Sexual dimorphism and seasonal changes of leaf gas exchange in the dioecious tree *Ilex paraguariensis* grown in two contrasted cultivation types

M. Rakocevic¹, M.J.S. Medrado², S.F. Martim¹,³ & E.D. Assad¹

¹ Embrapa Informática Agropecuária, Avenida André Tosello, Campinas, São Paulo, Brazil
² Embrapa Florestas, Estrada da Ribeira, Colombo, Paraná, Brazil
³ UNICAMP – IMECC, Department of Statistics, Rua Sérgio Buarque de Holanda, Campinas, São Paulo, Brazil

Keywords: Dioecy; female; growth pause; *Ilex paraguariensis*; leaf age; male; periodicity; photosynthesis; sexual dimorphism; shade; stomatal conductance.

Correspondence
Dr M. Rakocevic, Embrapa Informática Agropecuária, Avenida André Tosello 209, PO Box 6041, 13083-886 Campinas, SP, Brazil. Email: miroslava@iapar.br

Received: 20 June 2008; revised version accepted: 4 October 2008.


Abstract

Yerba maté (*Ilex paraguariensis*, Aquifoliaceae) is a subtropical, evergreen, dioecious, South American tree. In one preliminary study, it was observed that the functional strategy of yerba mate females, aiming to finish reproductive process, was increased transpiration relative to photosynthetic rates compared with males, on self-shaded leaves. We hypothesised that the long-term gas exchange response of males and females can evolve independently of phenological stage and cultivation type. In this spirit, the primary aim of the study was to analyse the physiological sexual dimorphism of this species, evaluating fluctuations of gas exchanges related to microclimate and phenological stages. A field study was conducted on adult plants of yerba maté cultivated in monoculture (MO) and in forest understorey (FUS), and measurements carried out *in situ* on microclimate and leaf gas exchange parameters. The photosynthetic photon flux density that was attained at leaf level in FUS was reduced roughly 10-fold compared with that in MO. Various leaf age populations were observed during a 2-year period at 2-month intervals and grouped into four categories: young, young-fully-expanded, fully-expanded and old. Young and young-fully-expanded leaves were the most active in photosynthesis. Leaves of female plants showed greater photosynthetic rate than those of male plants, which was expressed on all leaf age categories in MO, but only during vegetative stages previous to flowering and fruit ripening. The photosynthesis of young-fully-expanded leaves of females grown in FUS was superior to males but only during winter growth pause. The stomatal conductance differed in relation to cultivation type and leaf age but did not show the sexual differentiation. Physiological sexual dimorphism in yerba mate is shown to be plastic, responding to environmental conditions. The cost associated to the reproduction of yerba maté could be most easily met showing physiological differentiation of both sexes. A higher reproductive investment of females might be compensated for by exhibiting greater leaf photosynthesis than males that occurs in vegetative stages that precede flowering and fruit ripening.

Introduction

The existence of physical differences between the sexes, other than differences in the sex organs, or sexual dimorphism, is less evident in plants than in animals. In about 6% of angiosperm species (Renner & Ricklefs, 1995), the male and female reproductive organs occur in different individuals. Once dioecy appears, the diverse character separation of males and females not related directly to gamete production is initiated, developing a phenomenon
called secondary sexual dimorphism (Charlesworth, 1999). Secondary sexual dimorphism of dioecious species can be expressed by morphological diversification, which is most obvious during reproductive stages. Generally, males produce more flowers (Gross & Soule, 1981) and larger ones than do females (Vaughton & Ramsey, 1998). The sexual investments change the game when fruit production is included: females’ reproductive investments are often greater than males (Rocheleau & Houle, 2001), especially considering biomass and minerals (Cipollini & Whigham, 1994). Secondary sexual dimorphism can also be expressed by physiological diversification, which is most obvious during reproductive stages. Generally, sexual investments change the game when fruit production is included: females’ reproductive investments are often greater than males (Rocheleau & Houle, 2001), especially considering biomass and minerals (Cipollini & Whigham, 1994). Secondary sexual dimorphism can also be expressed by physiological (Obeso et al., 1998; Dudley, 2006; Palumbo et al., 2007) and phenological diversification (Espírito-Santo et al., 2003).

Yerba mate (Ilex paraguariensis St Hil., Aquifoliaceae) is a subtropical, evergreen, dioecious, South American tree and an economically important species whose leaves represent the primary material in the preparation of diverse beverages. In its natural habitat, I. paraguariensis grows in subcanopy (Carpanezzi, 1995) of subtropical rainforest with Araucaria angustifolia. Yerba mate growth responds strongly to cultivation type, showing less intensive leaf production (Rakocevic et al., 2006a), leaf area formation and leaf shed in forest understory (FUS) compared with monoculture (MO). Previous pilot data on a few isolated measurements of ecophysiological parameters carried out in six genotypes of yerba mate indicated the leaf gas exchange seasonality (Rakocevic et al., 2005), a phenomenon well defined in some other important agronomic species grown in tropical and sub-tropical climates, as in coffee (Silva et al., 2004).

Because sexual dimorphism in this species is not controlled by an XY system and markers have as yet not been developed, it has been impossible to identify sex in yerba mate plants before they attain a flowering age (Scherer, 1997), which is achieved in the third to fourth year after planting. For adult plants, yerba mate males show greater leaf area per plant than females because of less intensive leaf shedding and slightly bigger individual leaf surfaces (Rakocevic et al., 2006b). In yerba mate populations, constituted by advanced age plants, the sex ratio (males : females) was found to be 7–8.5 (Sturion et al., 1995). Male-biased genetic ratio in yerba mate was related to higher mortality among female plants (Wendt, 2005). As in other dioecious species such as Juniperus communis (Ortiz et al., 2002), preliminary evidence for yerba mate suggests higher levels of endogamy in males than in surviving females (Wendt, 2005).

A plant, not being able to relocate itself, relies often on its morphological plasticity and physiological adjustment (Givnish, 1988). Physiological responses in gas exchange can be used as performance indicators of physiological adjustments under different environments (Aranda et al., 2008). Acer negundo demonstrated the existence of physiological and morphological sexual adjustments in response to water availability and the importance of a seasonal effect on the manifestation of differences in gender-specific physiology (Dawson & Ehleringer, 1993). Most comparisons of the performance between sexes of dioecious species have focused on isolated or short-term physiological measurements, while only a few studies treated the instantaneous gas exchange responses across a range of temporal scales (Dawson et al., 2004).

We hypothesised the existence of sexual dimorphism in yerba maté gas exchange responses and sex-differential plasticity to cultivation type. In particular, the main objectives of this study were to determine seasonal variations of leaf gas exchange in males and females of yerba maté grown in two contrasted cultivation types and to correlate fine microenvironment variations with gas exchange responses while considering leaf phenology.

**Materials and methods**

**Local study**

The experimental field is situated in Barão de Cotegipe (27°37’ 15” S and 52°22’ 47” W, 765 m above sea level), Rio Grande do Sul State, Southern Brazil. Two contrasted areas were chosen (distance 100 m one from the other), a rainforest enriched with yerba mate in its FUS and MO. The climate is defined as subtropical humid (Cfa) by Köppen’s classification, with a regularly distributed rainfall during the year and an average temperature greater than 22°C in the hottest month. The soil is classified as Rhodic Hapludox.

**Leaf gas exchange and microclimate measurements**

Yerba maté plants for the two cultivation types (FUS and MO) were originated from the same seed collection. Seeds were collected in the summer of 1998, originated from the same ‘mother tree’. Seeds were reared in a nursery maintained by Barão, a company specialising in yerba maté production and industrial processing. In the spring of 1999, seedlings were planted out in the field in two sites using different cultivation methods: MO or FUS.

Pruning of formation was carried out in 2001. The pruning of production (plate form), retaining only 10–15% of foliated branches on a 0.8–1.2 m height, was conducted by yerba mate industry, in April 2003, in both cultivation types. Only 2–10% of photosynthetic photon flux density (PPFD) reached the yerba maté leaves under the forest shade (FUS) compared with the open area, while in MO, the PPFD that was attained at the leaf tips (2.0 m) and
inside the crown (1.2 m) were on average 62–90% and 31–71% of the PPFD in the open area, respectively (Rakocevic et al., 2008).

Fifteen yerba mate plants were identified in each cultivation type (MO and FUS) in April 2003. Three buds were marked on each of 30 identified plants. These buds were then followed for 2 years for growth; gas exchange measurements were taken on leaves originating from these buds. Leaves were marked by plastic labels, allowing repeat identification and tracking of leaf production and shedding at 2-month intervals. Plant sex was identified only during the first flush of flowering (January 2004) represented by 10/5 males/females in FUS and 5/10 males/females in MO.

Photosynthetic photon flux density (µmol m\(^{-2}\) s\(^{-1}\)), leaf temperature (\(T_l\), °C), leaf net photosynthesis (\(A\), µmol CO\(_2\) m\(^{-2}\) s\(^{-1}\)) and stomatal conductance (\(g_s\), mol H\(_2\)O m\(^{-2}\) s\(^{-1}\)) were measured \(in situ\) with a LI-6200 analyzer (LI COR, Lincoln, NE, USA). The measurements were carried out during the period of highest diurnal assimilation (10:00–14:30 h). This period showed the minimum daily variation in leaf gas exchange in yerba mate (Rakocevic et al., 2007b).

Ecophysiological measurements were conducted at 2-month intervals in a period from September 2003 to May 2005, which resulted in 11 sets of data. Data sets were grouped into four measurement seasons considering their biological and climate significance, that is variations related to seasonal fluctuations and phases of growth and development (Rakocevic et al., 2006a). The first measurement season occurred during spring regrowth (November 2003 and 2004), the second during the summer flowering and fruit ripening (January 2003 and 2004), the third during autumn flush of regrowth (March and May 2004 and 2005) and the fourth during winter growth pause (July 2004 and September 2003 and 2004). We used two-sample t-tests to determine that there was no evidence for a difference between pairs of data sets (two to four data sets) in a same growth stage (analysis not shown).

Leaf age classification

During this ecophysiological study, on 498 leaves 2440 measurements were carried out, with a maximum of 11 repetitions for the same leaf (11 data sets). The sprouting time occurred at the same time for both males and females. Dependent on the periodicity of leaf production, growing pauses and leaf shedding, not all leaf populations were represented in all data sets (measurement periods). Moreover, not all observed leaf populations were present on each measured branch. Lower leaf production and shedding were observed in yerba mate plants cultivated in FUS compared to MO. This permitted the presence of diverse leaf-age populations (1, 3, 7, 13, 15, 17, 19 and 21 months) on plants grown in FUS at the end of the experiment (May 2005). In the same measurement time, in MO, only a few leaf populations (1, 3, 7 and 17 months) were present. Mean number of measured leaves per plant, considering sex (males and females), cultivation type (MO and FUS) and four main growth stages, is shown in Table 1.

Table 1 Mean number of measured leaves per plant, considering sex (males [M] and females [F]), cultivation type (monoculture [MO] and forest understory [FUS]) and four main growth stages

<table>
<thead>
<tr>
<th>Cultivation Type and Plant Sex</th>
<th>Spring Regrowth Flowering and Fruit Ripening (summer)</th>
<th>Autumn Regrowth</th>
<th>Winter Growth Pause</th>
</tr>
</thead>
<tbody>
<tr>
<td>FUS – F</td>
<td>12.5</td>
<td>11.0</td>
<td>14.5</td>
</tr>
<tr>
<td>FUS – M</td>
<td>14.6</td>
<td>13.4</td>
<td>15.5</td>
</tr>
<tr>
<td>MO – F</td>
<td>11.4</td>
<td>7.8</td>
<td>11.1</td>
</tr>
<tr>
<td>MO – M</td>
<td>11.4</td>
<td>7.2</td>
<td>11.4</td>
</tr>
</tbody>
</table>
Sexual dimorphism and seasonal changes in *Ilex paraguariensis*  
M. Rakocevic et al.

data. The models had random effects at two levels: one for the plants and another for the leaves within plants. The techniques used in the models for parameter estimation do not depend on the data being balanced because we had sufficient information in the data sets to estimate the variance components and the fixed-effect parameters (Pinheiro & Bates, 2000). The ANOVAR was used to test the significance of light environment, growth stage, sex and leaf age associated with the residuals from the regression of $A$ and $g_s$, and these terms were tested sequentially in the order that they were entered in the models. The statistical correlation between physiological and environmental parameters was evaluated by Pearson correlation analysis using the same software. The results are presented graphically as means ± SE.

**Results**

**General view**

All researched factors (cultivation type, growth stage, gender and leaf maturity) showed significant effect on leaf net photosynthesis (Table 2), while stomatal conductance was not influenced by plant sex. The systems of yerba mate’ cultivation (MO and FUS), as expected, influenced strongly both net photosynthetic rate and stomatal conductance.

The PPFD that was attained at leaf level in FUS was reduced roughly 10-fold compared with that in MO. In addition to having a reduced PPFD in FUS relative to MO, self-shading reduced incident light on old leaves (Fig. 1D) compared with that which appeared to the light environment of young and young-fully-expanded leaves in FUS (Fig. 1A and Fig. 1B). In the shade of forest, the $g_s$ was reduced mostly for young-fully-expanded and fully-expanded leaves compared with MO, while $A$ diminished roughly threefold (Figs 1 and 2).

Also, a periodicity to responses was observed (Table 2, Figs 1 and 2). The $A$ increased in spring and decreased in autumn and winter (Fig. 1A to Fig. 1D). The $g_s$ increased in spring, continued to increase in summer and decreased in autumn and winter (Fig. 2A to Fig. 2D). Analysing the whole-year distribution, leaf photosynthesis was shown to be most intensive during spring sprouting (Fig. 1A to Fig. 1D). The periodicity in leaf gas exchange parameters is expressed by the growth stage main effect (Table 2).

**Sexual dimorphism and growth stage effect**

Female leaves photosynthesised significantly more than males in MO (Fig. 1) but only during spring sprouting and winter growth pause (Table 3). The assimilation decreased for all leaf ages and both sexes in forest shade for the stages of flowering and fruit ripening and autumn sprouting, then increased in the winter growth pause (Fig. 1A to Fig. 1D). This pattern was also observed for fully-expanded and old leaves in MO (Fig. 1C and Fig. 1D); however, during flowering and fruit ripening, the young and young-fully-expanded leaves in MO maintained their photosynthetic rate that was reached in spring sprouting (Fig. 1A and Fig. 1B).

**Table 2** Analysis of variance applied to the fitted linear mixed-effect models for repeated measures data for the residuals from the regression for leaf photosynthesis ($A$) and stomatal conductance ($g_s$) upon the simple additive effects of leaf temperature ($T_l$) and photosynthetic photon flux density (PPFD). Yerba mate’ leaves were followed during 2 years (between two successive prunings), during four principal stages of development, on 30 plants of two sexes, cultivated in two cultivation types (monoculture and forest understory).

<table>
<thead>
<tr>
<th>Factors</th>
<th>Residuals from $A$ upon $T_l +$ PPFD</th>
<th>Residuals from $g_s$ upon $T_l +$ PPFD</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>DF</td>
<td>F</td>
</tr>
<tr>
<td>Cultivation type</td>
<td>1</td>
<td>106.5893</td>
</tr>
<tr>
<td>Growth stage</td>
<td>3</td>
<td>9.0887</td>
</tr>
<tr>
<td>Sex</td>
<td>1</td>
<td>2.1492</td>
</tr>
<tr>
<td>Leaf age</td>
<td>3</td>
<td>34.5069</td>
</tr>
<tr>
<td>Cultivation type × growth stage</td>
<td>3</td>
<td>53.4912</td>
</tr>
<tr>
<td>Cultivation type × sex</td>
<td>1</td>
<td>0.0196</td>
</tr>
<tr>
<td>Development stage × sex</td>
<td>3</td>
<td>3.9971</td>
</tr>
<tr>
<td>Cultivation type × leaf age</td>
<td>3</td>
<td>24.3978</td>
</tr>
<tr>
<td>Growth stage × leaf age</td>
<td>9</td>
<td>5.4951</td>
</tr>
<tr>
<td>Sex × leaf age</td>
<td>3</td>
<td>0.5511</td>
</tr>
<tr>
<td>Cultivation type × growth stage × sex</td>
<td>3</td>
<td>1.3492</td>
</tr>
<tr>
<td>Cultivation type × growth stage × leaf age</td>
<td>9</td>
<td>4.7928</td>
</tr>
<tr>
<td>Cultivation type × sex × leaf age</td>
<td>3</td>
<td>1.8031</td>
</tr>
<tr>
<td>Growth stage × sex × leaf age</td>
<td>9</td>
<td>2.3711</td>
</tr>
<tr>
<td>Cultivation type × growth stage × sex × leaf age</td>
<td>9</td>
<td>1.8713</td>
</tr>
</tbody>
</table>

n.s., not significant.

Codes for statistical significance levels: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, $P < 0.1$.  

Journal compilation © 2008 Association of Applied Biologists
The pattern in stomatal conductance (Fig. 2) was different than for the photosynthetic rate. In MO, the increasing values were registered during the period of highest temperatures (late spring sprouting and summer growth pause). Differences in $g_s$ between two cultivation types were less evident than in photosynthesis. The $g_s$ of young female leaves was superior to males in FUS but only in autumn sprouting (interaction between sex and leaf age is shown in Table 3 and Fig. 2A).

Sexual dimorphism and leaf age effect

The leaf age effect on gas exchange was expressed practically during the whole year both in MO and FUS (Table 3). Young and young-fully-expanded leaves were statistically the most active in $A$ in MO, while in FUS, the first place is occupied with fully-expanded leaves. The old leaves are significantly inferior to other age categories (Fig. 1) in both cultivation types. The sexual photosynthetic dimorphism was expressed on all leaf age categories in MO during two stages previous to flowering and fruit ripening and on the young-fully-expanded ones in FUS during winter growth pause (interaction between ‘cultivation type × growth stage × leaf age’ is shown in Table 2, and sex × leaf age in Table 3). Oppositely, the sexual difference in stomatal conductance was manifested only on youngest leaves (Fig. 2A).
Correlation between leaf gas exchange and leaf microclimate

The strong correlation was established between PPFD at leaf level and leaf photosynthesis of yerba maté for the whole annual distribution measured on males and females in the two cultivation systems (Table 4).

The stomatal conductance in FUS was slightly correlated with local leaf PPFD only for females during spring sprouting, summer and winter growth pause, while the correlation was significant with leaf temperature for males during sprouting (spring and autumn) and winter growth pause. The temperature variation between two cultivation systems attained 4–5.5°C and was generally about 2°C, related to leaf localisation into the plant crown and stage of growth (Fig. 2). The $g_s$ correlated with $T_l$ for both sexes during two vegetative stages that precede flowering and fruit ripening in MO (Table 4). The correlation between $T_l$ and $g_s$ was observed even for males in flowering and fruit ripening in MO. Sexual dimorphism in leaf photosynthesis response to leaf temperature was

![Figure 2](image-url)
observed in two vegetative stages, intensive spring re-growth and winter growth pause. Strong correlation between $A$ and $g_s$ was observed in both genders and cultivation types (Table 4). The lack of correlation between $A$ and $g_s$ occurred only in males and females in the autumn sprouting in FUS.

The additive effect of two observed microclimate factors generally explained more than 50% of leaf photosynthesis in both cultivation types (Table 4 – fitted $A$), while $g_s$ is strongly dependent on PPFD and $T_l$ only in flowering and fruit ripening in MO (fitted $g_s$). Extremely low correlation between two microenvironmental factors and $g_s$ was registered in autumn sprouting; however, the sexual dimorphism was expressed in this vegetative stage in FUS.

**Discussion**

The fluctuations of yerba mate’ leaf gas exchange responses during a year were shown in both cultivation types (Figs 1 and 2). They can be defined as seasonal and related to climatic changes, leaf maturity and phenological stages (Tables 1 and 2). The adjustment of the growth periodicity to temperature and water availability is well known and has been observed in other subtropical tree species (Heinrich & Banks, 2006). Growth fluctuations are strongly reduced in yerba mate’ when grown in climatic chamber compared with plants cultivated in natural conditions (Bazzo & Rakocevic, 2005).

The importance of cultivation type prevailed in comparison to other factors (Table 2, Figs 1 and 2). To understand the gender behaviour for each cultivation type, the physiological responses were analysed separately for each cultivation type and growth stage (Table 3). Female leaves assimilated significantly more than males considering all leaf age categories in MO (Fig. 1A to Fig. 1D), but only during two stages prior to flowering and fruit ripening, while in FUS, this difference was reserved only for young-fully-expanded leaves during winter growth pause.

The importance of leaf maturation on the gas exchange was expressed practically during the whole year (Table 3). Growth of very young leaves depends on the photosynthetic import from chronologically older leaves (Hanson et al., 1988). Generally, reduced metabolic activity of chronologically old leaves is because of the amino acid export and is linked to protein degradation (Tetley & Thimann, 1974) and to stomatal closure in old leaves (Satler & Thimann, 1977). The decrease in leaf gas exchange with leaf maturation and senescence is also related to the leaf demography and the dynamic change of the leaf position in the plant canopy (Planchais & Sinoquet, 1998). Yerba mate’ manifests monopodial rhythmic growth, defined by Rauh’s plant architectural
model (Hallé et al., 1978). The probability that yerba maté young leaves appeared shaded in spring sprouting is lower than during following stages (considering summer growth pause and autumn sprouting) related to branching process occurring predominantly on lower and shaded tree crown layers, bearing flushes of young leaves. This was reflected in a local variation of PPF and leaf gas exchange (Fig. 1A).

Photosynthetic sexual dimorphism occurs at all leaf ages in MO (Fig. 1A to Fig. 1D) but for only young and young-fully-expanded ones in FUS (Fig. 1A and Fig. 1B). This study corroborates our previous observation that females have higher photosynthetic and transpiration rates on self-shaded leaves in MO (Rakocevic et al., 2007a). Dawson & Bliss (1989) suggested that those sex-specific differences in Salix arctica have an underlying genetic basis, which can be most easily met through physiological differentiation (as different seasonal and diurnal patterns of water use and water use efficiency).

Surprisingly, the physiological sexual differentiation of yerba maté occurred in spring during the active vegetative growth and in the winter growth pause (Tables 2 and 3, Fig. 1). When vegetative growth was analysed, in some species, females allocated more resources to vegetative tissues, for example in Amaranthus cannabinus (Bram & Quinn, 2000), and had a longer growing period than in males, as in Baccharis dracunculifolia (Espírito-Santo et al., 2003). However, yerba maté males and females manifested synchronisation in terms of leaf production, while a sexual dimorphism was clearly expressed in values attributed to leaf area parameters (Rakocevic et al., 2006b). Leaf area per individual plant and area of individual leaf were higher in males, while leaf shed was more important in females, which occurred intensively at the beginning of spring and autumn sprouting. The strategies of greater photosynthetic rate (Fig. 1) and more intensive leaf shed in female parameters (Rakocevic et al., 2006b) are probably related to important structural investment in females (Rakocevic et al., 2006c) and higher reproductive allocation, which may help explain the higher mortality among adult female plants (Wendt, 2005). Females of Acer negundo are less frequent on dry sites because of a drought-induced mortality, especially of young trees, while lower male abundance in wet and closed-canopy sites was related to a higher rate of carbon gain in females, and the notion that females outcompete males under those conditions (Dawson & Ehleringer, 1993).

Considering that the evidence of differential costs of reproduction in dioecious plant species is still a controversial question, the responses have to be searched separately for each case. The cost associated with reproduction could be most easily investigated and demonstrated by (a) physiological differentiation of sexes and (b) greater

---

### Table 4

Pearson correlation coefficient for leaf gas exchange and microenvironment [photosynthetic flux density (PPFD) and leaf temperature (T)l] and the fitted values from the regression upon the simple additive effects of T, and PPF, including the correlation between leaf gas exchange parameters, calculated for males and females grown in monoculture (MO) and forest understory (FUS) and separated by growth stages.

<table>
<thead>
<tr>
<th>Factors</th>
<th>Spring Regrowth</th>
<th>Flowering and Fruit Ripening (summer)</th>
<th>Autumn Regrowth</th>
<th>Winter Growth Pause</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Female</td>
<td>Male</td>
<td>Female</td>
<td>Male</td>
</tr>
<tr>
<td>MO</td>
<td>PPF 0.43***</td>
<td>0.55***</td>
<td>0.49***</td>
<td>0.52***</td>
</tr>
<tr>
<td></td>
<td>Tl -0.04 n.s.</td>
<td>0.33***</td>
<td>-0.18 n.s.</td>
<td>-0.07 n.s.</td>
</tr>
<tr>
<td></td>
<td>Fitted A 0.52**</td>
<td>0.55***</td>
<td>0.53***</td>
<td>0.59***</td>
</tr>
<tr>
<td></td>
<td>g L 0.38***</td>
<td>0.26**</td>
<td>0.75***</td>
<td>0.87***</td>
</tr>
<tr>
<td>FUS</td>
<td>PPF 0.28***</td>
<td>0.42***</td>
<td>0.58***</td>
<td>0.55***</td>
</tr>
<tr>
<td></td>
<td>Tl 0.06 n.s.</td>
<td>0.13*</td>
<td>-0.12 n.s.</td>
<td>0.17*</td>
</tr>
<tr>
<td></td>
<td>Fitted A 0.29**</td>
<td>0.42***</td>
<td>0.58***</td>
<td>0.55***</td>
</tr>
<tr>
<td></td>
<td>g L 0.21**</td>
<td>0.28***</td>
<td>0.46***</td>
<td>0.38***</td>
</tr>
<tr>
<td>Factors</td>
<td></td>
<td></td>
<td>Stomatal conductance (gL)</td>
<td></td>
</tr>
<tr>
<td>MO</td>
<td>PPF 0.12 n.s.</td>
<td>0.01 n.s.</td>
<td>0.22*</td>
<td>0.35**</td>
</tr>
<tr>
<td></td>
<td>Tl 0.24**</td>
<td>0.33***</td>
<td>-0.19 n.s.</td>
<td>-0.25*</td>
</tr>
<tr>
<td></td>
<td>Fitted gL 0.24**</td>
<td>0.39***</td>
<td>0.50***</td>
<td>0.54***</td>
</tr>
<tr>
<td>FUS</td>
<td>PPF 0.21*</td>
<td>0.02 n.s.</td>
<td>0.24*</td>
<td>0.12 n.s.</td>
</tr>
<tr>
<td></td>
<td>Tl 0.05 n.s.</td>
<td>0.21***</td>
<td>0.04 n.s.</td>
<td>0.11 n.s.</td>
</tr>
<tr>
<td></td>
<td>Fitted gL 0.21*</td>
<td>0.22***</td>
<td>0.24*</td>
<td>0.15*</td>
</tr>
</tbody>
</table>

n.s., not significant.

Codes for statistical significance levels: ***P < 0.001, **P < 0.01, *P < 0.05, 1P < 0.1.
photosynthetic rate in females compared with males, but not affecting the stomatal conductance. Obeso et al. (1998) observed that the efficiency of photosynthesis of leaves on non-fruiting branches of females of *Ilex aquifolium* (another species from the same genus) was higher than for the leaves on branches of male plants under low light conditions. This sexual dimorphism was attributed to the higher cost of reproduction in females. In the case of yerba maté (Fig. 1), female leaves of all age categories, emerging in different branching order, and submitted to different degrees of shading, exhibited greater photosynthetic rate. Sexual dimorphism of yerba maté was observed in two vegetative stages, intensive spring regrowth and winter growth pause (Fig. 1). Also, the lack of correlation between physiological parameters and leaf temperature in females in vegetative stages (Table 4) indicates the diversification in sexual physiological adaptation of sexes. It appears that more intensive photosynthesis during vegetative stages permits females to meet higher costs of reproduction.

Physiological sexual dimorphism in yerba maté was shown to be plastic, responding to the environmental conditions in a variety of combinations. When plants were grown in MO submitted only to intraspecific light competition, the female leaves showed more physiological adaptivity to local conditions than male leaves. Under the FUS, the environmental requirements of both sexes appeared to be similar, and yerba maté leaves showed a reduced amplitude in physiological responses to low light conditions compared with MO. The competitive physiological differences between yerba maté males and females varied with environmental conditions (low light in FUS versus high light in MO), which could play a role in the determination of the pattern of environmental sexual segregation, as in the case of dioecious grass *Distichlis spicata* (Eppley, 2006). Sexual dimorphism in *I. paraguariensis*, expressed through the strategy of a more intensive photosynthesis during vegetative stages that precede flowering and fruit ripening and through the lack of any sexual differentiation of stomatal conductance, indicates some genetic sex-specific differences and diversification in sexual physiological plasticity. Continuum in ecophysiological studies and initial steps in research of sex demography, stability in sex expression, sex-specific traits, and the effects of salinity on growth and reproduction of *Amaranthus cannabinus* (Amaranthaceae); a dioecious annual. *American Journal of Botany*, 87, 1609–1618.


Acknowledgements

We thank Giampaolo Pellegrino and two unknown reviewers for their helpful comments about manuscript, yerba mate industry Barão for permission to work on its property and to technicians from Embrapa Florestas for field assistance. Also, we are grateful to professors and students from Regional University – Erechim for their technical disposition and to Ms Celia Goodwin for English revision. This study was supported by grants for the invited researcher (M. R.) by the National Council for Scientific and Technological Development (CNPq/305406/02-7) and Foundation for Research in State of São Paulo (FAPESP/06434-9/2006) whose assistance we gratefully acknowledge.

References


Sexual dimorphism and seasonal changes in *Ilex paraguariensis*

M. Rakocevic et al.


