generations.
- *Methods:* We measured leaf size in adult trees in a natural population, in their adult F_1 offspring in two experimental populations, and in their F_2 offspring at the seedling stage. Individual trees were measured at various times over 20 yr.
- *Results:* Leaves of female trees averaged 8% longer and 12% greater in area than those of males. Leaves were sexually dimorphic at reproductive maturity. Leaf size declined during the lifetime of most trees. Heritability estimates for leaf length were positive although not statistically significant ($h^2 = 0.63$, SE = 0.48, $P = 0.095$).
- *Conclusions:* We ruled out the ecological causation hypothesis for sexual dimorphism in leaf size because male and female trees co-occurred in the same habitats. Sexual dimorphism appeared not to result from genetic or phenotypic correlations with other traits such as height or flower size. Rather, females appear to compensate for higher costs of reproduction and diminished photosynthetic capacity by producing larger leaves. Additive genetic variance in leaf size, a prerequisite for an evolutionary response to selection for sexual dimorphism, was suggested by positive (although only marginally significant) heritability estimates.

Key words: leaf size and shape; heritability; *Ocotea tenera*; Lauraceae; sexual dimorphism; tropical trees.

Optimal leaf size and shape depend upon a leaf's environment, especially physical factors such as light levels, heat dissipation, and water availability, conductance, and loss. Biological interactions such as competition with other plants, herbivory, pollination, and seed dispersal also influence optimal leaf size and shape (Givnish, 1979; Bond and Midgley, 1988; Brown et al., 1991; Dawson and Geber, 1999; Geber et al., 1999; Westoby et al., 2002; Bañuelos et al., 2004; Delph et al., 2009; Malhado et al., 2009; Harris and Pannell, 2010). In dioecious species, selection would be expected to favor different leaf sizes in males and females whenever the sexes experience distinct physical or biological environments. For example, because female plants generally invest more than males in reproduction (Obeso, 2002; Wheelwright and Logan, 2004), they may be restricted to more benign habitats with higher light levels or water availability, or

their growth rate, compromised by the costs of reproduction, may limit their height, thereby exposing them to more shady environments. In either case, males and females would be expected to differ in leaf traits (ecological causation hypothesis). Alternatively, intrasexual competition among males may favor branching patterns that enhance pollen dispersal and, indirectly, leaf sizes distinct from females (sexual selection hypothesis) (Midgley, 2010). Genetic correlations between morphological traits or between life-history stages may influence leaf traits differently in males or females, or correlations between sexes may constrain the independent evolution of sex-specific leaf traits (genetic correlation hypothesis) (Slatkin, 1984; Poorter, 2007). For example, artificial selection on flower size can result in correlated evolutionary responses in leaf traits (Delph et al., 2009). Such constraints could partly explain why leaf traits generally show lower sexual dimorphism than reproductive traits even though phenotypic variation is greater in leaves than in flowers (Arendt, 2007). Nonetheless, sexual dimorphism in leaf size has been shown to occur in a small number of species, mostly wind-pollinated shrubs (Harris and Pannell, 2010; Midgley, 2010). Almost nothing is known about how sexual dimorphism may change with age in long-lived plants.

We investigated sexual dimorphism in the leaves of *Ocotea tenera* (Lauraceae), a dioecious neotropical plant species. Unlike most species in which sexual dimorphism has been examined, *O. tenera* is a tree whose seeds are dispersed by large fruit-eating birds. Taking advantage of experimental plots of plants

of known-maternal parentage established in the early 1980s, we also measured changes in leaf size over the lifetime of individual trees and made a preliminary evaluation of the quantitative genetic basis of variation in leaf size.

MATERIALS AND METHODS

Study species—*Ocotea tenera* is endemic to the lower montane moist forests of Costa Rica, mostly between 1000 and 1400 m a.s.l. (Burger and van der Werff, 1990). Although sex expression may be labile in the first years of reproduction in young trees (Wheelwright and Bruneau 1992) and a small proportion (<3%) produce hermaphroditic flowers throughout their lives, the species is effectively dioecious, and the gender of all but a few trees can be unambiguously determined by floral morphology and levels of fruit production (Gibson and Diggle, 1997, 1998; Wheelwright and Logan, 2004). Based on a morphometric analysis of flowers, Gibson and Diggle (1997, 1998) characterized the species as gynodioecious, but long-term studies of marked individuals have revealed that most trees with apparently hermaphroditic flowers produce few or no fruits and are in fact functionally male. As in previous papers on this species (e.g., Gibson and Wheelwright, 1996, Wheelwright and Logan, 2004), we refer to plants that consistently bear staminate flowers with viable pollen as males and plants that bear pistillate flowers devoid of pollen and that produce fruits with viable seeds as females.

Male and female trees of *O. tenera* co-occur in the same habitats. The fact that a tree's nearest neighbor is commonly of the opposite sex emphasizes the similarity in habitat distribution between the sexes (Wheelwright and Bruneau, 1992). Under favorable conditions (sufficient moisture, location on the forest edge or in a light gap), males and females reach reproductive maturity at the age of 5 yr, when they are only 2–3 m tall and have a trunk diameter of 1–2 cm. Thereafter, trees reproduce annually. In deep shade, growth is slowed and maturity may be delayed by several years. For females, the cost of producing dozens to thousands of bulky fruits (ca. 3 cm long, 6.5 g) results in lower photosynthetic capacities and slower overall growth than males, presumably as a result of females having to divert nutrients from the photosynthetic apparatus to seeds and other reproductive tissues (Wheelwright and Logan, 2004). For most trees, maximum height (3–12 m) and trunk diameter (2–20 cm) are reached by the time the trees are 15 yr old, after which growth is negligible. Although trees can apparently live a half century or more, few survive more than 25 yr as the canopy closes over them (N. T. Wheelwright, unpublished data).

Leaves are simple, entire, and elliptic, a shape typical of many neotropical trees (Malhado et al., 2009). New leaves are produced throughout the year. We did not quantify how long individual leaves persist, but because a tree's leaves vary widely in their epiphyll loads (indicating a range of leaf ages) and a proportion of leaves are dropped each dry season, we estimate that leaves have a longevity of 1–2 yr. Once leaves are fully formed, they show no sign of changing size with age (e.g., freshly expanded leaves appear no smaller or bigger than leaves that are dark green, sclerophyllous, and accumulating epiphylls). Peak flowering occurs in the early to mid rainy season (July, August) and fruits ripen in mid dry season (February, March). Inflorescences are borne in leaf axils, with males producing more inflorescences, more flowers per inflorescence, and bigger, shorter-lived flowers than females (Wheelwright and Logan, 2004). Levels of herbivory seem low other than periodic attacks by stem-sucking coccoid Homoptera (Alcock, in Nadkarni and Wheelwright, 2000). Pollinators are small generalized insects, mainly Diptera, Hymenoptera, and Lepidoptera; seed dispersers are large specialized fruit-eating birds (Gibson and Wheelwright, 1996).

Study site, measurements, and analyses—We studied *O. tenera* trees in a natural population and in two experimental plots in Monteverde, Costa Rica (10°15′N latitude, 84°46′W longitude) (Nadkarni and Wheelwright, 2000). The plots were established in 1981 and 1984 by planting seedlings grown from seeds gathered from marked trees in the wild. Thereafter, size (trunk diameter, height) and fruit production of all trees were measured annually through 1997 and, after that, every few years through 2010. Over the course of the study, light levels in the plots dropped slightly as the canopy partially closed and the experimental trees grew taller, but most locations within the plots still received direct sunlight at several points during the day and moderate light throughout the day.

In 1990 we measured leaves of 12 female trees from the natural population (parental generation), along with leaves from their sexually mature 6- and 9-yr-old male and female offspring in the experimental plots (F_1 generation) ($N = 756$). In 1991 we measured leaves of F_1 trees in the plots plus their 1-yr-old seedlings grown from seeds (F_2 generation); the sex of seedlings was not determined

($N = 1841$). F_1 leaves were measured again in 2002 and 2010 ($N = 55$ and 974, respectively), when trees were 18-, 21-, 26- and 29-yr old (depending whether they were from the 1981 or 1984 cohort). From each parental and F_1 tree, 10 haphazardly chosen leaves were collected from at least three different branches 1.5–2.5 m off the ground. We avoided small or incompletely expanded newly emerged leaves such as those found at the tips of branches, or unusually big leaves such as those on stump sprouts. For F_2 seedlings, we could only measure three leaves per seedling. We used dial calipers to measure leaf length (from the base of the leaf blade, where it joined the petiole, to the leaf tip, in millimeters) and width (at the widest point, ca. 40% of the way from the base of the blade to the leaf tip, in millimeters). All leaves were sampled and measured at the same time of year (mid dry season) following the same protocol, without reference to the sex of the tree from which they were collected.

In total, we measured 3626 leaves from 129 individual plants (12 females from the natural population, plus 25 females, 39 males, and two hermaphrodites, all reproductively mature F_1 offspring, plus 51 F_2 seedlings of unknown sex). The original data set is on file in the online repository Dryad ["Leaf measurements of *Octea tenera* (Lauraceae)"; Provisional DOI: doi:10.5061/dryad.271cs]. For half of the leaves ($N = 1885$), area was also quantified using a leaf area meter. Linear regressions showed that leaf length × width, and even leaf length alone, were highly accurate predictors of leaf area ($r^2 = 0.97$ and 0.78, respectively; $P < 0.0001$; area [cm^2] = 0.0066 length × width [mm^2] − 0.506; area [cm^2] = 0.4168 length [mm] − 19.52). Consequently, hereafter, we focus mainly on the more easily measured leaf length as an index of leaf size. Specific leaf area (g·cm^{-1}) did not differ between males and females (Wheelwright and Logan, 2004). To identify factors affecting leaf size and shape, we used linear mixed models and standard model selection procedures based on Akaike information criterion (AIC$_c$) values (Demidenko, 2004). Tree identity was treated as a random effect to avoid pseudoreplication due to the inclusion of an average of 40.9 leaves per adult tree. Fixed effects included year of measurement, age, sex, and site. Statistical analyses (linear mixed effects models, linear regressions, ANOVAs, t tests, nonparametric tests) were performed using SPSS Statistics 19 (IBM, Tulsa, Oklahoma, USA). All P values are two-tailed. For comparisons between males and females, we applied both t tests and nonparametric Mann–Whitney U tests, given that variances between groups were not always homogeneous. In all cases, results were equivalent, so here we report only the results of t tests.

Heritability (narrow-sense, h^2) is the proportion of phenotypic variation (V_P) due to additive genetic variance (V_A) ($h^2 = V_A/V_P$) (Falconer and Mackay, 1996). It is an important concept because if a trait has very low heritability, there can be little evolutionary response (R) even in the face of strong directional selection (S, selection differential) (breeder's equation: $R = h^2S$). We estimated h^2 of leaf length with *H2boot*, quantitative genetics software that uses bootstrapping to estimate errors and test for statistical significance (Phillips, 2012; Phillips and Arnold, 1999). Maternal parent–offspring regression incorporated the phenotypic variance calculated from a full-sib ANOVA. We compared these results with traditional estimates of h^2 based on doubling the slope of the regression of the average of offspring leaf dimensions on the average leaf dimensions of their maternal parent (Falconer and Mackay, 1996). The intraclass correlation and the regression variance with uncorrected weighting yielded weighting factors that were very similar to family size. Leaves measured across a tree's adult lifetime were averaged to calculate individual means. Note that we used single parent–mid-offspring regressions because pollen donors (paternal parents) were not known. Unfortunately, this approach leaves open the possibility of biases such as maternal effects (e.g., provisioning of seeds by the parent plant could have long-term effects on leaf size). For that reason, we also attempted an animal model approach (Kruuk and Hadfield, 2007), but because our pedigree was relatively shallow (only three generations of trees) and paternity was not known, the results were not meaningful. Accordingly, our heritability estimates should be interpreted cautiously.

RESULTS

Sexual dimorphism—Leaves of female *Ocotea tenera* trees were on average 8% longer, 5% wider, and 12% larger in area than leaves of males ($N = 2847$ leaves, 76 trees; Table 1). Petiole length did not differ between the sexes. To control for tree age, growing conditions, and number of leaves measured per tree, we repeated the analysis using only trees planted at the same time in the experimental plots and calculating mean leaf dimensions per tree. As in the entire sample, females had leaves that were

Table 1. Leaf dimensions of reproductively mature male and female trees of *Ocotea tenera*.

Leaf character	Males				Females					
	Mean	SD	N_{leaves}	N_{trees}	Mean	SD	N_{leaves}	N_{trees}	t	P
Leaf length (mm)	106.2	18.5	1678	39	114.9	21.7	1169	37	11.2	<0.001
Leaf width (mm)	37.9	6.9	1678	39	39.8	8.2	1169	37	6.3	<0.001
Leaf area (cm^2)	26.5	9.6	679	29	29.8	10.3	448	19	5.5	<0.001
Petiole length (cm^2)	10.0	2.2	919	36	9.8	2.5	638	33	−1.4	0.15

longer and larger in area than males (*t* tests; length: $t = 2.4$, $P = 0.02$, $N = 23$ females, 38 males; area: $t = 2.0$, $P = 0.05$, $N = 19$ females, 29 males), but differences in leaf width and petiole length were not significant (width: $t = 1.7$, df = 59, $P = 0.10$; petiole: $t = −1.3$, df = 46, $P = 0.20$). Finally, to control for genotype as much as possible, we averaged the mean leaf dimensions of female siblings and compared them to the average of their male siblings (i.e., trees that shared the same mother and, given the moderately wide dispersion of trees in the wild, quite likely the same father in many cases). Consistent with our previous results, females had leaves that were longer and larger in area on average than their brothers (paired *t* tests; length: $t = 2.5$, $P = 0.038$; area: $t = 2.9$, $P = 0.02$; $N = 9$ sibling groups). Leaves of female trees averaged longer than those of male trees within 7 of 9 sibling groups (each group consisted of an average of 2.4 female and 3.8 male siblings) (Fig. 1). However, differences in leaf width and petiole length were not significant among the sexes across sibling groups (width: paired $t = 1.5$, $P = 0.15$; petiole: paired $t = 0.48$, $P = 0.64$).

On average, leaves of female trees were 5–9% longer than those of male trees in every year that they were measured (1990:
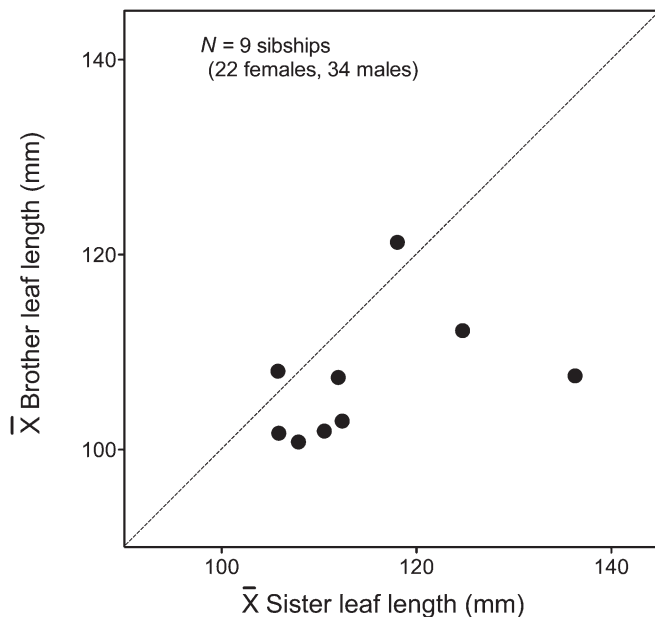

Fig. 1. Mean leaf length of female trees of *Ocotea tenera* vs. mean leaf length of their male siblings. Trees were reproductively mature, similar in age and grown under the same conditions within experimental plots. Females had significantly longer leaves than their male siblings within 7 of 9 sibships (collectively comprising 22 females and 34 males), as shown by points falling below the diagonal line representing equality in leaf sizes between siblings.

$P < 0.0001$, $t = 5.0$, $N = 355$ leaves from female trees, 391 leaves from male trees; 1991: $t = 6.8$, $P < 0.0001$, $N = 429$, 654; 2010: $t = 6.9$, $P < 0.0001$, $N = 355$, 610; in 2002, differences, although in the same direction, were not significant, possibly because of small sample sizes: $t = 1.4$, $P = 0.17$, $N = 32$, 23). In both sexes, leaf width showed a negative allometric relationship with length—longer leaves were relatively narrow—as indicated by slopes of less than 1 for regressions of log(leaf width) on log(leaf length) (slope = 0.87 and 0.84 for females and males, respectively; 95% confidence intervals = ± 0.02).

Effects of age, life-history traits and reproductive effort— After the age of reproductive maturity and as trees increased in height, leaf size tended to decline slightly in most individuals (Fig. 2). The slopes of regressions of leaf length vs. tree age were negative in 22 of 27 trees (binomial test: df = 26, $P = 0.01$), although some of the between-year variability within trees may have been due to sampling error and only two of the individual regressions were significant (presumably due to low statistical power, given that individual trees were measured in no more than four years). In general, leaf size and shape showed greater variation in females than males (Figs. 2, 3, Table 1). ANOVAs of leaf length of trees in the experimental plots showed significant effects of both sex and age (sex: $F_{1,2728} = 138.5$; age: $F_{7,2722} = 19.8$, $P < 0.0001$) but no effect of plot ($F_{1,2728} = 19.8$, $P = 0.55$). We also found a significant effect of sex and age on leaf width (sex: $F_{1,2728} = 39.3$; age: $F_{7,2722} = 11.3$, $P < 0.0001$). There was an effect of age but not sex on petiole length (sex: $F_{1,2728} = 2.8$, $P = 0.09$; age: $F_{7,2722} = 17.1$, $P < 0.0001$). Compared to leaf length, leaf shape (length to width) showed less variation over a tree's lifetime (Fig. 3), although there was a significant effect of age and sex (sex: $F_{1,2728} = 66.5$; age: $F_{7,2722} = 14.7$, $P < 0.0001$). The model that most powerfully explained variation in leaf length (based on AIC$_c$) included the random effect of tree and the fixed effects of age, sex, and site (Appendix S1, see Supplemental Data with the online version of this article). Leaf length varied between age classes ($F_8 = 22.7$, $P < 0.001$) and sex ($F_1 = 4.0$, $P = 0.048$). With regard to other leaf traits, age but not sex had a significant effect for leaf width ($F_7 = 10.6$, $P < 0.001$; $F_1 = 1.3$, $P = 0.26$), leaf area ($F_7 = 135.6$, $P < 0.001$; $F_1 = 3.9$, $P = 0.055$), and petiole length ($F_8 = 11.9$, $P < 0.001$; $F_1 = 0.6$, $P = 0.45$).

We found no relationship between a female tree's mean leaf size (length, width, or area) and any life history trait (size of seed from which the tree was grown; age of first reproduction) or measure of reproductive effort (previous-year fruit production; lifetime total fruit production) (univariate linear regressions: $P > 0.10$; multiple regressions: $P > 0.30$). Likewise, there was no relationship between leaf size and any other morphological structure we measured in females (mean fruit length or width, mean seed length or width, mean number of leaves, maximum trunk diameter) (all $P > 0.10$). Nor was there any relationship
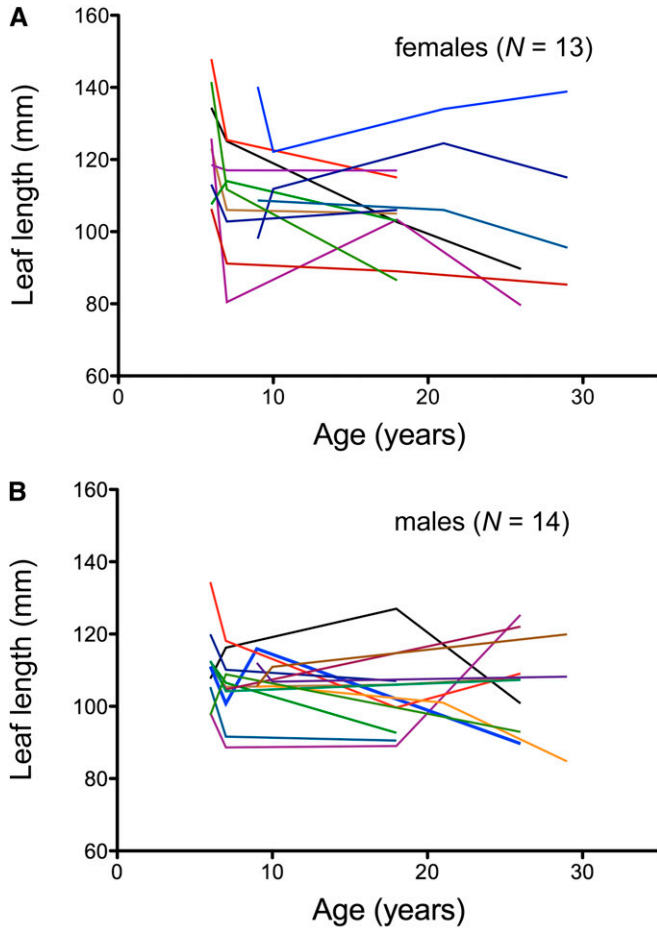
Fig. 2. Relationship between tree age and leaf length in (A) female and (B) male trees of *Ocotea tenera*. Each line represents leaf length versus age within a single individual measured in at least 3 years over 12–20-yr. Twenty-two of 27 trees showed a decrease in leaf size with age. Compared to males, females had leaves that were significantly longer and more variable in mean size between years.
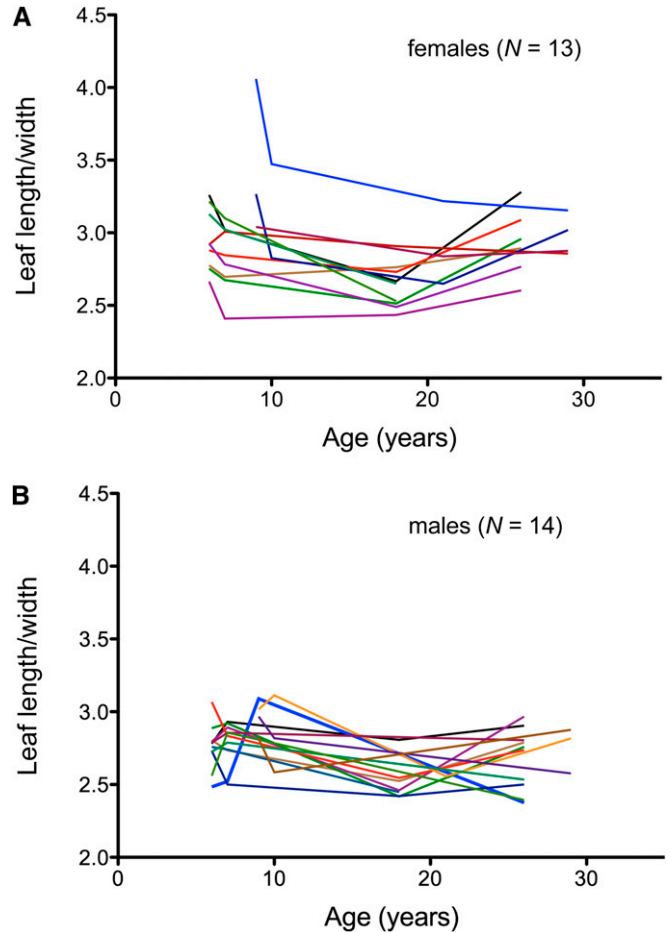

Fig. 3. Relationship between tree age and leaf shape (length/width) in (A) female and (B) male trees of *Ocotea tenera*. Each line represents leaf length/width on age within a single individual measured in at least three different years over 12–20-yr. Colors correspond to the same individuals as in Fig. 2. Most trees maintained relatively constant leaf shapes throughout their lives, although females varied more in leaf shape with age.

in males between leaf length and width and factors such as number of leaves, maximum trunk diameter, or age or size at first reproduction ($P > 0.10$).

Heritability estimates—Heritability estimates for leaf length using *H2boot* (Phillips, 2012) with data from 11 female trees and their reproductively mature male and female offspring were positive although not statistically significant ($h^2 = 0.63$, SE = 0.48, $P = 0.095$). A regression of mid-offspring leaf length on maternal leaf length yielded a slope of 0.29, which yielded a similar estimate ($h^2 = 0.58$, $P = 0.14$). When we restricted the analysis to female trees and their female offspring alone (in effect, treating female leaf size as a character distinct from male leaf size), the regression estimate of h^2 declined to 0.20 ($N = 10$ sibling groups, $P = 0.20$). The length of the leaves of reproductively mature F_1 trees was a poor predictor of the length of the leaves of their one-year-old (seedling) offspring (F_2 generation; Fig. 4B; $y = -0.19x + 107$, $P = 0.12$). The lack of a positive correlation between parents and offspring at the seedling stage most likely reflects nonlinear ontogenetic changes in leaf length.

Given that our estimates of h^2 were not statistically significant, they should be considered only tentative. Nonetheless, they suggest that a sizeable portion (ca. 60%) of the phenotypic variation in leaf length of adult trees could be due to additive genetic variance (Fig. 4A). The positive correlation between mean leaf lengths of male and female siblings, although not significant because of small sample sizes (Spearman rank: $r_s = 0.52$, $N = 9$, $P = 0.16$; Fig. 1), also suggests that there is additive genetic variation for leaf length.

DISCUSSION

Female trees of *Ocotea tenera* have leaves that are roughly 10% bigger than male leaves (8% longer, 5% wider, 12% larger area). By observing trees planted as seedlings of known-maternity in experimental plots, we were able to eliminate the possibility that sex differences in leaf size were due to the habitat in which a tree occurred, its age or the genotype of its mother. Sexual dimorphism in leaf size is rare among plants but where it occurs (e.g., *Silene latifolia*, *Simmondsia chinensis*) (Kohorn, 1994; Delph et al., 2002), females tend to have bigger leaves
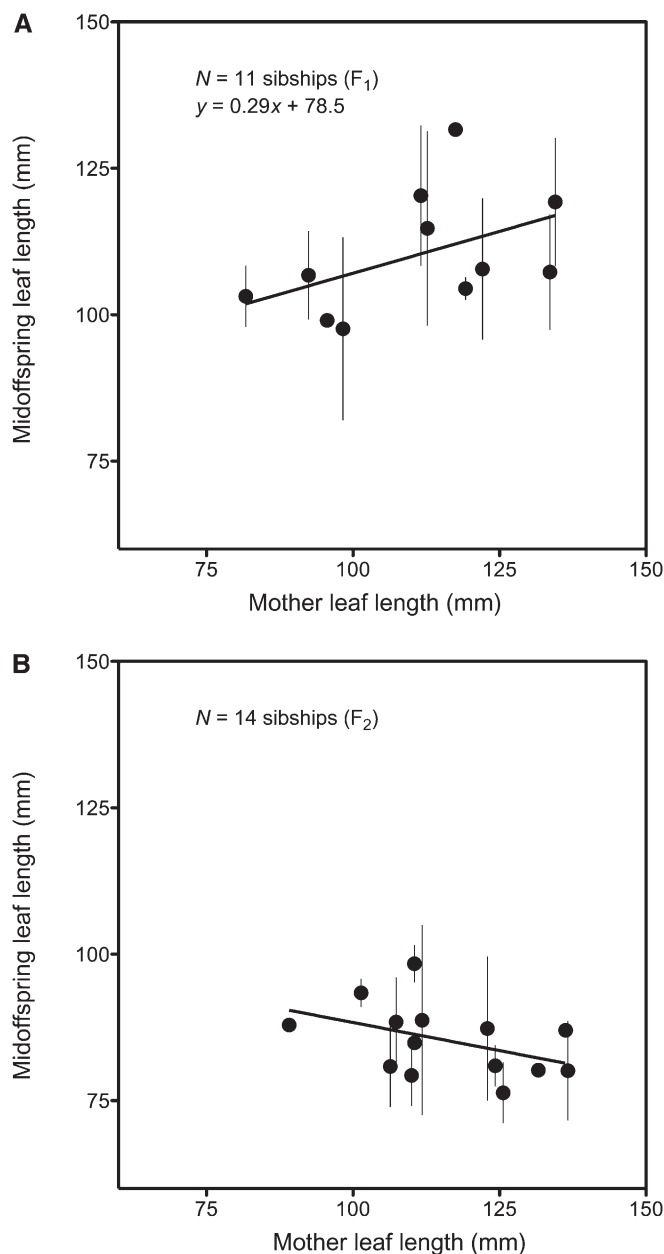
Fig. 4.   Regression of mean offspring leaf length (±1 SD) on mean maternal leaf length in *Ocotea tenera*. (A) Female trees (parental generation, $N = 11$) and their reproductively mature offspring (F_1 generation, $N = 60$). (B) Female trees (F_1 generation, $N = 10$) and their seedling offspring (F_2 generation, $N = 44$; $y = -0.19x + 107$, $P = 0.12$). Narrow-sense heritability (h^2) of adult leaf length was estimated as 0.58 (twice the slope of single parent–offspring regressions) in (A).

than males, as we found in this study. The degree of sexual dimorphism in *O. tenera*, although statistically significant and presumably biologically meaningful, is miniscule compared to some members of the genus *Leucadendron* (Proteaceae), wind-dispersed woody shrubs and small trees in which female leaves are more than 10 times the size of male leaves (Bond and Midgley, 1988; Harris and Pannell, 2010; Midgley, 2010).

Of the hypotheses proposed for the evolution of sexual dimorphism in leaves in general, most can be ruled out in the case of *O. tenera*. Male and female trees co-occurred in the same

habitat under natural conditions, commonly as nearest neighbors (Wheelwright and Bruneau, 1992), and trees grown in the experimental plots shared the same environment, so sexual differences in leaf dimensions were not due to spatial segregation of the sexes in distinct habitats (Midgley, 2010). Nor were ecophysiological differences at a local scale a likely explanation because we collected leaves of males and females in the same habitat and from the same height above ground, where they presumably experienced similar light, heat dissipation, water transport and water loss conditions. Thus, the ecological causation hypothesis seems unlikely. We cannot rule out changes in leaf shape as a correlated response to sexual selection on flower or stem size (Midgley, 2010), but this seems improbable because male leaves of *O. tenera* are smaller than in females even though their flowers, trunk diameter, and height are bigger (Wheelwright and Logan, 2004). We did not quantify branching patterns, but even if they differ between the sexes, inflorescences are axial, not terminal, so architectural constraints alone (Bond and Midgley, 1988) are unlikely to drive the evolution of sexual dimorphism in leaf size in this species.

The most compelling explanation for sexual dimorphism in leaf size in *O. tenera* may relate to gender differences in reproductive investment. As in the case of *Leucadendron* spp. (Harris and Pannell, 2010), female trees of *O. tenera* have to support the development and maintenance of relatively expensive fruits over a period of months. Perhaps females must produce bigger leaves to compensate for having to divert scarce nutrients to fruits and seeds and for having lower per-area photosynthetic capacities than males (Wheelwright and Logan, 2004). By having larger—but fewer and more widely spaced—leaves than males, females may also increase light exposure to their fruits, which would allow fruits to make photosynthetic contributions to their own construction costs (Wheelwright and Logan, 2004). In addition, a more open canopy could make females' fruits more visible to avian seed dispersers. On an ecological (as opposed to evolutionary) time scale, however, we failed to find any relationship within individual trees between leaf size and reproductive effort or life history traits. In the absence of any relationship between leaf size and lifetime seed production (a proxy for fitness), our study sheds little light on how natural selection currently acts on leaf size.

The hypothesis that large leaves in females may be an adaptation to increase photosynthesis does not explain why leaf size declines slightly with age. Given slightly reduced light levels in the experimental plots over the course of the study due to closing canopies and increased self-shading, this was an unexpected result: leaves are normally larger under low-light conditions (Horn, 1971). Conceivably, the decline in leaf size with age could reflect cumulative costs of reproduction. Interestingly, with a few exceptions (mostly in female trees), leaf shape remained quite constant over a tree's lifetime. Length to width ratios may be more developmentally canalized and less phenotypically plastic than leaf length or width alone, which could indicate that, compared to leaf size, leaf shape is more constrained by factors such as heat dissipation or water-shedding (Givnish, 1979; Malhado et al., 2009).

Although our heritability analyses provided only tentative evidence of appreciable heritability of adult leaf size in *O. tenera*, plant breeding studies of commercially important species have demonstrated high h^2 for leaf length (Stommel and Griesbach, 2008). Our study cannot rule out maternal effects, which can inflate h^2 estimates (Falconer and Mackay, 1996), but the fact that we found no relationship between the size of the seed from which a tree was grown and the size of its leaves years later eliminates at least one potential maternal effect. Despite

the limitation of small sample sizes, this study provides some of the first estimates of heritability of leaf traits in a dioecious tropical tree. Larger leaves in female *Ocotea tenera* trees, and steeper age-related declines in their mean leaf size may reflect selection on heritable variation in leaf traits in response to the higher costs of reproduction in females (Wheelwright and Logan, 2004).

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