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SCIENTIFIC ARTICLE

Exposition of three *Cattleya* species (Orchidaceae) to full sunlight: effect on their physiological plasticity and response to changes in light conditions

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Abstract

In order to establish a link between the evolutionary history and the photochemical attributes, measurements of chlorophyll (Chl) *a* fluorescence were made in *Cattleya warneri*, *C. shofieldiana* and *C. harrisoniana* exposed to high irradiance for 5, 35, and 120 min (hereafter referred to as treatments T_5, T_{35}, and T_{120}, respectively). The following questions are addressed: (1) Is the increased energy dissipation enough to counterbalance the excess energy that drives photosynthesis at different times of high irradiance exposure? (2) Is there an influence of the incidence and duration of light radiation on *Cattleya* species in full sunlight, compared to *Cattleya* species submitted to low irradiance? Higher relative variable fluorescence at the J-step (Vj) values followed by the lower quantum yield of electron transport (ψ_{Eo}) indicate the accumulation of reduced Quinone A (Q_A) proportionally of sunflecks exposure time in *C. warneri*. The higher performance index (PI_{ABS}) and plasticity index values in *C. schofieldiana* indicate higher efficiency in modulating the photosynthetic apparatus under sunflecks. *C. harrisoniana* shows the lowest plasticity index, suppression of maximum fluorescence (F_m), and no recovery of PI_{ABS} after sunflecks. This study evidences the importance of physiological plasticity in the current geographic distribution of *Cattleya* in response to light pulses in species derived from fragmented habitats and the maintenance of shade to species of more primitive clades.

Keywords: Chlorophyll *a* fluorescence, orchids, sunflecks.

Resumo

Exposição de três espécies de *Cattleya* (Orchidaceae) a pleno sol: efeito sobre sua plasticidade fisiológica e resposta a mudanças nas condições de luz

Com o objetivo de estabelecer uma ligação entre a história evolutiva e os atributos fotoquímicos, medidas de fluorescência da clorofila (Chl) *a* foram feitas em *Cattleya warneri*, *C. shofieldiana* e *C. harrisoniana* expostas à alta irradiância por 5, 35 e 120 min (T_5, T_{35} e T_{120}, respectivamente). As seguintes questões são abordadas: (1) O aumento da dissipação de energia é suficiente para contrabalançar o excesso de energia que impulsiona a fotossíntese em diferentes tempos de exposição à alta irradiância? (2) Existe influência da incidência e duração da radiação luminosa em espécies de *Cattleya* a pleno sol, em comparação com espécies de *Cattleya* submetidas a baixa irradiância? A maior fluorescência variável relativa no ponto J (Vj) seguida do menor rendimento quântico do transporte de elétrons (ψ_{Eo}) indicam o acúmulo de Quinona A (Q_A) reduzida proporcionalmente ao tempo de exposição às manchas solares em *C. Waeneri*. Os maiores valores de índice de desempenho (PI_{ABS}) e do índice de plasticidade em *C. schofieldiana* indicam maior eficiência na modulação do aparato fotossintético em resposta às manchas solares. *C. harrisoniana* apresenta menor índice de plasticidade, supressão da fluorescência máxima (F_m) e nenhuma recuperação de PI_{ABS} após exposição às manchas solares. Este estudo evidencia a importância da plasticidade fisiológica na distribuição geográfica atual de *Cattleya* em resposta a pulsos de luz em espécies derivadas de habitats fragmentados e a manutenção do sombreamento para espécies de clados mais primitivos.

Palavras-chave: Fluorescência da clorofila *a*, manchas solares, orquídeas.

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Introduction

In their natural habitat, plants are exposed to light intensities that fluctuate considerably during the day and year (Pinheiro et al., 2019; Kükenbrinck et al., 2021). Many tropical orchid species are shade-loving plants and, therefore, occur in habitats of low light intensity (80 to 100 µmol m^{-2} s^{-1}). The ability of shade-loving plants to respond to changes in their light environment, *e.g.,* dynamic events of opening and closing of forest clearings, has a significant repercussion on their performance, being critical and decisive in the competition for natural resources (Craine and Dybzinski, 2013). Therefore, higher photosynthetic efficiency is observed in orchids that grow under low luminosity (Zampirollo et al., 2021). On the other hand, high-light irradiation reduces photosynthetic efficiency due to photoinhibition of them (Wu et al., 2020). Under these circumstances, the photosynthetic apparatus becomes inefficient in light trapping and use of the excited energy, reducing the activity of the photosynthetic electron transporters and accumulating excited energy, which can ultimately lead to oxidative damage by the formation of reactive oxygen species (Leme et al., 2021).

Under the forest canopy, plants can grow under brief, short and intermittent periods of short high photon flux density (PFD) exposition because of the occurrence of sunflecks (Pearcy and Way, 2012). Generally, sunflecks occur through openings in the canopy (ranging from seconds to some or several minutes), allowing PFD to penetrate the forest canopy and reach the floor. Although short-term, these sunfleck exposes the plant species to direct sunlight, favoring their growth and development under the forest canopy (Shao et al., 2010). In contrast, depending on the clearing geometry, leaves are exposed to sunlight for longer periods, which ultimately results in damage to the photosynthetic apparatus or photoinhibition. At the same time, many plants have a high acclimation capacity to different light regimes (Feng et al., 2021). Thus, the efficiency of utilization of sunflecks is determined genetically; therefore, the responses to sunfleck exposition are species-specific and often genotype-specific.

In nature, quantifying and controlling sunflecks is difficult because the threshold above the diffuse light level varies depending on the species or canopy conditions. Furthermore, the height and structural characteristics of the canopy, the flexibility of branches and petioles, and leaf size alter sunfleck characteristics (Way and Pearcy, 2012). However, in non-natural conditions, it is possible to simulate the effects of sunflecks on plant performance. In a study made by Dias and Marenco (2006), two young tropical trees, *Swietenia macrophylla* King (Meliaceae) and *Minquartia guianensis* Aubl. (Olacaceae), a gap-demanding and shade-tolerant species, respectively, were exposed to full sunlight (1,800 – 2,000 µmol m^{-2} s^{-1}) during 5, 35, and 120 min. The authors assessed the effect of the exposure to sunflecks simulated on chlorophyll *a* fluorescence parameters (F_0, F_m, F_v/F_m) and recovery from photoinhibition. Such information permits us to evaluate plants' ability to utilize light during sunflecks and their recovery capacity after strong exposure.

In this study, we used Chl a fluorescence techniques to investigate the photoinhibition response of three *Cattleya* species (van den Berg, 2016) to high light intensity for varying periods. We hypothesized that the ecological implication of the energy flow blockage across the transient OJIP might be associated with physiological plasticity and the ability to respond rapidly and efficiently to the conditions imposed by abrupt and unpredictable changes caused by clearing openings in *Cattleya*'s Lindl. habitat (van den Berg and Cribb, 2014). Additionally, we expected to observe greater resistance to high light stress in more derived species of *Cattleya* Lindl. (van den Berg et al., 2009). Thus, this paper addresses the following questions: (1) Is the increased energy dissipation higher enough to counterbalance the energy in excess of that driving photosynthesis at different times of high irradiance exposure? (2) Is there an influence of the incidence and duration of light radiation on *Cattleya* species in full sunlight, compared to *Cattleya* species submitted to low irradiance?

Materials and Methods

Plant material and growth conditions

Mature plants (with similar ages and sizes) of orchid *Cattleya warneri* T. Moore (*C. labiata* complex), *C. shofieldiana* Rchb. f. and *C. harrisoniana* Batem. *ex* Lindl. (an alliance of *C. intermedia*) were obtained from a private shadehouse (São Mateus, Espírito Santo State, Brazil) where they were cultivated under 400-600 µmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD) and temperature ranging from 24 to 30 °C (minimum and máximum, respectively) at the time of the experiment. The plants were watered daily and fertilized twice weekly with 1.6 g L^{-1} of commercial NPK 10-10-10, containing the following macro and micronutrients: N (10%), P_2O_5 (10%), K_2O (10%), B (0.02%), Cu (0.05%), Fe (0.10%), Mn (0.05%), and Zn (0.05%).

The tropical conditions of the North of Espírito Santo State (Brazil) is characterized by constraining a dry winter distinct from a rainy summer with an average temperature of 24 ºC (Alvares et al., 2013). The mean of global radiation reaching the study site is about 5.11 - 5.20 kWh/m²/day, but in the summer, the mean of global radiation ranged from 5.89 to 6.04. However, during the sampling, the global radiation ranged from 6.00 to 6.26 kWh m^{-2} day^{-1}. The annual mean of photosynthetically active radiation (PAR) reaching the North of Espírito Santo State was about 1.89 - 1.93 kWh/m²/day, but during the summer, it can reach 2.19 - 2.26 kWh m^{-2} day^{-1}.

The methodology used in this study is according to that developed by Dias and Marenco (2006), as described below. Before the exposure of plants to high light intensity, one measurement of Chl *a* fluorescence was made at 8:00 a.m., designed as a control. This first measurement was made in the morning because the photosynthetic apparatus is not under the effect of photoinhibition. In this condition, full oxidation of photosynthetic units of plants occurs. Then, the studied species were exposed to full sunlight (1800 - 2000 µmol m^{-2} s^{-1}) on a clear day for 5, 35, and 120 min (hereafter referred to as treatments T_5, T_{35}, and T_{120}, respectively) and then made the new Chl *a* fluorescence measurement (which was made at 1:00 p.m.). After the Chl *a* fluorescence was monitored at 2, 4, and 6 h (with measurements being made at 3, 5, and 7:00 p.m., respectively) and at 8:00 h of the next day. This last measurement permitted us to evaluate the recovery capacity of the photosynthetic apparatus after exposure to high light intensity.

PPFD, polyphasic Chl *a* fluorescence, and JIP-test

Photosynthetic photon flux density (PPFD) was recorded with a quantum sensor (LI-250A, LI-COR, USA). Polyphasic Chl *a* fluorescence transients (OJIP) were measured with a plant efficiency analyzer (Handy PEA, Hansatech Instruments Ltd., King's Lynn, Norfolk). The leaves were previously dark-adapted using leaf clips for 30 min. The transients OJIP were induced by 1 s pulses of red light [650 nm, 3000 µmol (photons) m^{-2} s^{-1}], and the fluorescence kinetics (F_o to F_m) was recorded from 10 s to 1 s. The fluorescence signal recorded at 20 µs (O-step, F_o) indicates the minimal fluorescence value immediately reached the onset of illumination. The maximum fluorescence (P-step, F_m) was registered at around 300 ms. J (2 ms) and I (30 ms) steps are inflection points between the O and the P levels. These fluorescence signals were used to calculate the parameters of the JIP-test (Kalaji et al., 2017). A detailed description of parameters and their meaning can be found elsewhere (Strasser et al., 2004) and briefly addressed in Table 1.

Table 1. Abbreviations of the JIP-test parameters, formulas, and description of the data derived from the Chl a fluorescence

$F_o \cong F_{20ms}$	Minimal fluorescence, when all PSII RCs are open
$Fj \cong F_{2ms}$	Fluorescence intensity at the J-step (2 ms) of OJIP
$FI \cong F_{30ms}$	Fluorescence intensity at the I-step (30 ms) of OJIP
F_P $(=F_m)$	Maximal fluorescence at the peak P, when all PSII RCs are closed
$F_v \cong F_m - F_o$	Maximal variable fluorescence
Area	Total complementary area between the fluorescence induction curve and F_o and F_m
$Vj = (F_j - F_o)/(F_m - F_o)$	Relative variable fluorescence at the J-step
$ABS/RC = M_o.(1/Vj).(1/ \varphi P_o)$	Absorption flux per active reaction center (RC) at t = 0.
$TR_o/RC = M_o.(1/Vj)$	Trapped energy flux per RC (at t = 0)
$DI_o/RC = [(ABS/RC) - (TR_o/RC)]$	Dissipated energy flux per RC at t = 0.
$\varphi P_o = TR_o/ABS = [1 - (F_o/F_m)] = Fv/Fm$	Maximum quantum yield of primary photochemistry at t = 0).
$\psi_{Eo} = ET_o/ABS = [1 - (F_o/F_m)].\psi_o = \varphi P_o.\psi 1$	Quantum yield of electron transport (at t = 0)
$PI_{ABS} = RC/ABS.\varphi P_o/(1 - \varphi P_o).\psi_{Eo}/(1 - \psi_{Eo})$	Performance index based on absorption

For a review, see Strasser et al. (2004).

Statistical analysis

The experiment was performed following a completely randomized design, in a factorial scheme 3 x 3 x 6 [3 orchid species, 3 treatments of light (T_5, T_{35}, and T_{120}) and 6 times (8 a.m. (control), 1, 3, 5 and 7 p.m., and 8 a.m. (recovery)] for each orchid species. A second factorial scheme [3 x 3 (3 orchid species and 3 treatments of light (T_5, T_{35}, and T_{120})] was made to compare the photochemical performance, based on the performance index (PI_{ABS}), between orchid species after sunflecks. The data were tested for normal distribution and compared using the Scott Knott test (0.05%) to verify differences between treatments using the Sisvar software. Considering the significant result for the effect of interaction between factors, the probability value of the unfolding within each factor was used. Additionally, when no interaction effect between factors was found, the statistical difference of the isolated factor was considered.

Results

All species analyzed showed a typical polyphasic of transient OJIP during T_1, T_2, and T_3, with the fluorescence signal rising from the initial fluorescence level (F_o) to the maximal level (F_m) with well-defined intermediate J and I steps (Figure 1).

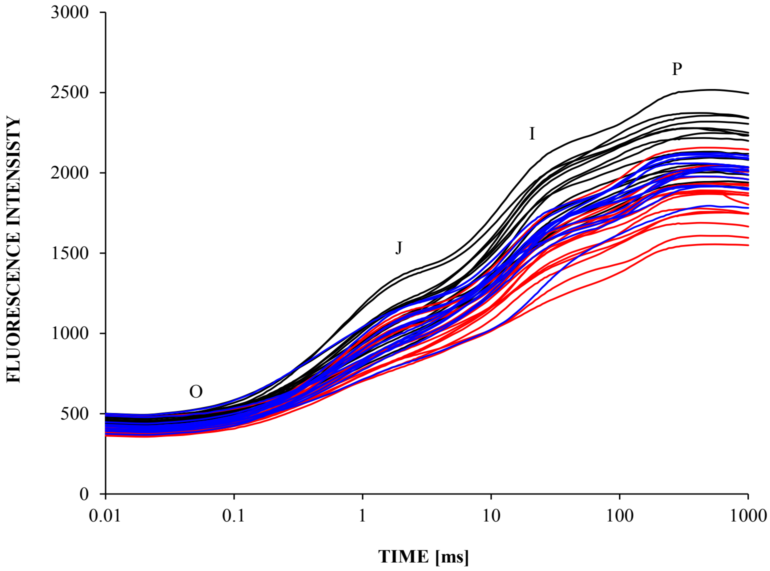

Figure 1. The OJIP chlorophyll *a* fluorescence transient curve (log time scale) in *Cattleya warneri* (black lines), *C. harrisoniana* (red lines) and *C. shofieldiana* (blue lines) orchid species submitted to high light intensity. Before the measurements, leaves were dark-adapted for 30 min. Values are means for eight plants.

As shown in Table 2, a significant triple interaction was observed for the variables Area ($p = 0.0017$) and TR_o/RC ($p = 0.0445$) (Table 2). A significant triple interaction was observed for the variables Area ($p = 0.0017$) and TR_o/RC ($p = 0.0445$) (Table 2). However, when the effects of the double interaction for the factor time were considered (See Figure 2 and Table 2), we observed an increase in Area inversely proportional to ψ_{Eo}, which was significantly higher in *C. harrisoniana*. This higher response's amplitude of Area in *C. harrisoniana* can also be visualized through the maximum fluorescence in the OJIP curves (red lines in Figure 1). In *C. warneri*, the results are presented as a percentage of change showing stability to the variable Area ($p > 0.05$, Table 2). Significant increases in Vj and reduction in ψ_{Eo} during T_{35} and T_{120} were observed in *C. warneri* (Figures 2A-C). On the other hand, considering the significant effect of the interaction between the analyzed factors (Table 2), *C. harrisoniana* orchid plants (Figures 2D-F) produced a marked increase in Vj ($p < 0.05$) during T_{35} and T_{120} in despite of the expenses of decreases in Area and energy conservation. A rapid response in maintaining the Vj and ψ_{Eo} was observed in plants of *C. schofieldiana* (Figures 2G-I) regardless of the sunfleck factor (Table 2).

Table 2. *P* values deduced by the JIP-test in *C. warneri*, *C. harrisoniana*, and *C. shofieldiana* orchid species submitted to high light simulating to sunflecks. The formulas and description of the data derived from the transient of Chl *a* fluorescence are shown in Table 1.

JIP-test parameters	Species (S)	Time (T)	Sunfleck (SF)	T x SF	T x S	S x SF	S x T x SF
Area	0.4504	0.0000	0.0386	0.1640	0.0000	0.9672	0.0017
Vj	0.0003	0.0000	0.0000	0.0042	0.0000	0.0261	0.1290
ABS/RC	0.0168	0.0000	0.0004	0.0079	0.0000	0.0518	0.0746
TR_o/RC	0.0003	0.0000	0.0000	0.4792	0.0000	0.0605	0.0445
Di_o/RC	0.0387	0.0003	0.0918	0.3799	0.0000	0.5171	0.5037
φP_o	0.0084	0.0000	0.1256	0.1702	0.0000	0.4136	0.1130
ψ_{Eo}	0.0003	0.0000	0.0000	0.0042	0.0000	0.0261	0.1290
PI_{ABS}	0.0093	0.0000	0.0000	0.0442	0.0000	0.5603	0.6355

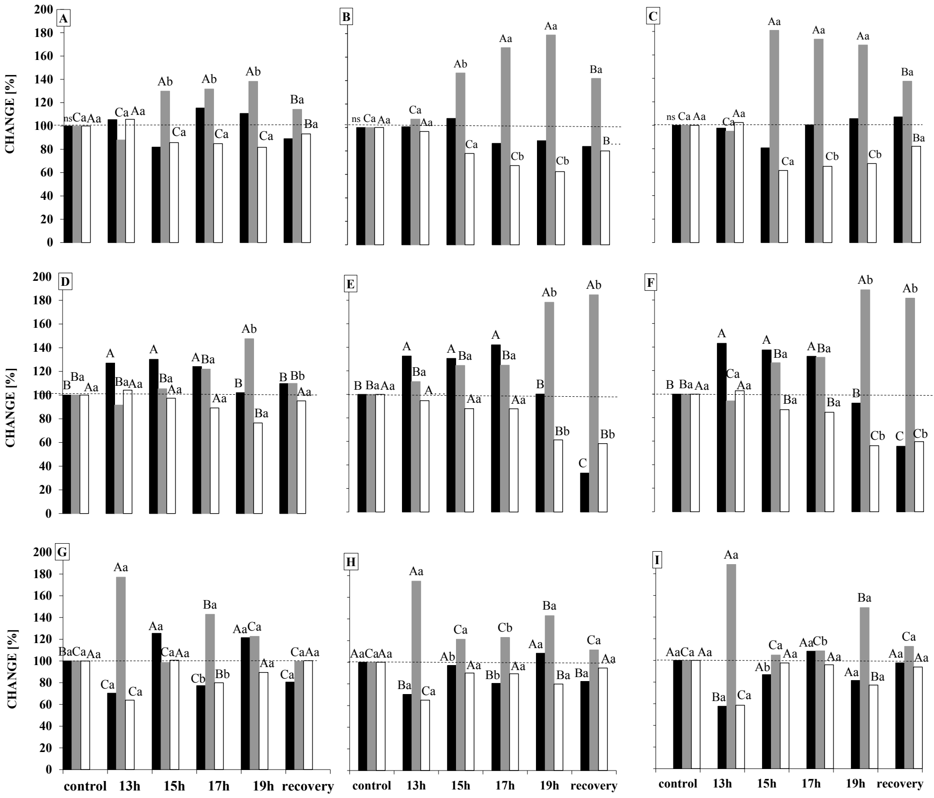

Figure 2. JIP-test parameters of *C. warneri* (A-C), *C. harrisoniana* (D-F), and *C. schofieldiana* (G-I) during exposure to high light during 5' (A, D, E), 35' (B, E, H) and 120' (C, F, I). Different upper-case letters indicate significant differences in each parameter between the time of exposure to high light within each treatment (5, 35, and 120'). Different lowercase letters indicate significant differences in each parameter between treatments (Scott Knott test, 5%, N = 72). Legend: ■ Area, ■ Vj, □ ψ_{Eo}. ns = not significant.

Correlations between the size of the light-harvesting complex functional antenna and the electron capture and heat dissipation show that species of *Cattleya* display different behaviors to the modulation of the photosynthetic apparatus under light pulses (Figure 3). Hence, *C. warneri* plants showed a positive correlation in contrast to *C. harrisoniana*. On the other hand, *C. schofieldiana* orchid plants had the highest amplitudes of responses to the aforementioned photochemical variables.

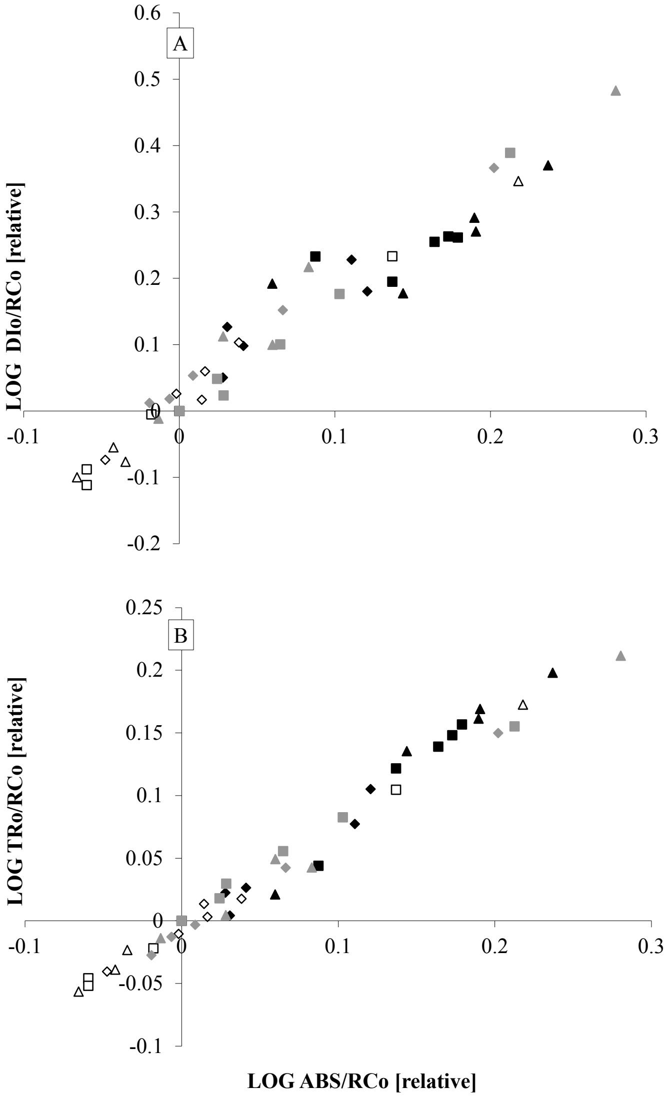

Figure 3. Energy transduction by reaction center in species of *Cattleya*. (A) correlations between ABS/RC and DI_o/RC, and (B) correlations between ABS/RC and TR_o/RC. The simbols ♦ - T_1, ■ – T_2 and ▲ - T_3 refers to *C. warneri*; ♦ - T_1, ■ – T_2 e ▲ - T_3 refers to *C. harrisoniana* and ◇ - T_1, □ – T_2 e △ - T_3 refers to *C. schofieldiana*.

Variations described in ABS/RC (Figure 3) resulted in alterations of both photochemical quantum yield (φ_{Po} or Fv/Fm) and performance index (PI_{ABS}) in the *Cattleya* species evaluated (Figure 4 and Table 2). PI_{ABS} values were significantly different between the orchid species ($p = 0.0000$). Higher PI_{ABS} values were reported in *C. schofieldiana* (≅ 38.56) compared to *C. warneri* and *C. harrisoniana* (≅ 20.79 and 26.48, respectively) after sunflecks. The treatment T_5 produced the highest PI_{ABS} values ($p = 0.0001$) after sunflecks. However, no interaction was observed between species and sunflecks' duration. Additionally, no significant alterations were observed in φ_{Po} or F_v/F_m for *C. warneri* (Figure 4A). Decreases of PI_{ABS} (post-pulse) in *C. warneri*, to which the magnitude of the responses was proportional to the duration of the light pulse at 1 pm, showed recovery at approximately 68%, 37%, and 31% in T_5, T_{35}, and T_{120}, respectively (Figure 4A).

No effect was produced by light pulse on φ_{Po} in *C. harrisoniana* during post-pulse. However, significant decreases of φ_{Po} were recorded 11 hours from the post-pulse (recovery) (Figure 4B). Significant reductions of φ_{Po} were observed in *C. schofieldiana* during the light pulse (13h) and recovery of the φ_{Po} values during all post-pulse and recovery periods (Figure 4C).

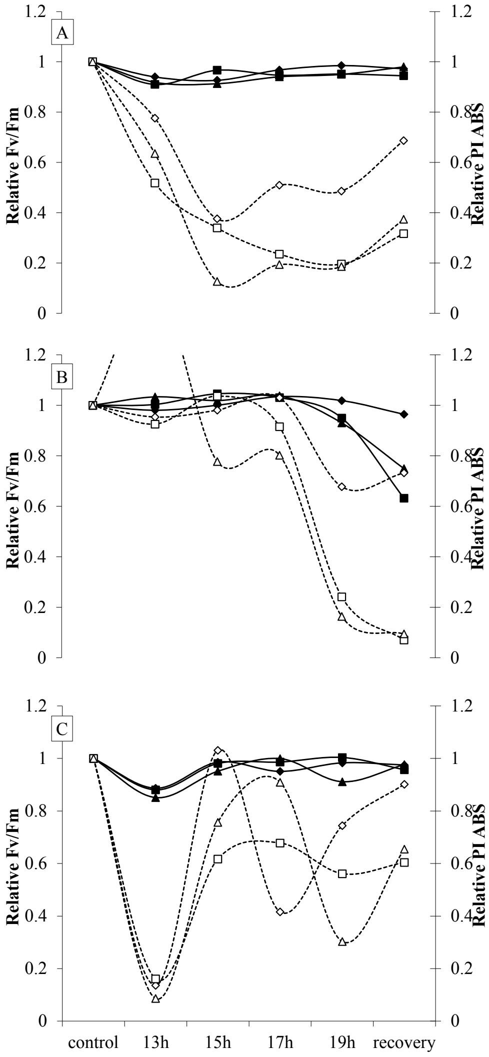

Figure 4. Relative maximum quantum yield and performance index in species of *Cattleya* Panels A-B-C refers to *C. warneri*, *C. harrisoniana,* and *C. schofieldiana,* respectively. The symbols ♦ - T_1, ■ – T_2, and ▲ - T_3 refer to relative Fv/Fm. The symbols ◇ - T_1, □ – T_2 e △ refers to relative PI_{ABS}.

Discussion

The typical OJIP polyphasic rise in the kinetic induction curves of the Chl *a* transient fluorescence emission during T_1, T_2, and T_3 varying from F_o to F_m demonstrate that all the samples remained photosynthetically active (Tsimilli-Michael, 2020). These measurements evidenced the characteristic polyphasic rise in the OJIP curves, representing the status of electron transport across the electron transport chain (Xiao et al., 2020). Phases O-J (50 µs – 2 ms), J-I (2 ms – 30 ms), and I-P (30 ms – 300 ms) represent the primary photochemical events of the photosynthesis from the acceptor side of the photosystem II (PSII), the processes of intersystem reduction, and the processes of pool reduction of final acceptors from the acceptor side of photosystem I (PSI), respectively (Xiao et al., 2020). The decrease in J, I, and P steps observed during light pulses can be attributed to the inhibition of electron transport from the donor side of PSII or to a decrease in the pool size of Q_A, which results in partial blockage in the energy flow (Zushi and Matsuzoe, 2017; Akhter et al., 2021).

The significant result obtained for the triple interaction suggests that structural changes in the light-harvesting complex associated with PSII were accompanied by modulations in the electron trapping rate (Table 2). Furthermore, in order to better understand the competing mechanisms of the photochemistry of photosynthesis, significant double interactions were considered (Table 2). The light pulse effect on the electron flow from the acceptor side of PSII can be calculated from Vj (Tsimilli-Michael, 2020; Chen et al., 2021). Therefore, an estimation of the total reaction centers that can be reduced can be obtained as the degree of blockage in the electron flow between photosynthetic subunits. Our results suggest that changes in electron transport after reduced Q_A led to alterations in the relative variable fluorescence emitted during 2 ms, as observed by Campos et al. (2021).

The results shown in figure 3 show that ABS/RC can represent the increase in the functional antenna size to higher capture and dissipation of the excess energy as a photoprotector mechanism. In the present study, *Cattleya* species showed a correlation between absorption and dissipation (Figure 3A) and absorption and capture (Figure 3B) as a physiological strategy in response to light pulse stimulus. The effective size of the antenna, ABS/RC, is calculated from the total number of photons absorbed by the chlorophyll molecule in all CRs divided by the total number of active CRs. Thus, this parameter is subject to variations in the rate of active and inactive reaction centers (Bussotti et al., 2020). Hence, the parameter ABS/RC can represent (1) inactive CRs transformed in non-reducting PSII Q_A when decreases in ABS/RC are observed in association with the electron capture stability, TR_o/RC, and decrease in φ_{Po} and $\gamma_{RC}/(1-\gamma_{RC})$; or (2) the antenna functional size when there is a proportional behavior to increases in φ_{Po} and ABS/RC (Bussotti et al., 2020). This experiment showed that plants of *C. warneri*, *C. harisoniana,* and *C. schofieldiana* exposed to light pulses in all three treatments had a conversion from reaction centers reducting of Q_A to non-reducting centers of Q_A in PSII.

These results are associated with the rapid response to the increase in the effective size of the antenna, ABS/RC, and to the non-reducting centers of Q_A activity (Strasser et al., 2004; Bo and Qing, 2008). According to Van Heerden et al. (2007), the energy loss signal is proportional to the time of exposure to a stressor factor. However, loss of energy in the form of heat can be an efficient mechanism of photosynthetic unit protection when facing an environment with excessive light (Wu et al., 2020). The degree to which plants adapt to light regimes is genetically determined, being species-specific, which may represent a selective advantage, defining their physiological plasticity in response to environmental factors, which can determine their photoinhibition susceptibility (Wu et al., 2020; Leme et al., 2021).

Chen et al. (2021) reported that the protecting effect to damages in the photosynthetic apparatus and its active subunits can be attributed to the dissipation of excess energy by the non-reducting quinone centers. Reaction centers can be converted into efficiently excited energy centers in response to a stressful factor and return to the reduced Q_A status once the environmental stressful stimulus conditions end. Within this scenario, a higher contingent of pigments (chlorophylls and carotenoids) can be recruited, increasing the antenna's effective size (Santos et al., 2020).

Physiological plasticity can be measured from an index that may be applied to the Chl *a* fluorescence parameters (Bo and Qing, 2008). Plants of *C. schofieldiana* showed the highest values to the physiological plasticity index (0.51) in comparison to *C. warneri* plants (0.42) and *C. harrisoniana* (0.38). Rapid reactions coordinated by the photosynthetic machinery are a prerequisite to the photosynthetic use of sunflecks (Lüttge, 1997). However, the photosynthetic limitation imposed by the high light exposition is gradually removed in the subsequent light pulses or during post-pulse. Hence, the plant may gain photosynthetic efficiency from light pulses (Durand et al., 2022). The highest range of responses from *C. schofieldiana* may be associated with a heliophyte behavior, which leads to a higher dispersive and resistant efficiency to the natural light stress factor (Bo and Qing, 2008).

The φ_{Po} may not be a sensible enough parameter to illustrate stress signals in ecophysiological studies (Campos et al., 2021). Thus, it suggests the use of the mathematical expression $PI_{ABS} = [\gamma_{RC}/(1-\gamma_{RC})].[\varphi_{Po}/1-\varphi_{Po})].[\psi_{Eo}/1-\psi_{Eo})]$ to infer the signal magnitude of the stress disturbance can be precise. Decreases in the φ_{Po} may be related to declines in F_m connected to photoinhibitory damages of the xanthophyll cycle or increases in F_o due to the conversion of reaction centers into non-reducting of Q_A (Zhang et al., 2021), which disturbances can confirm in the energy dissipation parameters by heat release $[DI_o/RC = (ABS/RC)-(TR_o/RC)]$ (Figure 3). As a result, it can be said that *C. warneri* and *C. schofieldiana* are likely more capable of modulating the maximum quantum efficiency of the PSII concerning sunflecks in all three treatments (Figure 4A-C). In addition, a 5 min light pulse confers the three species of *Cattleya* relative stability on the photochemical activities inherent to the PSII, as evaluated by φ_{Po} (Figure 4).

The performance index is one of the best parameters to describe plant responses to any cert stress type. It comprises the redox reaction in the photochemical phase O-J and the terminal phases J-I and I-P. The performance index, PI_{ABS}, can be calculated from three components, including: (1) $\gamma_{RC}/(1-\gamma_{RC})$, an expression related to the density of the active reaction centers in PSII; (2) $\varphi_{Po}/(1-\varphi_{Po})$ about the primary photochemistry; (3) $\psi_{Eo}/(1-\psi_{Eo})$, a component that describes the redox reaction in the intersystem (Kumar et al., 2020). We have distinguished the effects of light pulse-driven on individual components of PI_{ABS} and found that the ratio $\psi_{Eo}/(1-\psi_{Eo})$ presented more plasticity in three species of *Cattleya*, suggesting that the efficiency of the forward electron transport rates better explains the disturbances in PI_{ABS}. PI_{ABS} values are altered when an environment as stress affects one of the factors isolated or in combination, showing how efficiently this parameter is likely to describe the ecophysiological behavior of plants under stress (Spanic et al., 2021).

In conclusion, the ecological implication of the energy flow blockage across the transient OJIP may be associated with physiological plasticity and the ability to respond rapidly and efficiently to the conditions imposed by abruptand and unpredictable changes caused by clearing openings of 5, 35, and 120 min in *Cattleya*'s habitat. Within this scenario, the higher Vj values followed by lower ψ_{Eo} reported in *C. warneri* are indicative of the harmful effects of accumulation of reduced forms of Q_A proportional to sunflecks exposure time and establish a strong relationship with its current geographical distribution in montane forests of the central Atlantic rainforest corridor, restricting the occupation of more open forests where deciduous trees prevail or even the Cerrado.

Thus, a higher yield of the photochemical reactions of photosynthesis is expected in typical habitats of the species of the complex clade *C. labiata. C. schofieldiana* orchid plants have a higher efficiency in modulating the photosynthetic apparatus under light pulses concerning the rapid response and re-establishment of the physiological conditions close to the control compared to other species. These findings are confirmed by the higher PI_{ABS} values reported for this species (≅ 38.56) after sunflecks. Thus, these results evidence the critical role of physiological plasticity in response to the light pulse from the non-reducting reaction centers of Q_A. Hence, *C. schofieldiana* plants (plasticity index = 0.51) showed a photochemical behavior that corroborates the ecological findings on the current geographical distribution between the central Atlantic forest corridor and the Northeastern corridor, and given that this species is among those *Cattleya* species with the most derived characters.

Finally, the lowest plasticity index (0.38) values, the suppression at maximum fluorescence, the concomitant decrease in energy conservation or ψ_{Eo} and the absence of recovery fo PI_{ABS} after exposure to sunflecks reported for *C. harrisoniana* seem to reflect it distribution to regions of dense should ombrophilous forests, or associated with the central Atlantic rainforest corridor and the Serra do Mar corridor. On the other hand, more research is necessary involving a higher number of *Cattleya* to consolidate Orchidaceae's biogeographical and phylogenetical history.

Declaration of Competing Interests

The authors declare no conflict of interest

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Author Contribution

CLP: conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft; **JBZ:** conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft; **MMM:** conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft; **VFS:** conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft; **JPRM:** analysed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft; **DMS:** analysed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft; **MMPT:** conceived and designed the experiments, authored or reviewed drafts of the article, and approved the final draft; **DC**: designed the experiment and conceived the statistical analysis; **ARF:** conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.

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