

PHYSIOLOGICAL DIFFERENCES OF GREEN-LEAF AND VARIEGATED - LEAF IVY (*HEDERA HELIX* L.) CULTIVARS

TING ZHANG^{1*} AND YANRU FU¹

*Shanghai Engineering Research Center of Sustainable Plant Innovation,
Shanghai, 200231, China*

Keywords: Green-leaf, Variegated-leaf, Ivy, Chlorophyll contents, Chlorophyll fluorescence, Light adaptation range, Light tolerance, Photosynthesis

Abstract

To screen sun-resistant cultivars of ivy for the three-dimensional greening of urban roofs and balconies, the chlorophyll content, photosynthetic response index, and chlorophyll fluorescence parameters of 5 green-leaf and 5 variegated leaf cultivars of ivy were measured, and compared the photosynthetic characteristics of different cultivars. Results showed that ivy seedlings were very shade tolerant. The photosynthetic adaptation range, maximum net photosynthetic rate, and electron transfer efficiency of the PSII reaction center of the green-leaf ivy cultivars were significantly higher than those of the variegated ivy cultivars. The photochemical conversion efficiency and photosynthetic capacity of *Hedera helix* 'Shamrock' were higher than those of the other tested green-leaf cultivars, suggesting that *Hedera helix* 'Shamrock' had a strong light tolerance. The differences in photosynthetic characteristics among the variegated cultivars were greater than those within the green-leaf cultivars. Among the tested cultivars, *Hedera helix* 'Mini Kolibri' had a relatively high light adaptation range and high light efficiency potential.

Introduction

Ivy is a kind of evergreen vine of *Hedera* belonging to Acanthaceae. Ivy cultivars show significant differences in leaf color and shape. There are more than 600 cultivars of ivy recorded worldwide; most are distributed in Europe, and a small number of cultivars are found in Asia (Hugh *et al.* 2017). This plant is widely used in three-dimensional urban landscapes and indoor greening, and it can bring ecological benefits such as cooling and humidification. Although ivy cultivars are abundant, there are no more than ten common cultivars used for urban greening in China. A large number of ivy cultivars with different leaf colors and leaf shapes have not been developed and applied. This is mainly due to the intense light on terraces and rooves of urban vertical greening, as ivy is a shade-tolerant plant with leaves that are prone to wither and scorch under direct sunlight. Therefore, this study can provide a theoretical reference for selecting excellent ivy cultivars for three-dimensional greening in different lighting environments and provide the basis for the cultivation and configuration of ivy.

Some researchers have been carried out to study the photosynthetic physiological characteristics of ivy. Yeh and Hsu (2004) found that four ivy cultivars showed different growth and photosynthetic responses to the same light intensity. The light compensation points of Ingelise and Mini Adam were lower than those of Dark Pittsburgh and Evergreen. In a specific light intensity range 1.7-7.2 MJ/(m²·d), the internode length and leaf area of Ingelise, Dark Pittsburgh, and Evergreen decreased linearly with increasing light intensity, while the leaf thickness increased linearly. Zhang *et al.* (2022) mentioned that the decrease of the maximum quantum yield of

*Author for correspondence: <zhangting@shbg.org>. ¹Shanghai Botanical Garden, Shanghai 200231, China

photosystem II (Fv/Fm) in heat-sensitive ivy variety *Hedera helix* 'Shamrock' was more severe than that in heat-tolerant ivy variety *Hedera helix* 'Jessica'. Svoboda *et al.* (2005) compared the growth of three English ivy cultivars under three photosynthetic photon flux (PPF) treatments, corresponding to an average daily PPF of 3.2, 5.4 or 8.5 mol/(m²·d), and four fertilizer concentrations (0, 100, 200, or 300 mg/1 N) normally used in production. Results showed that 100 mg/1 N and 8.5 mol/(m²·d) were the most conducive to plant growth, and dry weight increased the most. Gold Dust, Gold Heart, and Goldchild grew the best under conditions of low light and low fertilizer use. The variegation proportion of Gold Heart under light levels lower than 8.5 mol/(m²·d) was less than that under 3.2 or 5.4 mol/(m²·d). Zhang *et al.* (2016) found a significant negative correlation between PSI activity and PSII activity of ivy leaves across daily and annual cycles. PSI decreased and PSII increased from summer to winter. Moreover, the PSI activity of ivy was not easily affected by temperature and could be active throughout the year, especially in winter.

In addition to ivy, some researchers found differences in photosynthetic response and growth caused by plant leaf color in another shade-loving foliage plant, coleus. Katherine *et al.* (2010) mentioned that the increase in leaf area was positively correlated with the intensity of sunlight. Under low light conditions, the coleus leaves are more likely to appear green, while under high light conditions, the leaf color is more likely to appear variegated. The levels of chlorophylls in plant leaf can indicate the tolerance to various stresses (Luo *et al.* 2019). Similar studies on the differences in the photosynthetic response between variegated leaves and pure leaves also occurred in Begonia and Chrysanthemum (Chang *et al.* 2013, Wang *et al.* 2019).

In the present study, the chlorophyll content, photosynthetic characteristics, and chlorophyll fluorescence characteristics of five green-leaf ivy cultivars and five variegated ivy cultivars were studied. The light adaptation range and light energy utilization ability of different cultivars were compared to provide a basis for screening and cultivating excellent ivy cultivars and promoting their application.

Materials and Methods

The experiment was conducted in the research nursery of Shanghai Botanical Garden (SBG) from July to September 2018. The plants were grown under 60% shading (light intensity of about 4000 lx). The annual average temperature is 18.5°C, and the average temperature from July to August is 28.7 °C. During the experiment, to avoid drought stress, supplemental water was added to maintain moisture.

Ten 2-year-old potted seedlings from cuttings of different cultivars of ivy were selected as experimental materials. The characteristics of the five green-leaf cultivars and five variegated cultivars are presented shown in Table 1 and Fig. 1. Each cultivar was planted in three pots; two robust and growing mature leaves were selected from each pot, and each leaf was recorded three times.

Fresh leaves were collected from each pot of ivy. After vein removal, 0.1 g was cut and weighed as the measurement sample. The determination of chlorophyll content was done (Hiscox *et al.* 1979), in which ethanol and acetone were mixed in a ratio of 1:2 (V:V) as the extraction solution.

A Li-6400 portable photosynthesis instrument (LI-COR Inc., Lincoln, USA) was used to measure the photosynthetic indexes of different ivy cultivars. The light response was measured at 9:00-11:30 a.m. on a sunny day. The gradient of photosynthetic photon flux density (PPFD) was set as 0, 20, 50, 80, 100, 150, 200, 400, 800, 1000, 1200, 1400, 1600, 1800 and 2000 μmol/(m²·s). The temperature of the leaf chamber was set at 28 °C, and the concentration of carbon dioxide was

set at 400 $\mu\text{mol/mol}$. The instantaneous net photosynthetic rate (P_n) was recorded. The diurnal process was measured every two hours in clear and cloudless weather from 7:00 to 17:00 using a natural light source and the normal carbon dioxide concentration in the air (Barman *et al.* 2008).

Table 1. Phenotypes of 10 ivy cultivars.

Leaf color	Variety name	Variety phenotype
Green	<i>Hedera helix</i> 'Gitte'	Dark green and glossy leaves with three ovate lobes.
	<i>Hedera helix</i> 'Jessica'	Dark green and shovel-like leaves. Stem or petiole green purple.
	<i>Hedera heibernica</i> 'Sark'	Dark green and glossy heart-shaped leaves.
	<i>Hedera helix</i> 'Shamrock'	Dark green leaves with three ovate lobes (occasionally five). Sometimes overlapping lateral and terminal leaves.
	<i>Hedera helix</i> 'Teardrop'	Dark green leaves similar to a teardrop with obvious veins.
Variegated	<i>Hedera helix</i> 'Ester'	Glossy leaves with a dark green and grayish-green center and milky yellow margin. Petiole purplish red.
	<i>Hedera helix</i> 'Goldchild'	Variegated leaves with dark green or bright green center, and milky white and yellow edge. Greenish purple.
	<i>Hedera helix</i> 'Mini kolibri'	Generally green leaves with a milky white or light green splash. Petiole purplish red.
	<i>Hedera helix</i> 'White wonder'	Glossy leaves with dark green and grayish green in the center, yellow or milky white in the margin.
	<i>Hedera helix</i> 'Yellow ripple'	Fan-shaped and glossy leaf with green center and yellow margin. Greenish purple.

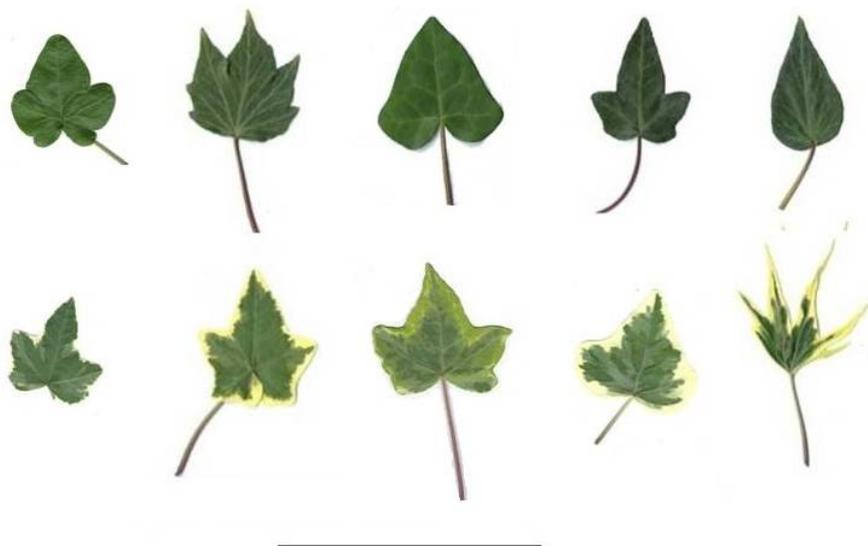


Fig. 1. Leaf morphology of 10 ivy Cultivars. The top row from left to right is Gitte, Jessica, Sark, Shamrock, and Teardrop; the bottom row from left to right is Ester, Goldchild, Mini Kolibri, White Wonder, and Yellow Ripple. The length of the ruler is 10 cm.

The chlorophyll fluorescence parameters of leaves were measured by the chlorophyll fluorescence chamber of an Li-6400 portable photosynthetic apparatus. The measurement was carried out from 9:00 to 11:00 a.m. The initial fluorescence (F_o) of PSII was measured after dark adaptation for one hour. The maximum photochemical quantum yield (F_v/F_m) and maximum fluorescence (F_m) of PSII were determined by saturation at $6000\mu\text{mol}/(\text{m}^2\cdot\text{s})$ for 0.8 s. Then, the tested plants were activated for 30 min under a $400\mu\text{mol}/(\text{m}^2\cdot\text{s})$ halogen lamp, and the stable fluorescence yield F_s , the maximum fluorescence value F_m' , the minimum fluorescence value F_o' , and the effective photochemical quantum yield F_v'/F_m' were determined. The Li-6400 can automatically calculate the photochemical quenching coefficient (qP), nonphotochemical quenching coefficient (NPQ) and optical quantum yield (ΦPSII).

Excel 2010 was used to process the data and draw charts. The nonrectangular hyperbolic model was used to fit the light response curve of the sample and was determined using SPSS 17.0 (SPSS Inc., Chicago, IL, USA). The light saturation point (LSP), light compensation point (LCP), maximum photosynthetic rate (A_{max}), apparent quantum yield (AQY) and dark respiration rate (R_{day}) of each ivy variety were calculated by linear regression within the range of $0\text{-}200\mu\text{mol}/(\text{m}^2\cdot\text{s})$.

Results and Discussion

There were no significant differences in the chlorophyll b content or the ratio of the chlorophyll a content to the chlorophyll b content among the 10 ivy cultivars, but the differences in the chlorophyll a content and total chlorophyll content among the ten ivy cultivars were highly significant ($p < 0.01$). LCP, LSP, A_{max} , and AQY among the cultivars were extremely highly different ($p < 0.01$), and R_{day} was significantly different ($p < 0.05$). There was no significant difference in NPQ among the cultivars, but there was a significant difference in F_o , F_m , F_v/F_m , qP , and ΦPSII ($p < 0.01$) (Table 2).

According to the leaf color, the ten kinds of ivy were divided into two groups: the green group and the variegated group. Comparing the two groups, only the content of chlorophyll a was significantly different among the different cultivars in the green group. In addition to the ratio of chlorophyll a/chlorophyll b, the total chlorophyll content of different cultivars in the variegated group was significantly different ($p < 0.05$), and the chlorophyll a content and chlorophyll b content were highly different ($p < 0.01$). The average total chlorophyll content in the green group was 1.99 mg/g (FW), which was 24.4% higher than that in the variegated group.

The total chlorophyll content of different cultivars of ivy from high to low is shown in Fig. 2. Jessica (green group) had the highest total chlorophyll content, followed by Goldchild (variegated group) and Teardrop (green group). The total chlorophyll content in the leaves of Ester was the lowest.

The diurnal dynamics of photosynthesis in 10 ivy cultivars showed a bimodal pattern, and the bimodal pattern of the variegated group was more apparent. The difference in the net photosynthetic rate among the different cultivars in the variegated group was more significant. In the green-leaf group (Fig. 3), the net photosynthetic rate reached a peak at approximately 9:00 a.m., decreased from 11:00 to 13:00, and showed a small peak again at 13:00 or 15:00, but the afternoon peak was smaller than the 9:00 peak. The variegated group entered dormancy at approximately 13:00 with a significantly decreasing photosynthetic rate and then reached a second peak at approximately 15:00 (Fig. 4). The peaks of Shamrock and Teardrop appeared at approximately 13:00, which was earlier than that of the other cultivars at 15:00, and the morning peak was higher than that in the afternoon. The diurnal variation range of P_n varied from 1.34 to $4.24\mu\text{mol}/(\text{m}^2\cdot\text{s})$.

Table 2. Differences in the physiological parameters of ivy leaves between the green and variegated group.

	Leaf color	Sum of squares	Mean square	F	Significance
Chlorophyll a	Green	0.637	0.159	4.039	0.033
	Variegated	0.921	0.230	24.712	0.000
Chlorophyll b	Green	0.048	0.012	1.078	0.418
	Variegated	0.133	0.033	19.964	0.000
Chlorophyll a/ Chlorophyll b	Green	0.231	0.058	1.225	0.360
	Variegated	0.091	0.023	2.118	0.153
Total chlorophyll	Green	1.029	0.257	2.871	0.080
	Variegated	1.748	0.437	24.226	0.000
LCP	Green	221.405	55.351	29.783	0.000
	Variegated	19.945	4.986	1.373	0.311
LSP	Green	12376.444	3094.111	8.214	0.003
	Variegated	8150.338	2037.584	10.458	0.001
A _{max}	Green	8.120	2.030	2.549	0.105
	Variegated	7.618	1.905	9.804	0.002
AQE	Green	0.000	0.000	2.854	0.081
	Variegated	0.000	0.000	25.049	0.000
R _{day}	Green	0.096	0.024	8.559	0.003
	Variegated	0.058	0.014	11.169	0.001
Fo	Green	4525.895	1131.474	5.864	0.011
	Variegated	4974.686	1243.672	6.190	0.009
Fm	Green	9174.880	2293.720	0.586	0.680
	Variegated	118882.822	29720.705	11.174	0.001
Fv/Fm	Green	0.006	0.001	8.391	0.003
	Variegated	0.003	0.001	7.851	0.004
qP	Green	0.027	0.007	5.049	0.017
	Variegated	0.013	0.003	8.978	0.002
PhiPSII	Green	0.072	0.018	2.848	0.082
	Variegated	0.074	0.019	7.149	0.005
NPQ	Green	2.623	0.656	6.665	0.007
	Variegated	0.828	0.207	2.032	0.166

The shape of the light response curve of different ivy cultivars was generally consistent (Fig. 5). In the lower range of light intensity 0-200 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$, Pn increased significantly with increasing light intensity. When the light intensity reached a certain range 200-400 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$, Pn increased significantly. When the light intensity exceeded a certain degree 400-2000 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$, the Pn value was almost unchanged and remained saturated. The characteristic photosynthetic parameters of the 10 kinds of ivy were significantly different ($p < 0.05$) (Table 3).

The average maximum net photosynthetic rate of the green group was higher than that of the variegated group. In the green group, Jessica had the highest net photosynthetic rate, followed by Teardrop. When the photosynthesis of each ivy variety reached the saturation level, the order of the Pn value from high to low was Jessica > Teardrop > Shamrock > Goldchild > Gitte > Yellow Ripple > Sark > White Wonder > Mini Kolibri > Ester.

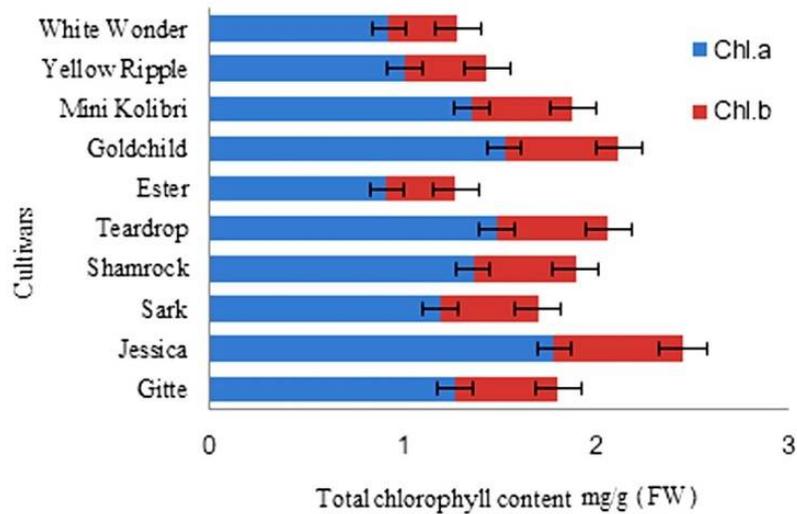


Fig. 2. Chlorophyll a and chlorophyll b contents in leaves of ten ivy cultivars. Different letters indicate the significance of differences between cultivars ($p < 0.05$).

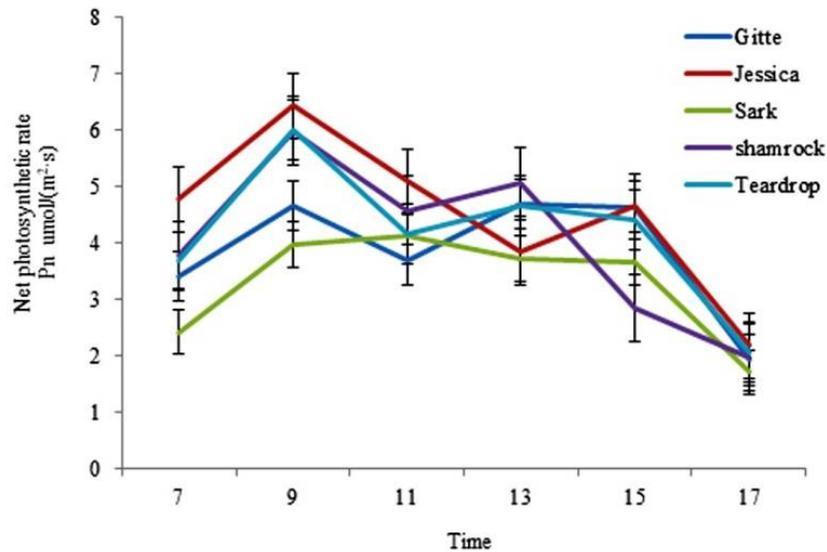


Fig. 3. Diurnal variation curve of the net photosynthetic rate for 5 green ivy cultivars.

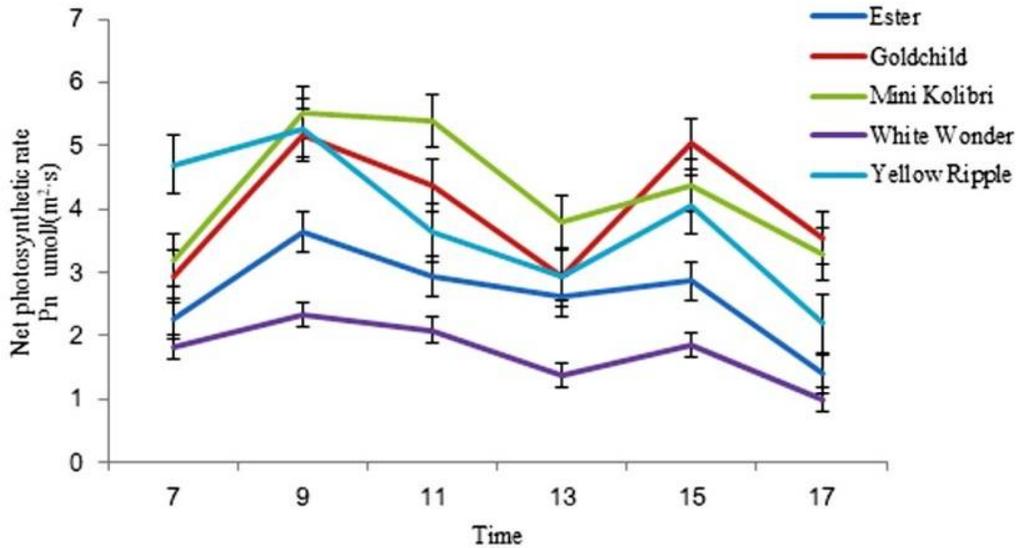


Fig. 4. Diurnal variation curve of the net photosynthetic rate for 5 variegated ivy cultivars.

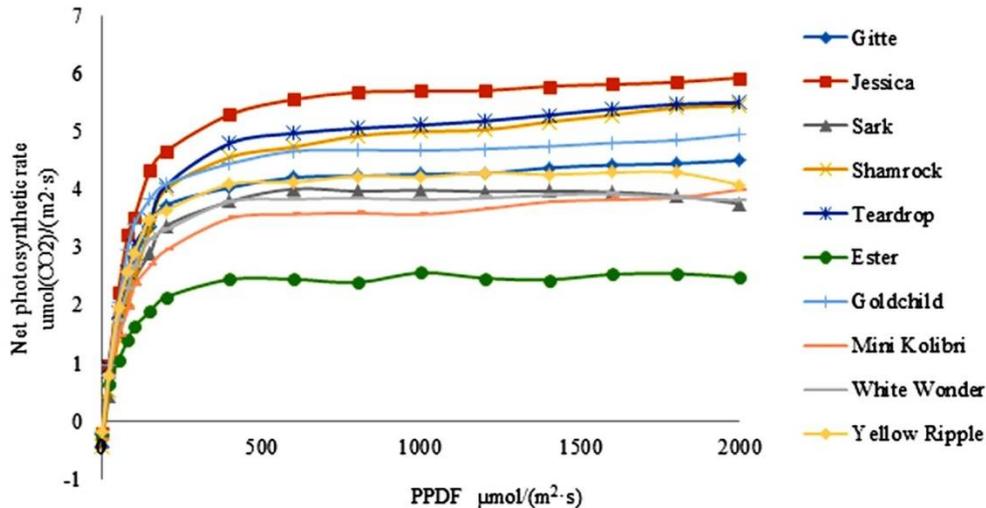


Fig. 5. Light responses curve of 10 ivy cultivars.

There were some differences in the light adaptation ranges of different cultivars, mainly due to the differences in LSP (Table 3). The results showed that the LCP of the tested cultivars was primarily concentrated at 6-16 μmol/(m²·s); Gitte was the lowest, and Shamrock was the highest. LSP was mainly concentrated at 170-262 μmol/(m²·s) among the different cultivars, and the difference was significant. The LSP of Shamrock was significantly higher than that of the other cultivars, followed by White Wonder and Teardrop. The seedlings of the 10 ivy cultivars are excessively shade-tolerant plants, and Shamrock has the widest light adaptation range.

Table 3. Physiological parameters of 10 ivy cultivars.

Cultivars	LCP	LSP	A _{MAX}	AQY	R _{DAY}
	μmol/(m ² ·s)	μmol/(m ² ·s)	μmol(co2)/(m ² ·s)	mol/mol	umol/m ²
Gitte	6.390±0.22a	204.763±20.39bc	5.983±0.82def	0.031±0.007cde	0.195±0.042ab
Jessica	6.677±1.09ab	192.691±24.21ab	6.805±1.09f	0.037±0.001e	0.243±0.034abc
Sark	13.858±1.89c	177.384±26.31ab	4.584±1.05bc	0.028±0.004bcd	0.385±0.051e
Shamrock	16.087±1.42d	262.246±13.64d	6.005±0.98def	0.025±0.005bc	0.391±0.060e
Teardrop	11.010±1.56c	206.291±1.75bc	6.279±0.28ef	0.032±0.002de	0.356±0.071de
Ester	12.524±1.93c	161.775±20.06a	3.237±0.32a	0.022±0.001ab	0.272±0.037bc
Goldchild	11.563±0.89c	170.640±2.36a	5.129±0.27cde	0.032±0.001de	0.372±0.029e
Mini kolibri	12.356±3.06c	192.735±15.34ab	4.271±0.64abc	0.024±0.001bc	0.289±0.058cd
White wonder	10.732±0.22bc	225.706±20.39c	3.562±0.82ab	0.017±0.007a	0.177±0.042a
Yellow ripple	9.392±1.72abc	168.880±4.75a	4.782±0.55bcd	0.030±0.004cde	0.278±0.027cd

LCP = Light compensation point, LSP = Light saturation point, A_{max} = Maximum net photosynthetic rate, AQY= Apparent quantum yield, R_{day} = Dark breathing rate.

The differences in A_{max} were obvious among the different cultivars, and the order from high to low was Jessica > Teardrop > Shamrock > Gitte > Goldchild > Yellow Ripple > Sark > Mini Kolibri > White Wonder > Ester, with Jessica ranking the highest, 110.2% higher than Ester, which ranked the lowest. In terms of the AQY index, all cultivars were concentrated in the range of 0.017-0.037 mol/mol. Additionally, the difference in R_{day} among the different cultivars was significant; Shamrock was the highest, and White wonder was the lowest. There was no significant difference in LCP, AQY, or R_{day} between the two groups of ivy cultivars, but there was a significant difference in LSP and A_{max}.

Results for the chlorophyll fluorescence parameters in the two groups of ivy (Table 4) showed that the Fo distribution of 10 ivy species was 157-232, and the difference was significant ($p < 0.05$); Jessica was the highest, the second was Teardrop, and Yellow Ripple was the lowest. The mean Fo of the green group was higher than that of the variegated group, and there was a significant difference between the two groups ($p < 0.05$). Fm reflects the electron transmission of PSII. The Fm of the five cultivars in the green group was higher than that of any variety in the variegated group. There was a significant difference in the Fm between the two groups ($p < 0.01$), among which Teardrop was the highest in the green leaf group, and Yellow Ripple was the lowest in the variegated group. The Fv/Fm of the leaves of the 10 ivy cultivars was 0.756-0.811. The Fv/Fm was not significantly different between the two groups, but the Fv/Fm difference among the cultivars was very significant ($p < 0.01$). The results showed that the values of PhiPSII and qP of the different cultivars were consistent, among which Gitte, Mini Kolibri and Shamrock had higher PhiPSII and qP values than the other cultivars, this finding indicated that the ratio of the light quantity was higher under saturated light intensity. There was no significant difference in PhiPSII, qP, or NPQ between the different groups, and the above indexes were all significantly different among the different cultivars ($p < 0.05$). In conclusion, the difference of the fluorescence parameters among the ten ivy cultivars is significant. However, for Fo and Fm, the green-leaf group had significantly higher values than the variegated group, and the other indicators showed no significant differences.

Table 4. Chlorophyll fluorescence parameters of 10 different ivy cultivars.

Cultivars	Fo	Fm	Fv/Fm	PhiPSII	qP	NPQ
gitte	185.918±12.38bc	969.437±82.98c	0.811±0.004e	0.172±0.036d	0.408±0.097cd	0.774±0.106a
Jessica	231.889±19.84d	917.929±77.23bc	0.756±0.027a	0.056±0.009a	0.220±0.033a	1.827±0.294d
Sark	190.313±13.25cd	933.599±35.48c	0.798±0.008cd	0.133±0.060bcd	0.367±0.094bcd	1.544±0.593abc
Shamrock	191.284±15.19bc	975.531±73.33bc	0.807±0.008cde	0.171±0.039bcd	0.410±0.099bcd	0.774±0.123bcd
Teardrop	212.286±3.42bc	979.419±8.44c	0.787±0.006 de	0.127±0.011d	0.361±0.052cd	1.171±0.165a
Ester	190.439±4.88bc	878.900±33.59bc	0.784±0.009bc	0.129±0.008bcd	0.387±0.005bcd	1.397±0.151bcd
Goldchild	211.816±7.21cd	895.390±29.78bc	0.765±0.012ab	0.113±0.008bc	0.347±0.033bc	1.386±0.094bcd
Mini Kolibri	173.129±15.01a	846.620±60.82a	0.798±0.004ab	0.171±0.014ab	0.481±0.048ab	1.522±0.187cd
White Wonder	187.933±3.97ab	895.016±32.54b	0.790±0.010cde	0.143±0.038d	0.393±0.080d	0.995±0.001bcd
Yellow Ripple	157.363±26.23bc	660.882±80.78bc	0.764±0.009cde	0.083±0.001cd	0.264±0.056cd	1.711±0.666ab

Fo = Origin fluorescence, Fm = Maximum fluorescence, Fv/Fm= Optimal/maximal photochemical efficiency of PS II in the dark, PhiPSII = Actual photochemical quantum efficiency of PSII, Qp = Quantum yield of photosynthesis, NPQ = Non photochemical quenching.

The leaf chlorophyll content is closely related to the plant physiological state and photosynthetic capacity (Ashraf and Harris 2013). Jessica, Goldchild, and Shamrock had the highest total chlorophyll content, and their A_{max} , Fo, and Fm values were also higher than those of other cultivars. Results showed that the total chlorophyll content of the green-leaf cultivars was higher than that of the variegated cultivars, and there was no significant difference in LCP between them. However, the LSP and A_{max} were significantly higher in the green-leaf cultivars than in the variegated cultivars. This observation indicated that the green-leaf cultivars had stronger light adaptability and photosynthesis ability and thus could carry out photosynthesis more efficiently, which was conducive to the accumulation of organic matter and plant growth. The results preliminarily confirmed Yeh's conjecture, to a certain extent, that there were differences in plant growth and light adaptability between green-leaf cultivars and variegated cultivars (Yeh and Hsu 2004). The difference in the chlorophyll-a content among the 10 ivy cultivars was more significant than that of the chlorophyll-b content, so the chlorophyll-a content became an important factor affecting the total chlorophyll content. Rose *et al.* (1996) and Brugnoli *et al.* (1998) reported that the photosynthetic rate of yellow or white leaves in English ivy cultivars was negative, which suggested that these leaves needed to be supported by green leaves. Jarle indicated that the leaf color change from green to violet-bronze of *Vaccinium myrtillus* was probably a protective response to the solar radiation (Bjerke *et al.* 2018).

The average light compensation point and the average light saturation point of the 10 ivy cultivars were $11.06 \mu\text{mol}/(\text{m}^2 \cdot \text{s})$ and $196.31 \mu\text{mol}/(\text{m}^2 \cdot \text{s})$, respectively. The light compensation points measured in the present study are similar to those reported by Yeh and Hsu (2004) because the ivy cultivars used in the present study were two-year-old seedlings. Bauer found that the photosynthetic rate of seedling leaves was lower than that of adult leaves, and the adaptability of seedlings to strong light was weaker than that of adult leaves (Bauer *et al.* 1980). Because lianas cannot grow upright, they exist in the lower layer of vegetation where there is weak light when they are young, so liana seedlings have stronger shade tolerance than liana adults (Li *et al.* 2000). Results showed that Fo and Fm had a significant positive correlation with the total chlorophyll

content of plant leaves; that is, the higher the total chlorophyll content was, the higher the values of F_o and F_m . F_v/F_m is the maximum photochemical quantum yield of PSII measured under dark adaptation, which reflects the light energy conversion efficiency of PSII. Shamrock and Mini Kolibri had higher F_v/F_m values, which indicated that these two cultivars had the highest potential PSII activity among the tested green-leaf cultivars and variegated cultivars, respectively.

The larger the Φ_{PSII} and qP values and the lower NPQ were, the higher the utilization of light energy and the higher the efficiency of photosynthesis. Among the ten ivy cultivars, Shamrock had higher Φ_{PSII} and qP values but the lowest NPQ. It was inferred that Shamrock had higher photosynthetic efficiency and promoted photosynthesis by increasing the photosynthetic electron transfer rate under higher light intensity. Although Jessica and Shamrock had the same A_{max} , the Φ_{PSII} and qP values of Jessica were significantly lower than those of Shamrock, and the NPQ of Jessica was the highest among the ten cultivars, indicating that Jessica resisted high light intensity through heat dissipation. The mechanism of resisting photoinhibition is different among different green-leaf cultivars in a strong light environment.

Different cultivars of ivy had different chlorophyll contents, photosynthesis parameters, and chlorophyll fluorescence parameters. This is mainly due to the complexity of photoelectron transfer and light energy transfer in photosynthesis. In addition, different genotypes can result in great differences in the process of photosynthesis among different cultivars, which is more evident in variegated cultivars (Stamps 1995, Rose 1996).

Results showed that the ivy seedlings were extremely shade-tolerant, and the light adaptation range of the ten tested seedlings was 6-262 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$. The results showed that the green-leaf ivy cultivars had a more comprehensive range of light adaptation and higher photosynthetic efficiency than the variegated ivy cultivars. The green-leaf cultivars also had a higher photosynthetic rate and electron transfer efficiency of the PSII reaction center than the variegated cultivars. Among the green-leaf cultivars, Shamrock had higher photosynthetic potential and stronger light resistance. Goldchild had a higher photosynthetic rate under suitable light intensity, but it was not tolerant to strong light. Mini Kolibri had a lower net photosynthetic rate, and it could resist strong light by increasing photorespiration and heat dissipation. Further research on different ivy cultivars under strong-light or high-temperature stress can be carried out to provide a reference for ivy breeding and application.

Acknowledgements

The project was supported by the projects from Science and Technology Commission of Shanghai Municipality (No. 23DZ2304600, No.21DZ1203005 and No. 18DZ2283500), and Traditional Chinese Medicine Culture Promotion and Education Base Project of Shanghai Municipal Health Commission.

References

- Ashraf M and Harris P 2013. Photosynthesis under stressful environments: an overview. *Photosynth.* **51**:163-190
- Barman TS, Baruah U and Saikia JK 2008. Irradiance influences tea leaf (*Camellia sinensis* L.) photosynthesis and transpiration. *Photosynth.* **46**: 618-621.
- Bauer H and Bauer U 1980. Photosynthesis in leaves of the juvenile and adult phase of ivy (*Hedera helix*). *Physiol Plant.* **49**: 366-72.
- Bjerke JW, Wierzbinski G, Tømmervik H, Phoenix GK and Bokhorst S 2018. Stress-induced secondary leaves of a boreal deciduous shrub (*Vaccinium myrtillus*) overwinter then regain activity the following growing season. *Nordic J. Bot.* **8**: 1-8

- Brugnoli E, Scartazzas A, De-Tullio MC, Monteverdi MC, Lauteri M and Augusti A 1998. Zeaxanthin and non-photochemical quenching in sun and shade leaves of C3 and C4 plants. *Physiol. Plant.* **104**: 727-34.
- Chang Q, Chen S and Chen Y 2013. Anatomical and physiological differences and differentially expressed genes between the green and yellow leaf tissue in a variegated chrysanthemum variety. *Molecul. Biotechnol.* **54**: 393-411.
- Hiscox JD and Israelstam GF 1979. A method for the extraction of chlorophyll from leaf tissue without maceration. *Can. J. Bot.* **57**: 1332-1334.
- Hugh M and Rosalyn M 2017. *Hedera: the complete*. The Royal Horticulture Society Media, Peterborough, UK, 33pp.
- Katherine FG, Stephanie EB, Lois BS and Donglin Z 2010. Minimum daily light integral for growing high-quality coleus. *Hort. Technol.* **20**(5): 929-933.
- Li JH, Gale J, Volokita M, Sinai T and Novoplansky A 2000. Effect of leaf variegation on acclimation of photosynthesis and growth response to elevated ambient CO₂. *J. Hortic. Sci. Biotechnol.* **75**: 679-83.
- Luo YY, Li RX, Jiang QS, Bai R and Duan D 2019. Changes in the chlorophyll content of grape leaves could provide a physiological index for responses and adaptation to UV-C radiation. *Nordic J. Bot.* **2**: 1-11 doi.org/10.1111/njb.02314.
- Rose PQ 1996. *The gardener's guide to growing ivies*. Timber Press, Portland, USA, 56 pp.
- Stamps RH 1995. Effects of shade level and fertilizer rate on yield and vase life of aspidistra relation 'Variegata' leaves. *J. Environ. Hortic.* **13**: 137-9.
- Svoboda VP, Marc WI and Stephanie EB 2005. Photosynthetic Irradiance and nutrition effects on growth of English ivy in subirrigation systems. *Hort. Sci.* **40**: 1740-1745.
- Wang N, Zhu T and Lu N 2019. Quantitative Phosphoproteomic and physiological analyses provide insights into the formation of the variegated leaf in *catalpa fargesii*. *Int. J. Molecul. Sci.* **20**: 1895.
- Yeh DM and Hsu PY 2004. Differential growth and photosynthetic response of selected cultivars of English ivy to irradiance. *J. Hortic Sci. Biotechnol.* **79**: 633-637.
- Zhang D, Zhang QS, Yang XQ, Sheng ZT and Nan GN 2016. The alternation between PSII and PSI in ivy (*Hedera nepalensis*) demonstrated by in vivo chlorophyll a fluorescence and modulated 820 nm reflection. *Plant Physiol. Biochem.* **108**(11): 499-506.
- Zhang T, Li P and Wei JL 2022. Transcriptome Analysis via RNA Sequencing Reveals the Molecular Mechanisms Underlying the *Hedera helix* Response to High Temperature. *Phyton-International J. Experim.Bot.* **91**(11): 2403-2417.

(Manuscript received on 31 March, 2023; revised on 26 June, 2023)