

# Photosynthetic efficiency of *Clusia arrudae* leaf tissue with and without Cecidomyiidae galls

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(With 2 figures)

## Abstract

Leaf galls induced by a still undescribed new species of Cecidomyiidae (Diptera) are frequent on leaves of *Clusia arrudae* Planchon & Tirana (Clusiaceae) in the rupestrian fields at 1400 m a.s.l. in Serra do Cipó, Minas Gerais, Brazil. Galls were  $7.1 \pm 0.7$  mm in diameter, one chambered with only one larva inside. Gall tissue is green and soft. Assessments of photosynthetic capacity using chlorophyll-*a* fluorescence measurements revealed that photosynthetic performance of gall tissue and healthy leaf tissue were rather similar. Hence, the morphological changes due to gall development were not associated with significant changes in the photosynthetic capacity of the tissue.

**Keywords:** insect galls, herbivore impact, photosynthesis.

## Eficiência fotossintética do tecido foliar de *Clusia arrudae* Planchon & Tirana com e sem galhas de Cecidomyiidae

### Resumo

Galhas induzidas por uma espécie nova ainda não descrita de Cecidomyiidae (Diptera) são frequentes nas folhas de *Clusia arrudae* Planchon & Tirana (Clusiaceae) em áreas de campos rupestres a 1400 metros de altitude na Serra do Cipó, Minas Gerais, Brasil. As galhas apresentaram um diâmetro médio de  $7,1 \pm 0,7$  mm e uma loja com uma larva dentro. As galhas são verdes e de tecido macio. Análises da capacidade fotossintética usando medidas de fluorescência da clorofila *a* revelaram que o desempenho fotossintético dos tecidos da galha e sadios foi similar. Assim, as mudanças induzidas pelo desenvolvimento das galhas não foram associadas a mudanças significativas da capacidade fotossintética do tecido.

**Palavras-chave:** galhas de insetos, impacto de herbívoros, fotossíntese.

### 1. Introduction

Herbivore impacts upon plants may range from harmful to positive (Belsky, 1986; Hendrix, 1979; Whitham et al., 1991; Paige and Whitham, 1987; Belsky et al., 1993; Cornelissen and Fernandes, 2001a,b) and vary according to herbivore type (Mattson et al., 1988). Gall inducing insects represent a special guild that develops in host plant meristematic tissues, where the gall-forming larvae modify the tissue growth processes, transforming the attacked cells into a gall structure that provides improved food and shelter for the larvae (Rohfritsch and Shorthouse, 1982; Ferreira et al., 1990; Price et al., 1987). Although galling insects are mostly considered true parasites of their host plants (Price et al., 1986, 1987), a spectrum of impact of gallers upon their host plants has been reported (Andrade et al., 1995; Fernandes, 1987).

Insect galls can cause important changes in host plant physiological processes. Galls are known to alter both carbon transport and allocation patterns of the plant, sometimes distant from the gall (Denill, 1985; Souza et al., 2001; Fay et al., 1996b; Fernandes, 1987; Fernandes et al., 1993; Sacchi et al., 1988). As an example, stem galls induced by the gall midge *Rhopalomyia hypogaea* on *Chrysanthemum leucanthemum* caused damage to the attacked stem and also reduced the production of the capitulum's ray florets (Mani, 1964). Gall induction on apical meristems may lead to the activation of dormant lateral meristems, affecting flower and fruit production secondarily (Craig et al., 1986; Fay and Hartnett, 1991; Silva et al., 1996). Insect gall growth and maintenance drain resources from the host plant and ultimately reduce flower head production

and/or decrease seed viability (Hartnett and Abrahamson, 1979; Fernandes and Ribeiro, 1990; Fernandes et al., 1993; Fay et al., 1996a). Numerous studies have shown that galls operate as physiological sinks for nutrients and assimilates, modifying tissues that otherwise could serve for growth and reproduction (Fourcroy and Braun, 1967; Janckiewicz et al., 1970; Kirst and Rapp, 1974; McCrea et al., 1985; Larson and Whitham, 1991; Fay et al., 1996a). Some galling cynipids (Hymenoptera) and cecidomyiids (Diptera) control the secondary metabolism of gall tissues, concentrating tannins and phenolics in the peripheral parenchyma, thereby leaving a highly nutritive inner layer consumed by the galling larva (Mani, 1964; Rohfritsch and Shorthouse, 1982). Because the sinks manipulated by gallers are physiologically linked to photosynthetic carbon fixation processes, galler impacts on leaf-level photosynthetic processes would be expected. In fact, gallers have been associated with both increased and decreased net leaf carbon gain (Fay et al., 1993; Larson, 1998). Net photosynthetic rates reflect the outcome of the dark and light and carboxylation reactions of photosynthesis. To date, there have been few studies examining these components independently with respect to insect galls (Fay et al., 1993; Larson, 1998; Florentine et al., 2005; Lemos Filho et al., 2007).

Chlorophyll-*a* fluorescence is a measure of the efficiency of the photosynthetic light utilisation in the light reactions with different applications, such as ecophysiology and crop productions (Baker and Rosenqvist, 2004; Lemos Filho et al., 2004). In this study, we compared the photosynthetic capacity of galled and healthy leaf tissue of *Clusia arrudae* Planchon and Tirana (Clusiaceae), measuring chlorophyll-*a* fluorescence parameters, on site, in the field. *Clusia* is the only genus of trees, sensu stricto, which has the Crassulacean acid metabolism (CAM). This special metabolism and the flexibility in the carbon acquisition under varying conditions are considered as ecophysiological advantages. Furthermore, the existence of ecotypes in high ecological amplitudes is associated with high rates of speciation within the genus (Lüttge, 2006).

Our hypothesis is that differences in the photosynthetic capacity between health and gall tissues do not exist, corroborating the argument proposed by Price et al. (1987) describing the vascular tissue from other parts of the plant as responsible for supplying the nutritional larvae requirements.

## 2. Material and Methods

### 2.1. Study site

The present study was performed in a rupestrian field vegetation area, at 1400 m a.s.l., in Serra do Cipó, located at the Southern portion of the Cadeia do Espinhaço, Minas Gerais State, Brazil (19° 12' S and 43° 29' W). The Serra do Cipó is dominated by cerrado and rupestrian field vegetation (Eiten, 1978; Giuliatti et al., 1987). *Clusia arrudae* occurs on the rocky outcrops of the area, in soils

with low water retention capacity, low concentration of nitrogen and phosphorus, and high aluminium concentration (Marques et al., 2002). The climate is characterised by rainy summers and dry winters, with high temperatures during the day, which, mainly during the winter, decrease drastically at night (Madeira and Fernandes, 1999). The habitat where *C. arrudae* occurs is also exposed to a high-light incidence (GWF, unpub. data).

### 2.2. Description of the system

The leaf galls on *C. arrudae* are induced by a still undescribed species of Cecidomyiidae (Diptera) and are found all year around. They are green and one-chambered, with only one larva inside. Galls are more or less globose, with the most pronounced portion on the abaxial leaf surface (Figure 1). Adult galling insects emerge from the adaxial portion of the gall, as observed by the emergence hole left on the gall walls (Figure 1). One to seven galls could be found on the leaf laminae during the study period (average of  $2.6 \pm 0.7$  galls per leaf,  $n = 30$ ). Galls occur singly, and coalescence was rarely observed. Galls averaged 7.15 mm in diameter when occurring singly ( $SE \pm 0.87$ ,  $n = 30$ ). Parasitism by an unidentified species of wasp on the gall midge was also observed but not quantified.

### 2.3. Sampling

Measurements of chlorophyll *a* fluorescence parameters were performed in the afternoon (from 3:00 PM to 4:00 PM) of a bright day in October 2002 on green gall tissue and adjacent tissue (hereafter called healthy tissue) of one leaf of three plants, totaling three (3) leaves of *C. arrudae*. The chlorophyll-*a* fluorescence measurements were performed using a miniaturised pulse-amplitude modulation fluorometer, Mini-PAM (H. Walz, Effeltrich, Germany) equipped with a standard 2030-B leaf clip holder (Bilger et al., 1995). Measurements of photosynthetic photon flux density (PPFD) ( $\lambda = 400-700$  nm) were taken by the micro-quantum sensor of the leaf clip calibrated against a LI-COR 190 quantum sensor (Li-COR, Lincoln, NE, USA).



**Figure 1.** Leaves of *C. arrudae* with galls of an undescribed species of Cecidomyiidae showing green gall tissue and the adjacent leaf tissue of which chlorophyll fluorescence parameters were measured.

#### 2.4. Data analysis

The effective quantum yield of PSII ( $\Delta F/F_m'$ ) was calculated as  $(F_m' - F) / F_m'$ , where  $F$  is the fluorescence yield of the light-adapted sample and  $F_m'$  is the maximum fluorescence obtained when a light pulse of 800 ms duration (intensity  $\approx 3000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) is superimposed on the prevailing environmental light level (Schreiber and Bilger, 1993). Instant light-response curves of  $\Delta F/F_m'$  were obtained using the light-curve programme of the Mini-PAM, where actinic light intensity was increased during 4 minutes in eight steps following each other after 30 seconds (Rascher et al., 2000). The internal halogen lamp of the instrument, using the fibre-optics and the leaf-clip holder, provided the light. Apparent electron transport rate was obtained as  $\text{ETR} = 0.5 \times 0.84 \times (\Delta F/F_m') \times \text{PPFD}$ . The factors in the equation for the ETR stand for an equal distribution of excitation energy to both photosystems I and (0.5) II, and for an assumed average light reflection of 16% (0.84) (Rascher et al., 2000).

### 3. Results and Discussion

Tissue temperature was 30 °C and ambient photosynthetic photon flux density (PPFD) c. 1000  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  during measurements (Table 2). At this PPFD photosynthetic performance, i.e. effective quantum yield ( $\Delta F/F_m'$ ) and apparent electron transport rate (ETR) were similar for both the galled and the non-galled tissue (Table 1). Comparison with light-dependence curves (Figure 1, Table 2) shows that

**Table 1.** Effective quantum yield ( $\Delta F/F_m'$ ) of PSII and apparent photosynthetic electron transport rate (ETR,  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) at ambient photosynthetic photon flux density (PPFD,  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) and temperature (T, °C) for gall tissue and adjacent healthy leaf tissue of *C. arrudae* ( $\bar{x} \pm \text{sd}$ ,  $n = 3$ ).

	Healthy tissue	Gall tissue
PPFD	905 $\pm$ 230	1040 $\pm$ 145
$\Delta F/F_m'$	0.20 $\pm$ 0.06	0.18 $\pm$ 0.07
ETR	76 $\pm$ 27	76 $\pm$ 25
T	30.4 $\pm$ 0.6	30.2 $\pm$ 0.7

**Table 2.** Cardinal points of light response curves (Figure 2) of gall tissue and adjacent healthy leaf tissue of *C. arrudae*.  $\text{ETR}_{\text{max}}$  is the apparent maximum electron transport rate.  $\text{PPFD}_{\text{sat}}$  and  $\text{PPFD}_{50}$  are the PPFD at  $\text{ETR}_{\text{max}}$  and at  $1/2 \text{ETR}_{\text{max}}$ , respectively.  $\Delta F/F_m'_{\text{-sat}}$  and  $\Delta F/F_m'_{\text{-50}}$  are the effective quantum yield at  $\text{PPFD}_{\text{sat}}$  and  $\text{PPFD}_{50}$ , respectively. PPFD and ETR are in  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  ( $\bar{x} \pm \text{sd}$ ,  $n = 3$  leaves).

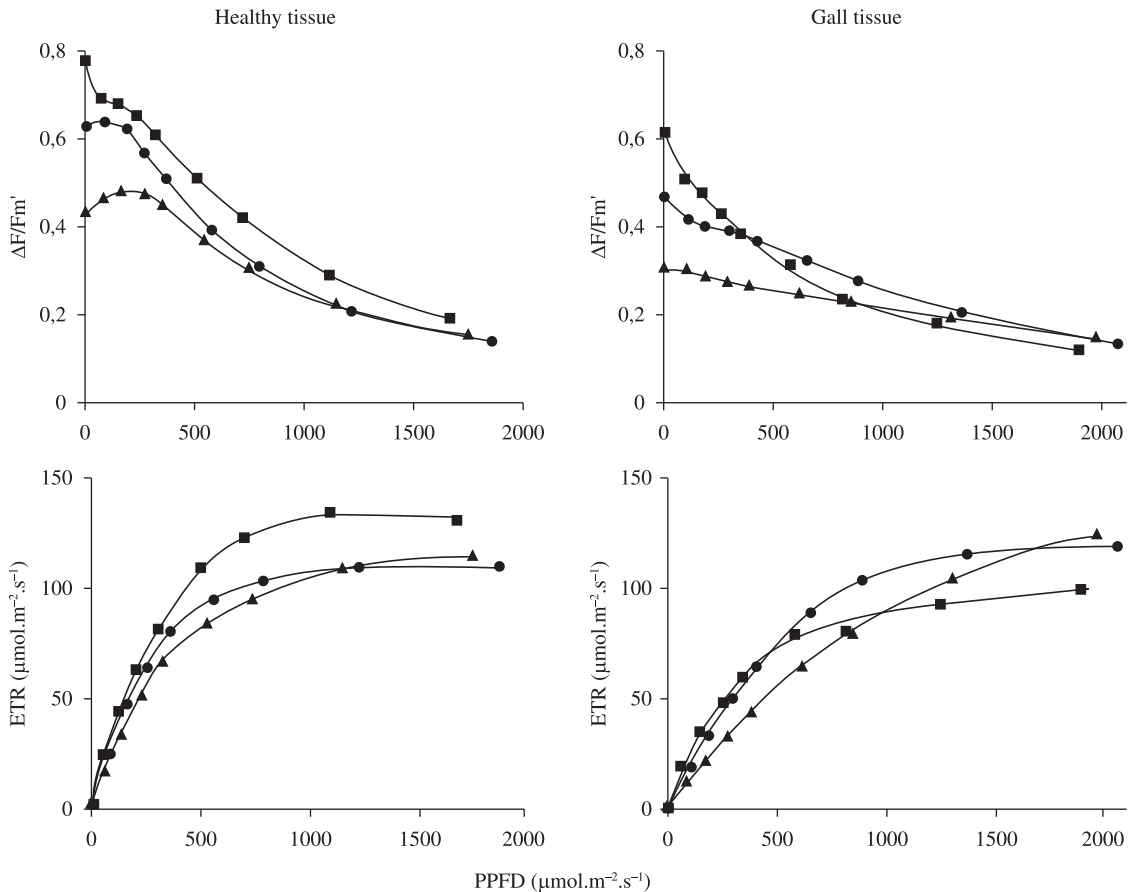
	Healthy tissue	Gall tissue
$\text{PPFD}_{\text{sat}}$	1230 $\pm$ 230	1900 $\pm$ 100
$\text{PPFD}_{50}$	250 $\pm$ 30	420 $\pm$ 185
$\text{ETR}_{\text{max}}$	120 $\pm$ 15	120 $\pm$ 15
$\Delta F/F_m'_{\text{-sat}}$	0.23 $\pm$ 0.06	0.14 $\pm$ 0.02
$\Delta F/F_m'_{\text{-50}}$	0.57 $\pm$ 0.09	0.35 $\pm$ 0.09

this PPFD ambient was close to saturation for the healthy and galled tissue. Although saturating PPFD was higher for the galled as compared to the healthy tissue, maximum ETR ( $\text{ETR}_{\text{max}}$ ) was similar and effective quantum yield of PSII even somewhat lower (Table 2). An inspection of the curves (Figure 2) and their cardinal points (Table 2) suggests, however, that at lower light intensities the healthy tissue has a somewhat superior performance compared to the galled tissue. At half saturating PPFD,  $\Delta F/F_m'$  is a little higher in the healthy than in the galled tissue.

The major result of the present measurement of photosynthetic capacity is the somewhat unexpected observation that photosynthetic performance of galled and healthy tissue was rather similar. It is clear that the morphological changes due to gall development were not associated with significant changes in the photosynthetic capacity of the tissue. Fay et al. (1993) reported increased leaf photosynthesis, stomatal conductance, and water potential over ungalled shoots in galls induced by *Antistrophus silphii* Gillette 1891 (Hymenoptera: Cynipidae) on *Silphium intergrifolium* Michx. (Asteraceae). Furthermore, galled plants experienced a smaller drop in leaf photosynthesis and stomatal conductance over a 4-day period after watering. The authors argued that while other guilds of herbivores consume the area of the attacked plant organ, galling insects leave their host organs intact. In addition, they argue that the gall-induced increase in leaf photosynthesis can be interpreted as a compensatory response by the plant, lessening the negative effect of galls on plant performance. Other measurements reported that the presence of galls caused a negative impact on photosynthesis when compared to the rates of healthy tissues (Larson, 1998; Florentine et al., 2005). They suggested that sink competition for nutrients between healthy leaves and gall tissue may account for the negative impacts on photosynthetic rates. In the same way, Lemos-Filho et al. (2007) did not find significant changes in photosynthetic activity between galled and ungalled tissues. However, they found changes in stomatal conductance due to the insect galling attack which can cause a decrease in carbon absorption, causing direct impacts on plant growth.

High concentrations of nitrogen, carbon and minerals in gall tissue were reported in many studies (Paquete et al., 1992; Raman et al., 2006). Morphological changes due to gall development were not associated with significant changes in the photosynthetic capacity of the tissue in this experiment. As the photosynthetic activity of the gall tissue is not increased to supply the needs of gall developing, our data support the hypothesis of adaptive value for insects by nutritional improvements, where these invertebrates control the nutrient levels in galls to their own benefit and the photosynthetic energy needed to supply gall growth and development may be being redirected from other host plant regions (Price et al., 1987).

Nonetheless, more studies on the physiology of gall induction throughout gall development and on the impact on their host plants are needed for a better understanding of the plant response to gall formation.



**Figure 2.** Light dependence (PPFD) curves of gall tissue and adjacent healthy tissue of *C. arrudae* with effective quantum yield ( $\Delta F/F_m'$ ) of PSII and apparent photosynthetic electron transport rate (ETR).

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