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An investigation of the photophysiology and phenology of cultivated African violet plants

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African violets (Streptocarpus ionanthus), originally native to the Eastern Arc Mountains of Africa and adjacent submontane or montane forests in Kenya and Tanzania, are commonly grown as ornamental plants and have been extensively studied by horticulturists. However, there is a lack of laboratory data regarding their ecophysiology. Given the growing interest in conserving African violets in their threatened natural habitats, it would be beneficial to establish baseline data on their physiological ecology, helping to document their response to changing environmental conditions in their natural environment. To address this need, we conducted an analysis of the net photosynthesis rate, respiration rate, and leaf fluorescence of mini and standard strains of African violet plants within a controlled laboratory setting. Additionally, we examined variations in the photosynthesis rate, respiration rate, and leaf fluorescence data for leaves of different ages (phenology) in the standard strain. The results showed that the mean net photosynthesis rate in the older whorl of leaves was approximately 50% of the rate observed in the younger leaves. Furthermore, the mature leaf respiration rate accounted for about 25 to 30% of the net photosynthesis. This particular metric, the ratio of respiration to net photosynthesis, is significant in estimating the carbon balance of the plants. It helps us understand how much carbon (C) is gained through photosynthesis compared to the amount of carbon lost through respiration.

Key words: Environmental carbon balance, leaf relative chlorophyll content analysis, leaf chlorophyll fluorescence analysis, photosynthesis rate, respiration rate, specific leaf area.

INTRODUCTION

African violets are among the most commonly cultivated ornamental plants in households and conservatories. From a taxonomic perspective, they belong to the Gesneriaceae family and were originally classified as *Saintpaulia ionantha* H. Wendl. However, based on molecular genetic analysis, African violets were reclassified under the *Streptocarpus* genus and renamed Streptocarpus ionanthus (H. Wendl.) Christenh (Christenhusz, 2012). Furthermore, there has been a growing interest in the molecular phylogenetics of *S. ionantha*, including the examination of phylogenetic relationships among various subspecies (Kyalo et al., 2002). African violet species are native to the Eastern Arc Mountains of Africa and are most prominently found in

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Figure 1. Laboratory cultured African violets. Standard plant (left) and mini plant (right). Marker = 6 cm. Source: Author.

the submontane or montane forests of Kenya and Tanzania. These regions are recognized as one of the 25 global biodiversity hotspots (Myers, 1988). Interestingly, a few African violet species are also found in lowland forests and have played a significant role as the primary source of species from which all horticultural cultivars have been developed (Clarke, 1998). Over the last century, African violets have been intensively cultivated, and new varieties have been bred through selective breeding, resulting in thousands of cultivated varieties that are mass-produced by the horticulture industry (Baatvik, 1993).

However, concerns have been growing regarding the conservation status of African violets in their natural habitat (Eastwood et al., 1998). To gain a comprehensive understanding of the environmental and anthropogenic factors that may pose a threat to the conservation of African violet species, additional research is needed to explore their physiological ecology. This research can provide evidence of their adaptive features, which are crucial for monitoring and documenting their status in their natural environment. It is worth noting that while considerable attention has been given to the horticultural aspects of their physiology, propagation, and growth (Faust and Heins, 1993; Yun et al., 1997; Boschi et al., 2000; Streck, 2004; Dewir et al., 2015; Teixeira et al., 2016; Ahamadi et al., 2023; Akbarian et al., 2023), there is only a modest representation of published laboratory research on their ecophysiology.

MATERIALS AND METHODS

Culture conditions and sampling methods

Mature African violet plants, including both mini and standard strains, were sourced from commercial plant distributors,

specifically Violet Barn in Naples, New York, and Valli Florist in New York City, New York, USA (Figure 1). These African violet plants were cultivated in plastic pots filled with commercially available potting soil formulated for African violets, specifically using Scotts Miracle-Gro from Marysville, Ohio, USA.

The plants were carefully nurtured in an environmentally controlled culture room at the Lamont-Doherty Earth Observatory of Columbia University. The growing conditions included a temperature of 25° C and a light cycle of 14 h of light followed by 10 h of darkness. The light was provided using fluorescent illumination with an intensity of 100 µmol photons m⁻² s⁻¹, and the relative humidity was maintained at 60%.

Each mature plant, whether of the mini or standard strain, had approximately four whorls of leaves. Individual mature leaves were collected in the morning and promptly transported to the laboratory within the same building for subsequent physiological analyses. Specifically, ten plants of the mini strain and ten plants of the standard strain were analyzed for their leaf morphology, photosynthesis rate, and respiration rate.

For the phenology study, leaves of the standard African violet plants were the focus of analysis. One leaf was collected from each of the four whorls present in the rosette of leaves from a total of six plants, resulting in a total of twenty-four leaves for physiological analyses. The youngest leaves were collected from the central whorl at the growing apex, while the oldest leaves were obtained from the outer peripheral whorl.

Morphology

African violet mean leaf thickness (mm) was assessed based on 40 leaf measurements of four plants, each of the mini and standard African violet plants, using a Micro-precision digital caliper (0.01 mm precision) manufactured by *iGaging* (San Clemente, California, USA). The mean leaf area (cm²) was based on 10 sampled leaves from each strain using a Leaf Area Meter (Model AM-350, Opti-Sciences, Inc., Hudson, New Hampshire, USA).

Leaf physiological and phenological analyses

The following variables were examined to document physiological

and phenological characteristics of the leaves:

1. Leaf chlorophyll fluorescence including evidence of quantum efficiency expressed as a ratio of variable fluorescence to maximum fluorescence (Fv/Fm) and electron transfer per reaction center beyond the quinone intermediate (Q_A) in the electron-transport chain (ET₀/RC).

 Leaf chlorophyll content index (CCI), a relative index measuring chlorophyll content per unit leaf area, and the specific leaf area (SLA), a measure of the ratio of leaf area to leaf dry mass.
Leaf net photosynthesis rate and dark respiration rate.

Understanding the relative rates of photosynthesis, respiration, growth, and carbon storage in vegetation is of paramount importance (Atkin et al., 2006). Such an analysis is crucial for gaining insights into the overall growth and carbon storage in plants. This study employs appropriate methods to obtain comparative data on net photosynthesis and respiration rates in both mini and standard strains of African violets. The goal is to incorporate this data into a broader analysis of the role of African violets in the carbon balance relative to their environment, particularly in the context of CO₂-based carbon balance. The net photosynthesis rate of the leaves was assessed using an infra-red gas analyzer (IRGA) system; specifically, model BTA from Vernier, Beaverton, Oregon. The system featured an optically clear, 163 cm³ assay chamber and was illuminated using a Light Emitting Diode (LED) source. The relative humidity within the sample cuvette was maintained within the range of 85 to 90% to reduce excessive vapor pressure deficit. The CO₂ concentration in the assay cuvette was set to match the ambient atmospheric concentration, which was 417 ppm. The measurement of each leaf took approximately 10 min.

Mean photosynthesis rates were assessed for both the mini and standard strains at four different light intensities, namely 10, 25, 50, and 100 μ mol m⁻² s⁻¹. These rates were measured and expressed in three different units: (1) based on leaf area (μ mol m⁻² s⁻¹), (2) based on fresh weight (FW) (nmol g FW⁻¹ min⁻¹), and (3) based on dry weight (DW) (μ mol g DW⁻¹ min⁻¹). The mean respiration rate was determined at a constant temperature of 25°C using the same apparatus. The assay chamber was completely darkened, and the results were expressed in the same three units: per leaf area, leaf fresh weight, and leaf dry weight. The leaf sample was kept in a dark condition within the respiration cuvette until the reaction centers of the photosystems in the leaves reached equilibrium with the darkened state (approximately 2 min). Measurements were initiated when a steady state respiration rate was achieved.

Each leaf sample's chlorophyll concentration index (CCI), expressed in mg m⁻² (Gitelson et al., 1999), and was obtained using a CCM-300 chlorophyll content meter (Opti-Sciences, Inc., Hudson, New Hampshire). At least ten measurements were made for each leaf sampled. The mean value, obtained from the ten measurements of leaves on one plant, was used to calculate the overall mean CCI value for a given plant. An OS-30p+ Chlorophyll Fluorometer (Opti-Sciences, Inc., Hudson, New Hampshire) was used to obtain the leaf fluorescence data. This included two assavs based on the JIP test application in the OS-30p+ instrument: 1) leaf quantum yield efficiency expressed as variable fluorescence/ maximum fluorescence (Fv/Fm), and 2) evidence of electron transport per reaction center (ET₀/RC) from photosystem II (PS II) to the guinone intermediate (Q_A) and beyond in the electron-transport chain. Leaf samples were dark adapted for 20 to 30 min. Before the measurements were made to ensure that the reaction centers (RC) had come to equilibrium with the darkened state. Following the leaf fluorescence assay, the area of the leaf, expressed as cm², was assessed using a Leaf Area Meter (Model AM-350, Opti-Sciences, Inc., Hudson, New Hampshire, USA). After drying overnight at 60°C in a laboratory oven, the leaf's fresh weight and the dry weight were determined using a Sartorius digital balance. This data was also

used to calculate the mean specific leaf area (leaf area in cm²/dry weight in g) (Wolf et al., 1972).

All results of the assays are presented as the mean \pm standard error of the mean (SEM) calculated using an Excel spreadsheet (Microsoft, Inc., Redmond, Washington State, USA). A t-Test (GraphPad Software, Boston, Massachusetts, USA) was used to test the statistical significance of mean differences for data presented in each of the Tables 1 to 4. The criterion level of significance was set at p \leq 0.05. A Kolmogorov-Smirnov test was used to verify that the data for each t-test analysis was sufficiently normally distributed to apply the parametric t-test.

RESULTS

Morphology

The mean leaf area (cm²) based on 10 sampled leaves from each strain was 7.7 \pm 0.4 for the mini strain and 17.1 \pm 1.6 for the standard strain. The difference in means is statistically significant (t = 5.70, p < 0.01, N =10). The mean leaf lamina thickness for the mini strain African violet plants (0.99 \pm 0.03 mm) was considerably thinner than for the standard strain (1.55 \pm 0.04 mm) (t = 11.2, p < 0.01, N =10). In both strains, leaf shape varied from ovate to cordate.

Physiology and phenology

Table 1 displays the mean net photosynthesis rates for both the mini strain and standard strain African violets. The data shows that there is no statistically significant difference in the photosynthesis rates between the two strains when expressed per unit area, per unit fresh weight, or per unit dry weight. This is evident from the comparable mean values and the results of t-tests, which confirm the lack of a significant difference.

Table 2 presents the mean dark respiration rates for the two strains, along with the results of statistical tests included in the table's footnote. The data indicates that the mean values are quite similar for both strains, and the statistical results do not show a significant difference. It is worth noting that even though the two strains differ substantially in plant size, leaf thickness, and leaf area (as shown in Figure 1), their mean respiration rates are not significantly different.

Given the similar leaf physiological properties observed in Table 2 for the African violet mini and standard strains, leaf phenology analyses were only conducted on the standard African violet strain. This strain is the most commonly cultivated and has larger leaves that are more suitable for laboratory analysis.

Table 3 presents mean data for leaf fluorescence (Fv /Fm, ET₀/RC), chlorophyll concentration index (CCI), and specific leaf area (SLA) from each of the four whorls of leaves in six plants. The mean values for the fluorescence leaf data (Fv /Fm and ET₀/RC) are statistically significant, with higher values observed in the younger leaves of whorl 1 compared to the older leaves in whorl 4. However,

Otrain	Photosynthesis rate				
Strain	(µmol CO ₂ m ⁻² s ⁻¹) ^b	(nmol CO ₂ g _{FW} ⁻¹ min ⁻¹) ^c	(µmol CO ₂ g _{DW} ⁻¹ min ⁻¹)		
Mini strain					
10	0.27 ± 0.04	22.0 ± 4.14	0.59 ± 0.11		
25	0.59 ± 0.07	48.0 ± 6.97	1.27 ± 0.21		
50	0.78 ± 0.10	64.9 ± 10.59	1.70 ± 0.28		
100	0.94 ± 0.10	76.9 ± 10.36	1.98 ± 0.25		
Standard strain					
10	0.27 ± 0.02	21.9 ± 1.51	0.52 ± 0.06		
25	0.57 ± 0.04	46.2 ± 4.66	1.15 ± 0.10		
50	0.83 ± 0.05	67.3 ± 6.02	1.67 ± 0.13		
100	0.96 ± 0.06	78.4 ± 7.40	1.91 ± 0.16		

Table 1. Mean ± SEM net photosynthesis rate for the mini and standard African violet strains^a.

^aN = 10 plants measured for each mean value. Light intensity expressed as photosynthetic photon flux density (PPFD) in units of µmol photons m⁻² s⁻¹, and mean leaf photosynthesis rate expressed per leaf area (m⁻²), per leaf fresh weight in grams (g FW⁻¹), and per leaf dry weight in grams (g DW⁻¹). Means for each of the three columns of data comparing the mini and standard strains are substantially comparable, and not significantly different. ^b(t = 0.17, p = 0.86), ^c(t = 0.08, p = 0.94), ^d(t = 0.42, p = 0.68).

Table 2. Mean \pm SEM Leaf respiration rate expressed per leaf area (m⁻²), per leaf fresh weight in grams (g FW⁻¹), and per leaf dry weight in grams (g DW⁻¹) for the mini and standard African violet strains^a.

Strain	(µmol CO ₂ m ⁻² s ⁻¹) ^b	(nmol CO₂ g _{FW} ⁻¹ min⁻¹) ^c	(µmol CO₂ g _{DW} -1 min ⁻¹) ^d
Mini strain	0.18 ± 0.02	23.77 ± 8.78	0.38 ± 0.03
Standard strain	0.24 ± 0.03	20.59 ± 3.78	0.48 ± 0.07

 a N = 10 plants measured for each mean value. Mean values for the mini and standard strains are substantially comparable, and not significantly different. $^{b}(t = 1.68, p = 0.11)$, $^{c}(t = 0.33, p = 0.74)$, $^{d}(t = 1.31, p = 0.21)$.

Table 3. Standard African violet leaf phenology	means ±	SEM for	fluorescence	data	(F _v /F _m ,	ET ₀ /RC),	chlorophyll
concentration index (CCI), and specific leaf area	(SLA) ^a .						

Whorl	F _v /F _m b	ET₀/RC°	CCI (mg m ⁻²) ^d	SLA ^e
1	0.75 ± 0.01	1.34 ± 0.06	11.60 ± 1.37	305.71 ± 1.04
2	0.71 ± 0.02	1.31 ± 0.05	10.30 ± 0.39	278.45 ± 21.25
3	0.72 ± 0.02	1.23 ± 0.04	12.83 ± 0.89	293.07 ± 17.05
4	0.62 ± 0.05	1.14 ± 0.06	8.34 ± 1.34	335.79 ± 14.82

^aN = 6 plants measured for each mean value per whorl. Statistical comparison of means for whorl 1 and whorl 4: ^b(t = 2.55, p = 0.03), ^c(t = 2.36, p = 0.04), ^d(t = 1.7, p = 0.12), ^e(t = 2.02, p = 0.07).

the mean values for CCI and SLA are not statistically different when comparing whorl 1 leaves to whorl 4 leaves.

Table 4 displays the variation in mean photosynthesis rates and mean respiration rates across the four whorls of leaves in six plants. It appears that both the mean photosynthesis rate and mean respiration rate tend to be higher in the younger leaves of whorl 1 compared to the older leaves of whorl 4. However, when subjected to ttest analysis for comparisons of means between whorl 1 and whorl 4, only the photosynthesis mean rates show a statistically significant difference between the two whorls. This significance is evident for each of the three column variables (μ mol CO₂ m⁻² s⁻¹, nmol CO₂ g FW⁻¹ min⁻¹, and μ mol CO₂ g DW⁻¹ min⁻¹). In contrast, the differences in mean respiration rates are not statistically significant.

DISCUSSION

Leaf morphology

As a context for this study, the leaf morphology (mean area and mean thickness) of the mini and standard

	Photosynthesis rate				
whori	(µmol CO ₂ m ⁻² s ⁻¹) ^b	(nmol CO ₂ g _{FW} ⁻¹ min ⁻¹) ^c	(µmol CO₂ g _{DW} ⁻¹ min⁻¹) ^d		
1	0.94 ± 0.11	72.1 ± 10.05	1.63 ± 0.19		
2	0.78 ± 0.10	52.7 ± 6.91	1.34 ± 0.23		
3	0.71 ± 0.11	50.2 ± 8.39	1.27 ± 0.21		
4	0.42 ± 0.12	33.0 ± 10.62	0.81 ± 0.20		
		Respiration rate			
	(µmol CO₂ m⁻² s⁻¹)e	(nmol CO ₂ g _{FW⁻¹} min ⁻¹) ^f	(µmol CO₂ g _{DW} -1 min ⁻¹) ^g		
1	0.28 ± 0.07	21.7 ± 5.84	0.52 ± 0.14		
2	0.24 ± 0.08	15.2 ± 5.0	0.39 ± 0.11		
3	0.22 ± 0.05	15.2 ± 3.78	0.38 ± 0.09		
4	0.11 ± 0.03	7.8 ± 2.42	0.20 ± 0.05		

Table 4. Standard African violet leaf phenology: net photosynthesis rate \pm SEM and respiration rate \pm SEM for leaves in whorls 1 to 4^a.

^aN = 6 plants measured for each mean value per whorl. The photosynthetic photon flux density (PPFD) for photosynthesis measurements was 100 μ mol m⁻² s⁻¹, equivalent to the light intensity in the environmentally controlled culture chamber. Statistical t-test results for each column of data are as follows: ^b(t = 3.16, p = 0.01); ^c(t = 2.67, p = 0.02); ^d(t = 3.93, p = 0.003); ^e(t = 2.16, p = 0.06); ^f(t = 2.20, p = 0.052); ^g(t = 2.15, p = 0.057).

African violet plants was examined. As may be expected, the mini strain had thinner leaves and smaller leaf area than the standard strain. A search of the literature suggests that this is the first report of these comparative data for leaf morphology in African violets. However, there have been substantial studies of variations of leaf morphology related to experimental treatments such as growth substrate (Ghehsareh et al., 2023), effects of light spectral quality on leaf area and thickness (Ahamadi et al., 2023), and effects of adding UV light in the visual spectrum on leaf expansion (Akbarian et al., 2023), including modelling studies of growth (Faust and Heins, 1993; Streck, 2004).

Photophysiology and phenology

A careful review of the literature indicated that few prior research studies have examined the photosynthesis rate of African violets in relation to light intensity. However, Dewir et al. (2015) reported that pot-grown plantlets of African violets exhibited maximum net photosynthesis at a moderate light intensity of 70 µmol m⁻² s⁻¹ when compared with either a lower or higher intensity (35 and 100 µmol m⁻² s⁻¹, respectively). The results reported here with mature mini and standard strains of African violets showed net photosynthesis was highest at a light intensity of 100 µmol m⁻² s⁻¹ across a light intensity range of 10 to 100 µmol m⁻² s⁻¹, with a mean assimilation rate of c. 2.0 μ mol CO₂ g $_{DW}^{-1}$ min⁻¹ at the highest light intensity. Based on this evidence, the carbon assimilation rate, when illuminated with a light intensity of 100 µmol m⁻² s⁻¹ is c. 23 μ g of C g_{DW⁻¹} min⁻¹. During a photoperiod of 12 h illumination, assuming a steady rate of photosynthesis, the gain in carbon during the 12-h photoperiod would be 16.5 mg C per g dry weight of the leaf. In general, a careful search of the literature indicated that very little, if any, research has been done on the photophysiology of species in the Gesneriaceae family. Given their significance in the natural environment and their horticultural value, more research is warranted to elucidate the ecophysiology of this widely occurring family of plants.

Using leaf fluorescence analysis, Dewir et al. (2015) reported that Fv/Fm values in African violet plantlets varied inversely, with light intensity being highest $(Fv/F_m =$ 0.80) at a light intensity of 35 µmol m⁻² s⁻¹ and lowest (0.75) at light intensity of 100 µmol m⁻² s⁻¹. In the present study, Fv/Fm was examined for leaves of varying maturity when grown at a PPFD of 100 µmol m⁻² s⁻¹. The mean Fv/Fm values varied from 0.68 for older leaves in whorl 4 to 0.75 for young leaves in whorl 1. This value for young leaves (0.75) is close to a value of 0.80 reported by Dewir et al. (2015) for the young leaves of African violet plantlets. The mean net photosynthesis rate in the current study also decreased with increasing maturity of the leaves in the four whorls of standard African. For example, the net mean photosynthesis rate (µmol CO2 assimilated m⁻² s⁻¹) when assessed at a light intensity of 100 μ mol m⁻² s⁻¹ was 0.94 ± 0.11 for young leaves (whorl 1) and 0.42 ± 0.12 for older leaves (whorl 4). Prior research with a wide variety of angiosperms has shown a similar decline in photosynthesis rate with leaf age, including studies of wheat (Suzuki et al., 1987), grape vines (Kriedemann, 1988), conifer trees (Freeland, 1952), and tropical canopy trees (Kitajima et al., 1997). The

mean dark respiration rate in the current study was not significantly higher for whorl 1 compared to whorl 4 leaves, although there was a statistically significant difference in the photosynthesis rate (Table 4). In general, the results indicated that respiration rates were not significantly different for any of the leaf variables examined in this study. Thus, in general, respiration rate appeared to be less variable compared to photosynthesis rates for the experimental conditions used in this research.

Overall, the respiration rate is approximately 25 to 30% of the net photosynthesis rate. Based on prior experimental research and modelling studies of plants, some variation in the ratio of respiration to photosynthesis can be expected depending on the species, temperature of growth, and the state of plant growth (Atkin et al., 2006; Van Oijen et al., 2010). This metric (ratio of respiration to net photosynthesis) is important in estimating the carbon balance of the plants; that is, how much C is gained through photosynthesis relative to the amount of C lost through respiration, and has significance for estimating climate change related to atmospheric CO₂ concentrations (Heskel, 2018). It may be an important measure of African violet vitality in different locales in its natural habitat in Africa, where this species is incurring environmental stress or other threats to survival.

A thorough literature search revealed few prior research studies have reported the SLA for African violets. Ahamadi et al. (2023) published SLA data for African violet plants grown with different wavelengths of light, but they calculated the SLA based on units of cm² per g fresh weight rather than units of dry weight as most typically used. Akbarian et al. (2023) reported SLA values based on leaf dry weight when African violet plants were grown with illumination of varying wavelengths in combination with UV irradiation. They found SLA values in the range of 140 to 240. In the current study, the SLA values based on dry weight were 300 to 465 for standard African violet plants with a mean SLA of 360. Given substantial evidence that SLA is positively correlated with photosynthesis rate in a variety of angiosperms, especially when the photosynthesis rate is expressed per units of dry weight (Poorter and Evans, 1998; Reich et al., 1998), additional attention should be given to studying the effects of environmental variables on the SLA of African violet plants in the natural environment as well as in laboratory-based studies.

In the current research, the mean net photosynthesis rate was expressed in three ways: related to leaf area, per leaf fresh weight, and per leaf dry weight. The net photosynthesis rate expression per leaf area unit is a widely used metric. It is particularly useful in accounting for the physiological fate of solar energy absorbed in plant ecosystems because the amount of solar radiation absorbed per unit area of the environment can be quantitatively related to the amount of the incident radiation absorbed and utilized to drive CO₂ assimilation

by photosynthesis per leaf area (either for individual plants or for stands of plants). However, expression of photosynthesis rates per unit of weight, particularly dry weight, is particularly useful in ecosystem carbon budget analyses because the amount of energy consumed to support carbon uptake by primary production can be related quantitatively to the total carbon biomass of a given plant or stand of plants in an ecosystem. Furthermore, as explained earlier, the best estimates of the prediction of photosynthesis rates based on SLA are obtained when the photosynthesis rate is expressed per unit of leaf dry weight (Poorter and Evans, 1998). With increasing interest in conserving African violets in the natural environment, it may be particularly important to make measurements of photosynthesis and respiration in the natural environment based on units of dry weight in addition to measurements based on units of leaf area. This will permit a more accurate accounting of the amount of gain or loss in carbon by the total biomass of plants in a given stand or regional ecosystem. This may be especially useful where changing environmental conditions may place the African violet plants at risk for survival, and a more accurate accounting of their C gain and loss is of importance in assessing their vitality.

CONFLICT OF INTERESTS

The author has not declared any conflict of interests.

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