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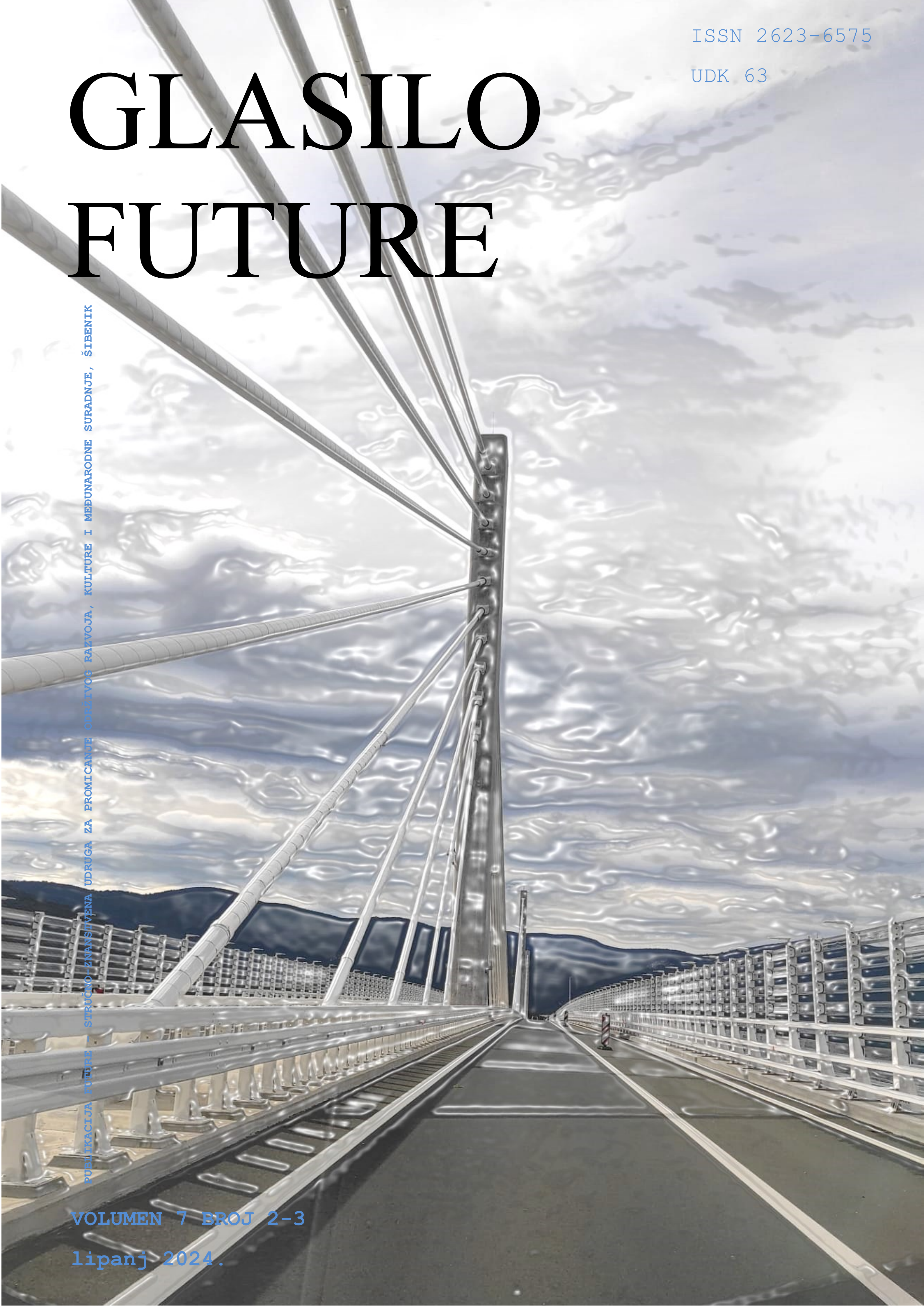

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SADRŽAJ:

Shading treatments affect the growth characteristics, ornamental value, and photosynthetic activities of various *Peperomia* species and cultivars

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Abstract

This study investigated the suitable shading levels for *Peperomia* species and cultivars, a genus within the Piperaceae family known for its ornamental value as an indoor plant. We examined the effects of four different shading levels (45, 60, 75, and 99 %) using polyethylene (PE) shading films on four *Peperomia* species and cultivars, namely: *P. obtusifolia* (L.) A.Dietr., *P. quadrangularis* (J.V.Thomps.) A.Dietr., *P. caperata* Yunck. 'Eden Rosso', and *P. caperata* 'Napoli Nights'. After an eight-week cultivation period, we assessed plant sizes, biomass (i.e. fresh and dry weight), leaf color, chlorophyll content (SPAD units), and five chlorophyll fluorescence parameters (F_v/F_m, Φ_{Do}, ABS/RC, DI_o/RC, and PI_{ABS}) in *Peperomia* species and cultivars. The results indicated that *P. obtusifolia* and 'Eden Rosso' exhibited the best growth performance within the 45-75 % shading range, whereas *P. quadrangularis* and 'Napoli Nights' showed optimal performance at the 45 and 60 % shading levels, respectively. All species and cultivars demonstrated reduced growth and biomass under the 99 % shading level, hypothesized to be due to restricted CO_2 assimilation under low-light conditions. Leaf color, measured by CIE76 color-difference (ΔE^*_{ab}) analysis based on the Commission Internationale de l'Eclairage Lab (CIELAB) color space, remained relatively constant across four different shading levels. Analyses of chlorophyll content and chlorophyll fluorescence revealed that high shading levels might deactivate some reaction centers, although the overall photosynthetic efficiency appeared largely unaffected. The performance index (PI_{ABS}) suggested that except for *P. quadrangularis*, which peaked at the 60 % shading level, *P. obtusifolia*, 'Eden Rosso', and 'Napoli Nights' generally performed well under the 45-75 % shading levels. Therefore, *Peperomia* plants are capable of tolerating broad shading conditions, except for excessively high shading (99 % shading level). These results indicate that providing suitable

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shading levels is effective in improving the growth and photosynthetic activity of those several *Peperomia* species and cultivars.

Key words: chlorophyll fluorescence, CIELAB, ornamental plants, *Peperomia*, shade tolerance.

Introduction

The genus *Peperomia*, a member of the Piperaceae family, is known to comprise around 1600 species (Samain et al., 2009). Genus *Peperomia* is recognized for its Crassulacean acid metabolism (CAM) plant and has resistance to drought stress (Herrera et al., 2000; Holthe et al., 1992). Exhibiting unique morphological characteristics across different species, most *Peperomia* species also have aesthetically appealing foliage, making them valuable as ornamental plants. These succulents or foliage plants are popular for indoor cultivation due to their ease of maintenance. The previous research has explored the use of *Peperomia* in bio-wall systems (Han and Shim, 2020), indoor introduction (Jeong et al., 2016), and in the reduce of particulate matter in the air (Paull et al., 2020), highlighting its versatility as an indoor and ornamental plant.

According to previous studies, *P. obtusifolia* is known to be rich in bioactive compounds (Ilyas et al., 2014; Mota et al., 2011; Tanaka et al., 1998), with several physiological studies available (Henny, 1985; Shen and Seeley, 1983; Woerner and Martin, 1999). Additionally, there have been reports of stem rot disease in *P. quadrangularis* (Han et al., 2014), and studies on the effects of temperature and photoperiod on flowering in *P. caperata* (Brøndum and Friis, 1990) as well as research on its propagation (Zaloga et al., 2005). However, further diverse physiological studies are necessary. The current number of physiological studies is still limited, and a broader understanding of the physiological characteristics of these species is essential for their effective cultivation and utilization. In addition to the physiological studies, various pharmacological studies have been conducted on *Peperomia*. It has been found to possess anti-cancer (Wei et al., 2011), antioxidant (Phongtongpasuk and Poadang, 2014), anti-diabetic (Hamzah et al., 2012), antipyretic (Khan et al., 2008), anti-inflammatory, and analgesic properties (De Fatima Arrigoni-Blank et al., 2004), and is known to produce various bioactive compounds (Alves et al., 2019; Gutierrez et al., 2016), confirming its utility. Moreover, it has been reported to produce a significant amount of phenolic compounds (Ho et al., 2022; Ware et al., 2022), raising expectations for its future use as an ingredient in health-promoting dietary supplements.

Previous studies on *Peperomia* have included cultivation under white LEDs with different color temperatures to enhance growth and external quality (Shin et al., 2023), and the effects of temperature and photoperiod (Brøndum and Friis, 1990). In another study on shading levels by Shen and Seeley (1983), two variegated *Peperomia* cultivars were used, but the levels of shading were not varied widely, being limited to two or three levels in each specific experiment. The purpose of shading cultivation is to protect plants from abiotic stress during the seedling or raising stage by creating artificial shading environments. These environments are usually formed using shade nets or shade films (Lee and Nam, 2022). Producing healthy plants is directly related to the income of farmers, hence the appropriate management of abiotic stress should be duly considered (Lee and Nam, 2023). Past research has reported that shading environments can protect plants from mechanical damage, heat stress, soil moisture loss, and photoinhibition (Nam et al., 2022; Semchenko et al., 2012). However, excessively high shading levels can negatively affect plant growth and physiological performance, necessitating research on appropriate shading levels for each species and cultivars (Lee and Nam, 2023). Continuous research has been conducted on shading cultivation to improve the growth and quality of ornamental plants (Lee et al., 2021; 2022; Park et al., 2023b). Shading cultivation can be widely applied to various plant species and used as an effective method to control abiotic stress.

The chlorophyll fluorescence analysis technique enables non-invasive assessment of plant stress levels and has been widely used to examine the link between chlorophyll fluorescence changes and plant physiological performance (Baker and Rosenqvist, 2004; Lechaudel et al., 2010; Serodio, 2004). Its effectiveness in evaluating plant physiological traits and stress responses, utilizing various fluorescence parameters, has been established in numerous studies (Jang et al., 2023; Oh et al., 2022; Shin et al., 2023). This study investigates the suitable shading levels for the cultivation of *Peperomia* by analyzing the growth characteristics and photosynthetic activity of four different species and cultivars (i.e. *P. obtusifolia* (L.) A.Dietr., *P. quadrangularis* (J.V.Thomps.) A.Dietr., *P. caperata* Yunck. 'Eden Rosso', and *P. caperata* 'Napoli Nights') used in this study.

Materials and methods

Selection of plant materials

In this study, *Peperomia obtusifolia* (L.) A.Dietr., *P. quadrangularis* (J.V.Thomps.) A.Dietr., *P. caperata* Yunck. 'Eden Rosso', and *P. caperata* 'Napoli Nights' were selected as experimental plants. Plants grown for six months were used, with an average height and width of 15 and 10 cm, respectively.

Treatments and experimental environment

The study was conducted over eight weeks, from May 4 to June 30, 2022, at the experimental greenhouse, Department of Environmental Horticulture of Sahmyook University, Seoul, Republic of Korea (37°38'40"N 127°06'25"E). Round plastic pots with diameters and heights of 11 × 10.5 cm were used, and plants were planted in the center of each pot. Fertilized horticultural substrate (Hanareumsangto, Shinsung Mineral, Republic of Korea) was used as the potting media. Using direct sunlight (0 %; 1960.9 ± 394.2 μmol m^{-2} s^{-1}) as the reference, shading levels were designed in four levels: within the greenhouse using one layer of clear polyethylene (PE) firm with greenhouse glass (45 %; 1083.21 ± 274.2 μmol m^{-2} s^{-1}), one layer of white PE firm with greenhouse glass (60 %; 731.4 ± 193.4

μmol m^{-2} s^{-1}), two layers of white PE firm with greenhouse glass (75 %; 472.8 ± 109.4 μmol m^{-2} s^{-1}), and one layer of black PE firm with greenhouse glass (99 %; 19.8 ± 5.4 μmol m^{-2} s^{-1}). The photosynthetic photon flux density (PPFD) at each relative shading level was measured weekly at 1 p.m. on clear days using a portable spectroradiometer (SpectraPen mini, Photon Systems Instruments, Czech Republic), and the results were represented in Table 1. The average temperature during the experiment was 21.5 ± 2.8 °C (Fig. 1A), relative humidity was 64.8 ± 14.6 % (Fig. 1B), and cloud cover index was 5.5 ± 2.7 (Fig. 1C). Irrigation was conducted three times a week until gravitational water drained.

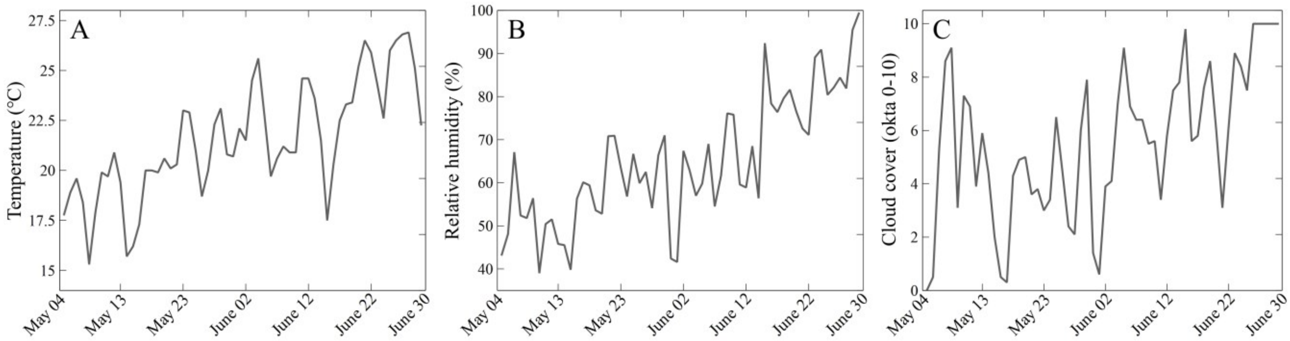

Figure 1. *Environmental conditions during the conduct of this study: A) temperature; B) relative humidity; C) cloud cover: 0 okta: sky clear; 1-2 okta: few clouds; 3-4 okta: scattered; 5-7 okta: broken; 8 okta: overcast; and 9 okta: sky obscured.*

Plant growth parameters and ornamental value

The types of growth parameters measured included shoot height, shoot width, root length, ground cover, fresh weight (FW), dry weight (DW), moisture content (MC), and Commission Internationale de l'Eclairage Lab (CIELAB) color space values (L^*, a^*, and b^*) and CIE76 color-difference (ΔE^*_{ab}). The moisture content was calculated using the following formula: MC = [(FW - DW) / FW] * 100. The measurement of CIELAB values (L^*, a^*, and b^*) followed the leaf color measurement method of Lee (2023), using a spectrophotometer (CM-2600d, Konica Minolta, Japan) set to CIELAB D65/10°, including specular component inclusion (SCI). Measurements were taken randomly from areas of the leaves not traversed by veins, with each measurement conducted ten times per treatment across three replicated. Subsequently, leaf colors were evaluated by converting the average values of CIELAB L^*, a^*, and b^* into converted colors using the Converting Colors designed by Zettl (2023). Additionally, to compare the effects of shading levels on color differences in *Peperomia* leaves, each shading level was set as a reference for calculating the color difference, using the following formula for ΔE^*_{ab} (CIE, 2004).

$$\Delta E^*_{ab} = \sqrt{(L^*_2 - L^*_1)^2 + (a^*_2 - a^*_1)^2 + (b^*_2 - b^*_1)^2}$$

(In this study, $\Delta E^*_{ab} \leq 1.5$ were considered 'no color difference' or 'subtle color difference', levels of 1.6-3.0 as 'very small color difference', 3.1-6.0 as 'small color difference', 6.1-9.0 as 'color difference', 9.1-12.0 as 'big color difference', and levels ≥12.1 as 'very big color difference' or 'completely different color').

Analysis of physiological activities

The chlorophyll content (SPAD units) and five fluorescence parameters (F_v/F_m, Φ_{Do}, ABS/RC, DI_o/RC, and PI_{ABS}) of *Peperomia* species and cultivars as affected by shading levels were analyzed. Chlorophyll content (SPAD units) was determined using a portable chlorophyll meter (SPAD-502, Konica Minolta, Japan), while chlorophyll fluorescence response was evaluated with a portable fluorometer (FluorPen FP 110/D, Photon Systems Instruments, Czech Republic). Measurements were taken from the central areas of fully expanded leaves, avoiding the veins. Each measurement was conducted ten times per repetition, randomly selecting leaves for each measurement, and this process was repeated three times. Before measuring the chlorophyll fluorescence parameters, plants were dark-adapted for approximately 15 minutes using dark-adaptation leaf-clips following the manufacturer's guidelines (PSI, 2023), and measurements were taken on the last day of the study. The five chlorophyll fluorescence parameters are as follows: F_v/F_m represents the maximum quantum yield of photosystem II (PSII), Φ_{Do} indicates the probability of absorbed photons being dissipated, ABS/RC signifies the absorption flux per reaction center, DI_o/RC denotes the amount of energy dissipated per reaction center, and PI_{ABS} indicates the performance index on an absorption basis. The parameters were calculated using the formulas provided by PSI (2023) and Stirbet and Govindjee (2011).

$$F_v \,/\, F_m = (F_m - F_o) \,/\, F_m$$

$$\Phi_{Do} = 1 - \Phi_{Po} = F_o \,/\, F_m$$

$$ABS \,/\, RC = M_o \cdot \left(1 \,/\, V_j\right) \cdot (1 \,/\, \Phi_{Po})$$

$$DI_o \,/\, RC = (ABS \,/\, RC) - (TR_o \,/\, RC)$$

$$PI_{ABS} = (RC \,/\, ABS) \cdot [\Phi_{Po} \,/\, (1 - \Phi_{Po})] \cdot [\Psi_o \,/\, (1 - \Psi_o)]$$

Statistical analysis

The experimental results were analyzed using ANOVA (analysis of variance) in SAS 9.4 (SAS Institute, USA). Comparisons between means were statistically analyzed using Duncan's multiple range test at a significance level of $p < 0.05$. The study was conducted in a completely randomized design, with three plants per replication and three replications per treatment.

Results and discussion

Analysis of growth characteristics

Peperomia species and cultivars, subjected to different shading levels, exhibited varying growth responses (Fig. 2 and Table 1). Results indicated that for *P. quadrangularis* (J.V.Thomps.) A.Dietr., shoot height was highest at the 60 % shading level, reaching 19.72 cm. The other remaining *Peperomia* species and cultivars showed the same significant level at the shading levels between 45-75 %, according to Duncan's multiple range test (DMRT). A previous study on *Orostachys malacophyllus*, a Crassulacean acid metabolism (CAM) species like *Peperomia*, indicated the highest shoot height and width at the 52 % shading level within the 52-97 % range of shading levels (Jeong et al., 2013). Similar trends were reported for *Delosperma cooperi* (Lee et al., 2022). In this study, for shoot width, *P. obtusifolia* (L.) A.Dietr. showed broader widths of 19.80-20.69 cm at the 45-60 % shading levels. *P. quadrangularis* and *P. caperata* Yunck. 'Eden Rosso' (hereafter 'Eden Rosso') exhibited the broadest widths of 30.90 and 21.10 cm at the 75 % shading level, respectively, indicating optimal shading levels vary for each species or cultivar to significantly increase shoot sizes. In previous studies, *O. iwarenge* for. *magnus* showed the widest shoot width at the 52 % shading level within the 52-97 % range (Jeong et al., 2012), and *Sedum zokuriense* showed the widest shoot width at the 65 % shading level (Lee et al., 2021). Meanwhile, it was observed that *Echeveria agavoides*, a type of ornamental succulent species, showed an increase in both shoot height and width as the shading level increased (Cabahug et al., 2017). For root length, *P. obtusifolia* was longer at the 45-60 % shading levels, measuring 16.20-17.32cm, while 'Eden Rosso' showed the longest root length of 14.03 cm at the 45 % shading level. According to Nam et al. (2022), *Hylotelephium telephium* 'Lajos' showed no significant shading effects on root length across 0-99 % shading levels, whereas *H. sieboldii* 'Mediovariegatum' exhibited significant root length reduction at the 99 % shading level, despite showing similar significant levels up to 75 % shading level. Additionally, Qi et al. (2019) reported a significant decrease in the root length of *Pinus koraiensis* at the 80 % shading level compared to direct sunlight, indicating that the impact of shading treatment on root length varies among species.

The ability of plants to alter their morphological characteristics in response to changes in the growth environment is known as phenotypic plasticity (Bradshaw, 1965; DeWitt et al., 1998; Sultan, 1987). Among such instances of phenotypic plasticity, the shade-induced phenotype enables plants to exhibit morphological traits suited to shading conditions (Weijschede et al., 2006). This shade-induced phenotype can lead to changes such as increased plant height, increased light-catching area like extension shoot width or ground cover, and larger leaf sizes (Lee and Nam, 2022), which can help mitigate the negative impacts on growth due to reduced light intensity in shading environments (Park et al., 2023b). Furthermore, the ground cover, showed that *P. obtusifolia* had a wider ground cover at the 45-60 % shading levels, measuring 392.3-427.4 cm^2, while *P. quadrangularis* and 'Eden Rosso' showed their widest at the 75 % shading level, with 987.1 and 450.8 cm^2, respectively. Previous research found that *Veronica pusanensis* had a significantly higher ground cover at the 35-45 % range of shading levels (Park et al., 2023b). Excessive shading levels beyond optimal shading levels can negatively affect plant growth and quality (Lee and Nam, 2023), as it can hinder carbon dioxide assimilation in chlorophyll and suppress plant growth, emphasizing the need to identify the appropriate shading levels for each species and cultivar.

Each species exhibits varying levels of shade tolerance. For example, species like *Veronica pusanensis*, which are native to coastal areas, appear to have lower shade tolerance compared to tropical forest-dwelling genus *Peperomia* (Forster, 1993; Park et al., 2023b; Shin et al., 2012). In terms of fresh weight, both *P. obtusifolia* and 'Eden Rosso' showed heaviest weights at shading levels between 45-75 % range. However, *P. quadrangularis* reached its heaviest weight of 84.1 g at the 45 % shading level, while *P. caperata* 'Napoli Nights' (hereafter 'Napoli Nights') peaked at 167.2 g at the 60 % shading level. Dry weight results are also similar to these trends, indicating varying preferred shading levels across species and cultivars. Previous studies reported a significant reduction in shoot and root biomass of *Pinus koraiensis* in shading environments (Qi et al., 2019), and *Codonopsis lanceolata* showed a significant increase in both fresh and dry weights of shoot and root parts at the 45 % shading level compared to direct sunlight, though showing similar levels to direct sunlight at the 75 % shading (Park et al., 2023a). However, *Phedimus takesimensis* 'Atlantis', a Crassulaceae cultivar, exhibited the highest fresh and dry weights of the shoot part at the 45 % shading level (Lee and Nam, 2022). In contrast to our findings, a study by Shen and Seeley (1983) reported that variegated cultivars of *P. obtusifolia* (i.e. 'Albo Marginata' and 'Variegata') showed the highest fresh and dry weights at the 20 % shading levels compared to 47 and 73 % shading levels. This discrepancy may be due to variegated plants requiring more light intensity than average due to chlorophyll deficiency. Regarding moisture content, *P. obtusifolia* and 'Napoli Nights' showed the highest values at the 99 % shading levels, reaching 94.1 and 95.3 % respectively, suggesting that under low-light conditions, some *Peperomia* species may experience cell elongation and thus higher moisture content.

Consequently, based on the results related to plant size, it is advisable to cultivate *P. obtusifolia* at the 45-60 % shading levels, while *P. quadrangularis* and 'Eden Rosso' are better suited to 75 % shading level. 'Napoli Nights' appears to be adaptable to any shading level. In terms of biomass analysis, it seems beneficial to grow *P. obtusifolia* and 'Eden Rosso' at the 45-75 % shading, and *P. quadrangularis* and 'Napoli Nights' at the 45 and 60 % shading, respectively.

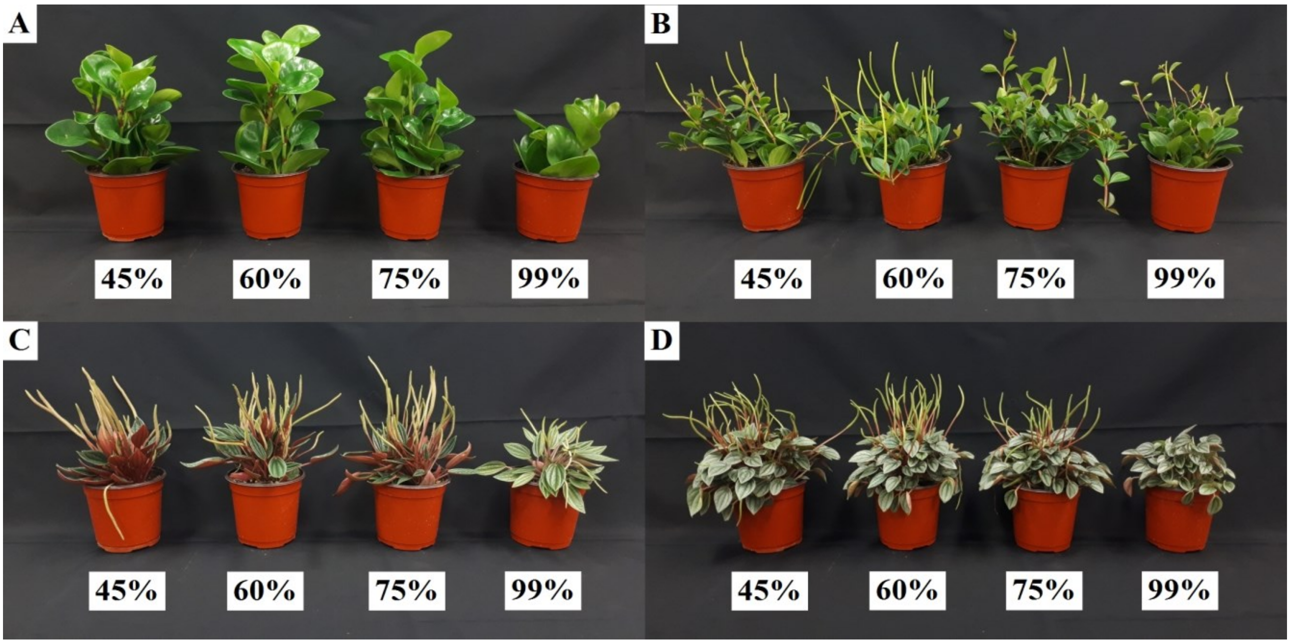

Figure 2. *Plants shape of Peperomia species or cultivars as affected by shading treatments for eight weeks: A) P. obtusifolia (L.) A.Dietr.; B) P. quadrangularis (J.V.Thomps.) A.Dietr.; C) P. caperata Yunck. 'Eden Rosso'; and D) P. caperata 'Napoli Nights'.*

Table 1. *Plant sizes, plant weight, and moisture content of Peperomia species and cultivars as affected by shading treatments for eight weeks.*

Plants	Shading levels (%)	Plant sizes (cm)			Ground cover (cm^2)	Plant weight (g)		Moisture content (%)
		Shoot height	Shoot width	Root length		Fresh weight	Dry weight	
Peperomia obtusifolia	45	19.98 a^z	20.69 a	17.32 a	427.4 a	191.6 a	15.92 a	91.7 b
	60	20.04 a	19.80 a	16.20 a	392.3 a	208.0 a	16.41 a	92.1 b
	75	22.71 a	19.14 ab	13.64 ab	368.2 ab	178.3 a	13.19 a	92.7 b
	99	13.41 b	16.88 b	8.81 b	285.0 b	96.2 b	5.61 b	94.1 a
P. quadrangularis	45	18.27 ab	27.53 ab	4.38 a	759.5 ab	84.1 a	7.96 a	90.1 a
	60	19.72 a	28.06 ab	4.40 a	791.5 ab	65.5 b	6.58 b	89.6 a
	75	17.20 ab	30.90 a	4.37 a	987.1 a	68.4 b	6.02 b	91.0 a
	99	15.24 b	20.96 b	4.56 a	442.4 b	63.0 b	5.89 b	90.5 a
P. caperata 'Eden Rosso'	45	17.82 a	17.75 b	14.03 a	312.2 b	68.2 a	2.78 a	95.8 a
	60	17.90 a	18.56 ab	12.16 ab	349.2 b	74.2 a	3.29 a	95.5 a
	75	18.85 a	21.10 a	12.54 ab	450.8 a	76.8 a	2.95 a	96.1 a
	99	11.91 b	19.50 ab	11.07 b	383.0 ab	38.0 b	1.32 b	96.4 a

P. caperata 'Napoli Nights'	45	16.86 a	18.79 a	16.31 a	354.2 a	149.1 ab	8.62 ab	94.1 b
	60	17.64 a	20.97 a	16.63 a	439.6 a	167.2 a	9.15 a	94.5 b
	75	17.70 a	21.02 a	14.54 a	442.9 a	123.9 b	6.99 b	94.3 b
	99	11.82 b	18.22 a	13.70 a	333.7 a	78.3 c	3.61 c	95.3 a
Significance[y]	Plants (A)	***	***	***	***	***	***	***
	Shading levels (B)	***	**	**	**	***	***	**
	(A) × (B)	NS	*	NS	*	**	**	NS

[z]Means separation within columns by Duncan's multiple range (DMRT) test at $p < 0.05$; same lowercase letters indicate no significant differences.
[y]NS, *, **, and ***: non-significant or significant at $p < 0.05$, 0.01, or 0.001, respectively.

Evaluation of ornamental value

Shading treatment was evaluated to have some minor effects on the leaf color of *Peperomia* species and cultivars used in this study (Table 2). Commission Internationale de l'Eclairage Lab (CIELAB) L^*, representing lightness, was highest for *P. quadrangularis* at the 60 % shading level with a value of 33.81. However, no statistically significant differences were observed in other remaining *Peperomia* species and cultivars. For CIELAB a^*, which indicates green-red colors, *P. quadrangularis* showed the highest value of -5.11 at the 75 % shading level, and 'Napoli Nights' had higher values of -3.26 and -3.02 at the 75 and 99 % shading levels, respectively, suggesting a tendency for leaf color to become redder under extremely low-light conditions. This result contradicts previous studies which showed an increase in a^* values under higher light level conditions (Lee et al., 2021; Park et al., 2023b). For CIELAB b^*, representing blue-yellow colors, *P. quadrangularis* and 'Napoli Nights' showed higher values at the 45-60 % shading range, whereas 'Eden Rosso' had higher values at the 45 and 99 % shading levels. Previous studies reported that *Veronica pusanensis* exhibited higher b^* values under direct sunlight compared to shading conditions (Park et al., 2023b). Generally, plants in unsuitable growth environments or under stress tend to show an increase in leaf lightness and a yellowing of leaf color (Lee et al., 2022). However, considering the results of L^* and b^* in this study, no consistent trend was observed across the *Peperomia* species and cultivars used in this study, suggesting that characteristics like thick leaf texture and leaf reflectivity of *Peperomia* may have influenced these results.

In the CIE76 color-difference (ΔE^*_{ab}) analysis to evaluate the color difference by shading levels, *P. obtusifolia* showed the highest ΔE^*_{ab} = 1.38 between 45 and 99 % shading levels, but this was assessed as 'no color difference'. On the other hand, *P. quadrangularis* and 'Napoli Nights' exhibited the most color difference with ΔE^*_{ab} = 2.84 and 2.91, respectively, between 60 and 75 % shading levels, which was evaluated as 'very small color difference'. Similarly, 'Eden Rosso' had the highest ΔE^*_{ab} = 2.70

between 45 and 75 % shading levels, but like *P. quadrangularis* and 'Napoli Nights', it was assessed as 'very small color difference', suggesting that the color difference in leaves due to shading levels is very minimal.

Based on the results of the leaf color qualities, it is concluded that shading treatment does not significantly impact the leaf color of *Peperomia* species and cultivars used in this study. Particularly, as the color differences (ΔE^*_{ab}) between treatments were not substantial, mostly rated as 'no color difference' or 'very small color difference', it seems that specifying a particular shading level for the purpose of modifying leaf color might not yield significantly meaningful results, unlike the findings of the analysis of growth characteristics.

Table 2. *Leaf color reading values of Commission Internationale de l'Eclairage Lab (CIELAB) values, converted color, and CIE76 color-difference (ΔE^*_{ab}) of Peperomia species and cultivars as affected by shading treatments for eight weeks.*

Plants	Shading levels (%)	CIELAB values			Converted color[z] (color chip)	CIE76 (ΔE^*_{ab}) by shading levels (%)			
		L^*	a^*	b^*		45	60	75	99
Peperomia obtusifolia	45	34.43 a[y]	-8.33 a	12.69 a		Reference	1.02	0.32	1.38
	60	34.74 a	-8.79 a	13.55 a		1.02	Reference	0.72	0.55
	75	34.55 a	-8.54 a	12.90 a		0.32	0.72	Reference	1.14
	99	34.71 a	-8.51 a	14.03 a		1.38	0.55	1.14	Reference
P. quadrangularis	45	32.95 ab	-5.86 b	9.14 a		Reference	1.06	1.97	1.38
	60	33.81 a	-6.20 b	9.66 a		1.06	Reference	2.84	2.40
	75	32.54 ab	-5.11 a	7.36 b		1.97	2.84	Reference	1.50
	99	31.79 b	-5.91 b	8.39 ab		1.38	2.40	1.50	Reference
P. caperata 'Eden Rosso'	45	33.49 a	-3.08 a	6.55 a		Reference	1.50	2.70	1.13
	60	32.60 a	-3.87 a	5.63 ab		1.50	Reference	1.46	0.88
	75	32.14 a	-3.66 a	4.26 b		2.70	1.46	Reference	2.31
	99	32.66 a	-3.86 a	6.51 a		1.13	0.88	2.31	Reference
P. caperata 'Napoli Nights'	45	39.81 a	-4.02 b	6.02 a		Reference	1.15	2.07	1.74
	60	40.96 a	-4.09 b	6.00 a		1.15	Reference	2.91	1.33
	75	38.59 a	-3.26 a	4.52 b		2.07	2.91	Reference	2.50
	99	40.99 a	-3.02 a	5.21 ab		1.74	1.33	2.50	Reference

Significance[x]	Plants (A)	***	***	***
	Shading levels (B)	NS	*	***
	(A) × (B)	NS	*	NS

[z]Colors converted using CIELAB L^*, a^*, and b^* values.
[y]Means separation within columns by DMRT at $p < 0.05$; same lowercase letters indicate no significant differences.
[x]NS, *, and ***: non-significant or significant at $p < 0.05$ or 0.001, respectively.

Chlorophyll Content and Chlorophyll Fluorescence

Peperomia species and cultivars affected by shading treatment showed varying results in chlorophyll content and chlorophyll fluorescence responses (Table 3). In terms of chlorophyll content (SPAD units), *P. obtusifolia* exhibited the highest value of 60.32 SPAD units at the 45 % shading level, while *P. quadrangularis* showed similar significance at shading levels between 45-75 % range. Meanwhile, 'Eden Rosso' and 'Napoli Nights' showed similar significance at the 60-75 % shading levels, indicating an increase in chlorophyll density per unit area at optimal shading levels. A previous study reported that *Phoebe bournei* had the highest chlorophyll content at the 78 % shading level (Tang et al., 2019), partly aligning with the findings of this study. Similarly, the 'Lane Late' cultivar of navel orange also exhibited the highest chlorophyll content at the 75 % shading level (Incesu et al., 2014). On the other hand, F_v/F_m, representing the maximum quantum yield of photosystem II (PSII), is known to be between 0.78-0.84 in higher plants not under stress (Asadi-Sanam et al., 2015; Björkman and Demmig, 1987; Ventura Zapata et al., 2023). In this study, F_v/F_m values ranged between 0.78-0.83, suggesting that the photosynthetic apparatus of all *Peperomia* species and cultivars was at a normal operational level regardless of shading levels. *P. obtusifolia* and *P. quadrangularis* showed the highest F_v/F_m values of 0.82 and 0.80, respectively, at the 60 % shading level, while 'Eden Rosso' exhibited the highest at 0.83 at the 75 % shading level. 'Napoli Nights' showed similar significance at the 45-75 % range of shading levels. Φ_{Do}, which is antagonistic to F_v/F_m and indicates the probability of absorbed photons being dissipated, was highest at the 99 % shading level for *P. obtusifolia*, 'Eden Rosso', and 'Napoli Nights'. However, *P. quadrangularis* exhibited the highest Φ_{Do} value of 0.21 at the 45% shading level, which represents the highest light intensity in the study. This suggests that the photosynthetic apparatus activity may decrease at elevated light levels in certain species. Although a value of 0.21 does not significantly deviate from the normal range, it is statistically higher compared to other species examined. This result suggests potential photoinhibition, likely due to a reduced rate of PSII photochemistry resulting from damage to the PSII reaction centers and/or an increased rate of non-radiative dissipation of excitation energy.

ABS/RC, representing absorption flux per reaction center, and DI_o/RC, denoting dissipated energy flux per reaction center, showed similar results to Φ_{Do}. *P. obtusifolia*, 'Eden Rosso', and 'Napoli Nights' exhibited the highest values at the 99 % shading level, while *P. quadrangularis* showed high values at the 45 and 75 % shading levels. This suggests that in *P. obtusifolia*, 'Eden Rosso', and 'Napoli Nights', some reaction centers may have been deactivated due to prolonged extremely low-light conditions over about eight weeks. Conversely, *P. quadrangularis* appears to have a reduced activity of reaction centers and stress responses at higher light conditions compared to low-light conditions. Meanwhile, PI_{ABS} is a performance index based on an absorption basis (Srivastava et al., 1999). PI_{ABS} showed similar significance at the 45-75 % shading levels for all but *P. quadrangularis*, which had the highest value of 8.52 at the 60 % shading level.

In summary, from the chlorophyll content and chlorophyll fluorescence responses analysis, the maximum quantum yield of *Peperomia* species and cultivars used in this study, regardless of shading level, is assessed to be unstressed. However, other parameters such as ABS/RC and DI_o/RC indicate that some reaction centers may have become inactive at the 99 % shading level. Nevertheless, based on the results for maximum quantum yield, it is expected that the activity level of the photosynthetic apparatus would rapidly recover with a substantial increase in light intensity. The performance index (PI_{ABS}) for *Peperomia* species and cultivars, except for *P. quadrangularis*, which was highest at the 60 % shading level, is assessed to be similar at the 45-75 % shading levels, suggesting that they can exhibit a favorable performance index within a relatively wide range of shading levels, as long as the shading level is not too high.

Table 3. *Chlorophyll content and five chlorophyll fluorescence parameters (F_v/F_m, Φ_{Do}, ABS/RC, DI_o/RC, and PI_{ABS}) of Peperomia species and cultivars as affected by shading treatments for eight weeks.*

Plants	Shading levels (%)	Chlorophyll content (SPAD units)	Chlorophyll fluorescence parameters				
			F_v/F_m	Φ_{Do}	ABS/RC	DI_o/RC	PI_{ABS}
Peperomia obtusifolia	45	60.32 a[z]	0.81 b	0.18 b	1.03 c	0.18 b	8.59 a
	60	53.64 ab	0.82 a	0.17 c	1.09 bc	0.18 b	9.04 a
	75	54.60 ab	0.81 b	0.18 b	1.16 b	0.21 b	8.00 a
	99	51.95 b	0.79 c	0.20 a	1.47 a	0.29 a	4.86 b
P. quadrangularis	45	62.72 a	0.78 b	0.21 a	1.39 a	0.29 a	6.41 b
	60	64.98 a	0.80 a	0.19 b	1.23 b	0.24 b	8.52 a
	75	65.48 a	0.79 ab	0.20 ab	1.38 a	0.28 a	6.95 b
	99	57.43 b	0.79 ab	0.20 ab	1.30 ab	0.26 ab	6.75 b

P. caperata 'Eden Rosso'	45	44.21 ab	0.80 c	0.19 b	1.28 b	0.24 b	8.27 a
	60	48.16 a	0.82 b	0.17 c	1.19 b	0.21 bc	9.22 a
	75	51.12 a	0.83 a	0.16 d	1.21 b	0.20 c	10.13 a
	99	36.99 b	0.79 d	0.20 a	1.75 a	0.35 a	4.93 b
P. capearata 'Napoli Nights'	45	55.98 b	0.81 a	0.18 b	1.10 c	0.20 b	11.59 a
	60	62.23 a	0.82 a	0.17 b	1.14 bc	0.19 b	11.56 a
	75	61.39 a	0.82 a	0.17 b	1.31 b	0.23 b	9.90 a
	99	52.08 c	0.79 b	0.20 a	1.87 a	0.38 a	5.57 b
Significance[y]	Plants (A)	***	***	***	***	***	***
	Shading levels (B)	***	***	***	***	***	***
	(A) × (B)	NS	***	***	***	***	***

[z]Means separation within columns by DMRT at $p < 0.05$.
[y]NS and ***: non-significant or significant at $p < 0.001$.

Conclusion

The genus *Peperomia*, belonging to the Piperaceae family, is commonly used as an indoor ornamental plant. While there have been various studies on the use of *Peperomia* as indoor ornamental plants, research on optimal growing conditions has been limited. Therefore, this study established four different shading levels using polyethylene (PE) shading films: 45, 60, 75, and 99 %. The experimental plants selected were *P. obtusifolia* (L.) A.Dietr., *P. quadrangularis* (J.V.Thomps.) A.Dietr., *P. caperata* Yunck. 'Eden Rosso', and *P. caperata* 'Napoli Nights'. Based on the results regarding plant sizes, it is advisable to cultivate *P. obtusifolia* at the 45-60 % shading levels, *P. quadrangularis* and 'Eden Rosso' at the 75 % shading level, and 'Napoli Nights' can be grown regardless of shading level. In terms of biomass analysis, *P. obtusifolia* and 'Eden Rosso' are better off at the 45-75 % shading levels, and *P. quadrangularis* and 'Napoli Nights' at the 45 and 60 % shading levels, respectively. Most *Peperomia* species and cultivars used in this study showed significantly lower plant sizes and biomass at the 99 % shading level, presumably due to limited carbon dioxide assimilation in extremely low-light conditions over the 8-week period. From the leaf color qualities, shading treatment was evaluated to have only minor effects on the leaf color of *Peperomia*. Particularly, the color difference analysis using CIE76 color-difference (ΔE^*_{ab}), which is based on the Commission Internationale de l'Eclairage Lab (CIELAB) color space, showed values ranging from 0.32 to 2.91 across all *Peperomia* species and cultivars, and shading levels, rated as 'no color difference' or 'very small color difference', indicating minimal differences in leaf color due to shading levels. Thus, unlike the results of the plant growth characteristics, setting specific shading levels for leaf color control may not yield significantly meaningful outcomes. Combining the results of chlorophyll content (SPAD units) and chlorophyll fluorescence responses, the maximum quantum yield (F_v/F_m) of *Peperomia*, regardless of the species and cultivars, or shading levels, is assessed to be relatively robust. However, based on the parameters ABS/RC and DI_o/RC, some reaction centers appear to be inactive at the 99 % shading level. Still, judging from the results for maximum quantum yield, it is expected that the activity level of the photosynthetic apparatus would quickly recover with a significant improvement in light intensity. The performance index (PI_{ABS}) for *Peperomia* species and cultivars, except for *P. quadrangularis* which was highest at the 60 % shading level, is assessed to be similar up to the 45-75 % shading levels, suggesting that they can exhibit a favorable performance index within a relatively wide range of shading levels, as long as the shading is not excessively high. These results indicate that providing suitable shading levels is effective in improving the growth and photosynthetic activity of those several *Peperomia* species and cultivars.

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