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Seasonal changes in *Elaeocarpus sylvestris* leaf colour and physiology

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Abstract: Leaves of *Elaeocarpus sylvestris* (Lour.) Poir. were sampled on five dates between autumn and winter and analysed to identify the factors causing progressive changes in leaf colour and physiological characteristics. Colour parameters L^*, a^*, C^*, and s^* increased significantly, particularly s^*, which changed from 8 518.79 to 13 044.77 (53.13%) over the sampling period. Changes in leaf colour parameters indicated that *E. sylvestris* leaves became reddish, and colour brightness and purity increased. Total chlorophyll and carotenoid contents decreased significantly, with mean values on December 30 being only 15.2% and 56%, respectively, of those recorded on October 30. Conversely, anthocyanin content increased 3.15-fold, and changes in pigment content ratio were the major factors explaining leaf reddening over the experimental period. Pigment content interacted with fluorescence and photosynthetic characteristics during leaf reddening. The decrease in chlorophyll and carotenoid contents weakened leaf fluorescence while decreasing light energy use efficiency and net photosynthetic rate. The allocation of light energy to regulatory processes (e.g., photochemical reactions) and heat dissipation pathways decreased, resulting in excess excitation energy that led to photodamage in photosystem II. These findings provide a scientific basis for gardening applications of *E. sylvestris* and novel theoretical insights into the mechanisms of leaf colouration in colourful ornamental plants.

Keywords: plant leaf colouration; colour parameters; photosynthetic physiology; leaf pigments; photochemical reactions; photodamage

Colour is one of the most important phenotypic characteristics of ornamental garden plants. Previous studies showed that organ colour and morphology in certain plants change in response to shifts in environmental physical factors such as temperature and light (Li 2016; Liu et al. 2018; Li et al. 2020). Simultaneously, plants with coloured leaves have become increasingly popular among landscape designers because they complement green plants and enrich landscape colour. Consequently, researchers have sought to elucidate the mechanisms of colour formation in garden plants. In particular, the growth habits and phenological changes in coloured-leaf plants require further study to determine the temporal regularity of ornamental characteristics and colour changes.

A case in point, *Elaeocarpus sylvestris* (Lour.) Poir., is a small, highly valued ornamental tree within *Elaeocarpaceae*, which develops a characteristic dense foliage, a graceful shape, and a spire-

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shaped crown. Additionally, in autumn, winter, and after frosts, some *E. sylvestris* leaves rapidly turn red, which can enrich garden design and enhance the garden atmosphere. Consequently, this species is widely used in urban planning, horticulture, and landscaping. Currently, the internal factors that cause *E. sylvestris* leaves to change from green to red, resulting in significant differences in the physiological characteristics of different-coloured leaves, remain unclear. Therefore, breeding new *E. sylvestris* cultivars with brightly coloured leaves and improved ornamental value requires that the mechanisms controlling leaf colouration under natural conditions are thoroughly elucidated.

To address this issue, we quantified and analysed the dynamic changes in *E. sylvestris* leaf-colour parameters and physiological characteristics as the leaves changed from green to red during the autumn-to-winter transition. Our study aimed to clarify the relationship between the changes in leaf colour under natural conditions and the internal physiological activity occurring during the transition from autumn to winter, such as to elucidate the mechanisms responsible for leaf colour changes, provide a scientific basis and reference data to support the application of *E. sylvestris* in gardens, and facilitate artificial interventions in leaf colour and breeding of superior varieties.

MATERIAL AND METHODS

Material. Five healthy and uniform *E. sylvestris* trees growing at Jiangxi University of Water Resources and Electric Power (28°41'23"N, 116°1'48"E) in Jiangxi Province, China, were selected for the study. These trees were not shaded and experienced minimal human interference. However, the lateral branch of one tree was crushed during the experiment; therefore, this tree was abandoned, and only the remaining four trees were used (average height, 4.3 m; average diameter at breast height, 12 cm). The experiment was conducted in the field, where the trees were subjected to natural ambient temperature and natural photoperiod throughout the entire study period. Leaf colour change in *E. sylvestris* is a continuous process from autumn to winter; therefore, five observation dates were selected (October 30, November 14, November 30, December 15, and December 30, 2022). Segmented observations were performed for leaf colour and physiological characteristics according to the law of leaf colour change from green to red.

Leaf colour parameters. Five fully expanded and healthy leaves were obtained from the same height (approximately 1.9 m above the ground) as replicates from each tree and used for analysis of leaf colour parameters. Five points on each side of the main leaf vein on each leaf were randomly selected for measurement, for a total of 10 measuring points, and values were recorded and averaged. Before measurement, leaves were wiped clean of dust. Colour-parameter values were recorded using an NH310 Portable Colourimeter (3nh Ltd., Shenzhen, China), and the standard of the International Commission on Illumination (CIE) $L^*a^*b^*C^*H^*$ measurement mode was applied.

Chlorophyll fluorescence parameters. Five, fully expanded, healthy leaves were selected from the same crown position on each sample tree between 09:00 and 11:00 h on sunny days, and leaf chlorophyll-fluorescence parameters were measured using a MINI-PAM-II Ultra-Portable Modulated Chlorophyll Fluorometer (Heinz Walz GmbH, Effeltrich, Germany; Hamani et al. 2020). Chlorophyll fluorescence parameters were automatically calculated and downloaded using Win Control-3 (version 3.32) software.

Gas exchange parameters. Leaf gas exchange parameters were measured on five leaves from each tree (the same leaves used for chlorophyll fluorescence measurements) using a Li-6400 portable photosynthesis system (Li-COR Inc., Lincoln, USA; Al-Gaadi et al. 2024) and the leaf limiting value of stomata (L_s) (Liu et al. 2020) and apparent CO_2 use efficiency (*CUE*) (Liu et al. 2023) were calculated based on the results. After measurements, leaves were stored at −80 °C to determine pigment contents.

Pigment contents. Photosynthetic pigments were extracted using dimethyl sulfoxide (Berhe et al. 2024). Leaf anthocyanins were extracted with a 1% hydrochloric acid-ethanol solution in the dark (Li 2016). A Spectra Max 190 microplate reader (Molecular Devices, Sunnyvale, USA) was then used to measure the absorbance of the extracts. Total chlorophyll (Chl (a + b)), carotenoids (Car), and anthocyanins (Ant) contents were calculated. Five replicates were analysed for each tree.

Statistical analysis. Differences in leaf colour, pigment content, chlorophyll fluorescence, and gas exchange parameters among sampling time-

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Figure 1. Leaf colour changes in *Elaeocarpus sylvestris* from October to December

points were determined using one-way analysis of variance and least significant difference tests. The statistical significance level was set at 5%. Correlations between different characteristics were determined using Pearson's correlation coefficients. All statistical analyses were performed using SPSS (version 20.0) for Windows (SPSS Inc., Chicago, IL, USA).

RESULTS AND DISCUSSION

Leaf colour. Over the period of observation, *E. sylvestris* leaves typically transitioned from green to greenish-yellow and eventually to red (Figure 1). The green colour started to become lighter on November 14; then, local leaf tissue turned yellow, leaf margins and tips shifted to red, and on December 30, when leaf colour change was complete, the brightness and purity of the reddish colour reached maximum intensity.

As leaf colour changed, both colour lightness or darkness (L^*), and the yellow and blue colour characteristic (b^*) values increased with time, peaking on December 15. The mean L^* value increased from 20.26 to 24.96, while the mean b^* value increased from 3.04 to 6.22 (Table 1), as leaves became brighter and developed a deeper yellow colouration. In turn, the values for red-green colour characteristics (a^*) and degree of colour vividness (C^*) showed the same increasing trend over time and were significantly higher at the end of the observation period. The colour light value (s^*) generally increased throughout the observation period. Although minor fluctuations occurred, the differences observed between October 30 and December 15 were not significant. The highest s^* value (13 044.77) was recorded on December 30, and was 53.13% greater than the lowest value (November 30). These findings were highly consistent with field observations, thus highlighting the reliability of the colour index for quantifying plant colour and indicating that leaves had a reddish and bright gloss with increased colour purity.

Leaf colour and pigment contents. In nature, visible leaf colours primarily depend on pigment type, content, and proportion within cells. Changes in the contents and proportions of these pigments are primarily influenced by a combination of environmental factors plant growth and development, and senescence (Li et al. 2020).

Table 1. Leaf colour parameters in *Elaeocarpus sylvestris* trees over the period

Date (2022)	L^*	a^*	b^*	C^*	s^*
October 30	20.26 ± 3.14^{b}	8.21 ± 2.70^{c}	3.04 ± 2.07^{d}	9.24 ± 1.62^{c}	8 545.37 ± 4 578.60^{b}
November 14	20.67 ± 1.78^{b}	8.46 ± 2.45^{bc}	3.37 ± 1.78^{cd}	9.44 ± 1.93^{c}	8 710.06 ± 4 872.25^{b}
November 30	21.44 ± 2.00^{b}	8.62 ± 1.37^{bc}	4.34 ± 2.38^{bc}	9.99 ± 1.42^{c}	8 518.79 ± 2 724.29^{b}
December 15	24.96 ± 1.55^{a}	9.59 ± 0.92^{b}	6.22 ± 2.18^{a}	11.60 ± 1.54^{b}	8 950.77 ± 1 481.87^{b}
December 30	23.86 ± 1.37^{a}	11.88 ± 1.59^{a}	5.06 ± 1.79^{ab}	12.97 ± 2.12^{a}	13 044.77 ± 3 167.16^{a}

L^* – lightness or darkness of a colour; a^* – red-green colour characteristics; b^* – yellow and blue colour characteristics; C^* – colour vividness; s^* – colour light value; values are means ± SD; different superscript letters within columns indicate significant differences in the same colour parameter among sampling timepoints ($P < 0.05$)

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Table 2. Leaf pigment contents in *Elaeocarpus sylvestris* trees during colour change

Index	October 30	November 14	November 30	December 15	December 30
Chl *a* (mg/g)	0.85 ± 0.22^{a}	0.70 ± 0.17^{b}	0.41 ± 0.12^{c}	0.21 ± 0.11^{d}	0.06 ± 0.03^{e}
Chl *b* (mg/g)	0.39 ± 0.08^{a}	0.34 ± 0.06^{b}	0.25 ± 0.06^{c}	0.17 ± 0.04^{d}	0.13 ± 0.03^{d}
Chl *a*/*b*	2.16 ± 0.29^{a}	2.07 ± 0.28^{a}	1.64 ± 0.22^{b}	1.20 ± 0.26^{c}	0.43 ± 0.14^{d}
Chl (*a* + *b*) (mg/g)	1.25 ± 0.29^{a}	1.04 ± 0.22^{b}	0.66 ± 0.17^{c}	0.37 ± 0.15^{d}	0.19 ± 0.05^{e}
Car (mg/g)	0.25 ± 0.04^{a}	0.23 ± 0.03^{b}	0.17 ± 0.03^{c}	0.14 ± 0.02^{d}	0.14 ± 0.04^{d}
Ant (mg/g)	4.12 ± 0.45^{b}	3.99 ± 0.45^{b}	4.16 ± 0.90^{b}	4.53 ± 0.97^{b}	17.11 ± 5.76^{a}
Ant/Chl	3.43 ± 0.69^{b}	4.00 ± 0.92^{b}	6.61 ± 2.05^{b}	13.19 ± 3.82^{b}	95.81 ± 38.95^{a}
Ant/Car	16.75 ± 2.33^{c}	18.09 ± 3.55^{c}	25.33 ± 5.38^{bc}	34.07 ± 8.96^{b}	119.64 ± 34.87^{a}
Car/Chl	0.20 ± 0.03^{d}	0.22 ± 0.02^{cd}	0.26 ± 0.04^{c}	0.38 ± 0.06^{b}	0.79 ± 0.17^{a}

Chl *a* – chlorophyll *a*; Chl *b* – chlorophyll *b*; Chl *a*/*b* – chlorophyll ratio; Chl (*a* + *b*) – total chlorophyll content; Car – carotenoids; Ant – anthocyanins; Ant/Chl – Ant-to-Chl ratio; Ant/Car – Ant-to-Car ratio; Car/Chl – Car-to-Chl ratio; values area means ± SD; different superscript letters within rows indicate significant differences among sampling timepoints ($P < 0.05$)

Mean Chl *a*, Chl *b*, and Chl (*a* + *b*) contents and Chl *a*/*b* ratio values in *E. sylvestris* leaves on December 30 were 0.06, 0.13, and 0.19 mg/g, and 0.43, respectively. These values were significantly reduced by 92.94%, 66.67%, 84.80%, and 80.09%, respectively, compared to those recorded on October 30 (Table 2). Furthermore, Car levels generally showed the same trend, with the lowest value recorded between December 15 and December 30 (approximately 0.14 mg/g, 44% lower than the value recorded on October 30).

The change in leaf colour from green to red represents gradual leaf senescence, which initiates with chlorophyll breakdown. Moreover, the increasingly low ambient temperatures in autumn and winter are alleged to intensify chlorophyll degradation (Yang 2020) and inhibit chlorophyll biosynthesis (Zhao et al. 2020), leading to a decline in chlorophyll content. Moreover, low temperatures promote Ant synthesis and its accumulation in leaves, further enhancing the gradual loss of green colour and the change to red (Li 2016). Both the Ant value and the anthocyanins to chlorophyll ratio (Ant/Chl) showed an upward trend during the observation period. However, the changes between October 30 and December 15 were relatively modest, with mean values ranging from 3.99 to 4.53 mg/g and 3.43 to 13.19, respectively. Then, a marked increase was observed from December 15 to December 30, when the values rose significantly to 17.11 mg/g and 95.81, respectively. Similarly, the mean value of the anthocyanins to carotenoids ratio (Ant/Car) increased from 16.75 to 119.64 over the same period, suggesting that a higher anthocyanin content played a decisive role at the end of the colour-change period, masking the colour-developing effects of chlorophyll and carotenoids, and intensifying the red colour of the leaves. Consistent with the significant increase in hue a^* values, which were used to verify the changes in leaves fading from green to red, in this study, the increase in anthocyanin content was the major factor responsible for *E. sylvestris* leaf-reddening over the sampling period.

Our correlation analysis revealed that L^*, a^*, C^*, and s^* were significantly, or highly significantly and positively correlated with Ant, Ant/Chl, Ant/Car, and Car/Chl, whereas colour phase b^* was not significantly correlated with Ant, Ant/Chl, or Ant/Car (Table 3). Thus, changes in Ant, Ant/Chl, and Ant/Car corresponded to changes in redness and brightness of leaf colour. Moreover, changes in anthocyanin content were seemingly the most direct cause of the reddish colouration of *E. sylvestris* leaves and had no direct effect on the yellow-blue colour. Anthocyanins, which are stored in vacuoles, are responsible for the pinkish-red colouration of most flower petals and fruits and are primarily responsible for the red colour of autumn leaves.

Leaf fluorescence parameters and pigment contents. Chlorophyll fluorescence can be used as a non-destructive, non-invasive tool to detect plant physiological responses (Hamani et al. 2020). In particular, chlorophyll fluorescence parameters are often used to characterise leaf absorption, transfer, dissipation, and distribution of light energy, and

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represent important indicators for studying plant photosynthesis (Liu et al. 2023). In this study, the maximum photochemical efficiency of photosystem II (PSII; F_v/F_m), effective quantum yield (F_v'/F_m'), and potential activity of PSII (F_v/F_o) in *E. sylvestris* leaves showed a decreasing trend over time (Figure 2). All parameters showed relatively constant high values from October 30 to November 14 followed by marked decreases. Generally, F_v/F_m values of normal plant leaves range from 0.75 to 0.85 (Liu et al. 2018). Further, a decrease in F_v/F_m value is considered to be a PSII reaction to biotic or abiotic stress factors (Wojciechowska et al. 2013). In this study, following leaf colour change from green to red, F_v/F_m values began to decline, and after November 14, the values fell below the normal range, decreasing from 0.51 to 0.15. This reduction was largely attributed to leaf senescence and a decline in chlorophyll content. Consistently, Wu et al. (2022) found that low-temperature stress impaired PSII reaction-centre activity in *Bougainvillea glabra* leaves, as evidenced by a decrease

Table 3. Coefficients for the correlations between colour parameters and various physiological indicators in the leaves of *Elaeocarpus sylvestris* trees

Group	Index	L^*	a^*	b^*	C^*	s^*
Pigment contents and ratios	Chl *a*	−0.71**	−0.36**	−0.55**	−0.54**	−0.18
	Chl *b*	−0.65**	−0.40**	−0.52**	−0.56**	−0.22*
	Chl *a*/*b*	−0.64**	−0.45**	−0.44**	−0.57**	−0.29**
	Chl (*a* + *b*)	−0.70**	−0.38**	−0.55**	−0.55**	−0.19
	Car	−0.62**	−0.36**	−0.52**	−0.52**	−0.18
	Ant	0.24*	0.49**	0.09	0.45**	0.39**
	Ant/Chl	0.32**	0.51**	0.18	0.50**	0.40**
	Ant/Car	0.34**	0.54**	0.18	0.53**	0.42**
	Car/Chl	0.46**	0.51**	0.28**	0.56**	0.38**
Chlorophyll fluorescence parameters	F_v/F_m	−0.59**	−0.48**	−0.39**	−0.57**	−0.31**
	F_v'/F_m'	−0.50**	−0.50**	−0.34**	−0.57**	−0.34**
	F_v/F_o	−0.66**	−0.33**	−0.50**	−0.48**	−0.15
	Y(*II*)	−0.28**	−0.48**	−0.18	−0.50**	−0.28**
	ETR	−0.28**	−0.49**	−0.18	−0.50**	−0.28**
	qP	−0.03	−0.29**	0.00	−0.25*	−0.19
	NPQ	−0.56**	−0.11	−0.38**	−0.28**	0.09
	Y(*NPQ*)	−0.48**	−0.13	−0.26*	−0.23*	0.06
	Y(*NO*)	0.45**	0.26*	0.26*	0.34**	0.04
Gas exchange parameters	P_n	−0.62**	−0.42**	−0.44**	−0.54**	−0.25*
	g_s	−0.56**	−0.31**	−0.41**	−0.44**	−0.16
	T_r	−0.56**	−0.41**	−0.40**	−0.52**	−0.25*
	C_i	0.28**	0.47**	0.13	0.45**	0.37**
	CUE	−0.52**	−0.49**	−0.36**	−0.56**	−0.32**
	L_s	−0.27**	−0.46**	−0.12	−0.44**	−0.37**

Chl *a* – chlorophyll *a*; Chl *b* – chlorophyll *b*; Chl *a*/*b* – chlorophyll ratio; Chl (*a* + *b*) – total chlorophyll content; Car – carotenoids; Ant – anthocyanins; Ant/Chl – Ant-to-Chl ratio; Ant/Car – Ant-to-Car ratio; Car/Chl – Car-to-Chl ratio; F_v/F_m – maximum photochemical efficiency of photosystem II (PSII); F_v'/F_m' – effective quantum yield; F_v/F_o – potential activity of PSII; *Y*(*II*) – actual photochemical quantum yield of PSII; *ETR* – electron transfer rate; *qP* – photochemical quenching coefficient; *NPQ* – non-photochemical quenching coefficient; *Y*(*NPQ*) – regulated energy-dissipation quantum yield; *Y*(*NO*) – non-regulated energy-dissipation quantum yield; P_n – photosynthetic rate; g_s – stomatal conductance; T_r – transpiration rate; C_i – intercellular CO_2 concentration; *CUE* – apparent CO_2 use efficiency; L_s – limiting value of stomata; *,**significant ($P < 0.05$) and highly significant ($P < 0.01$) correlations, respectively

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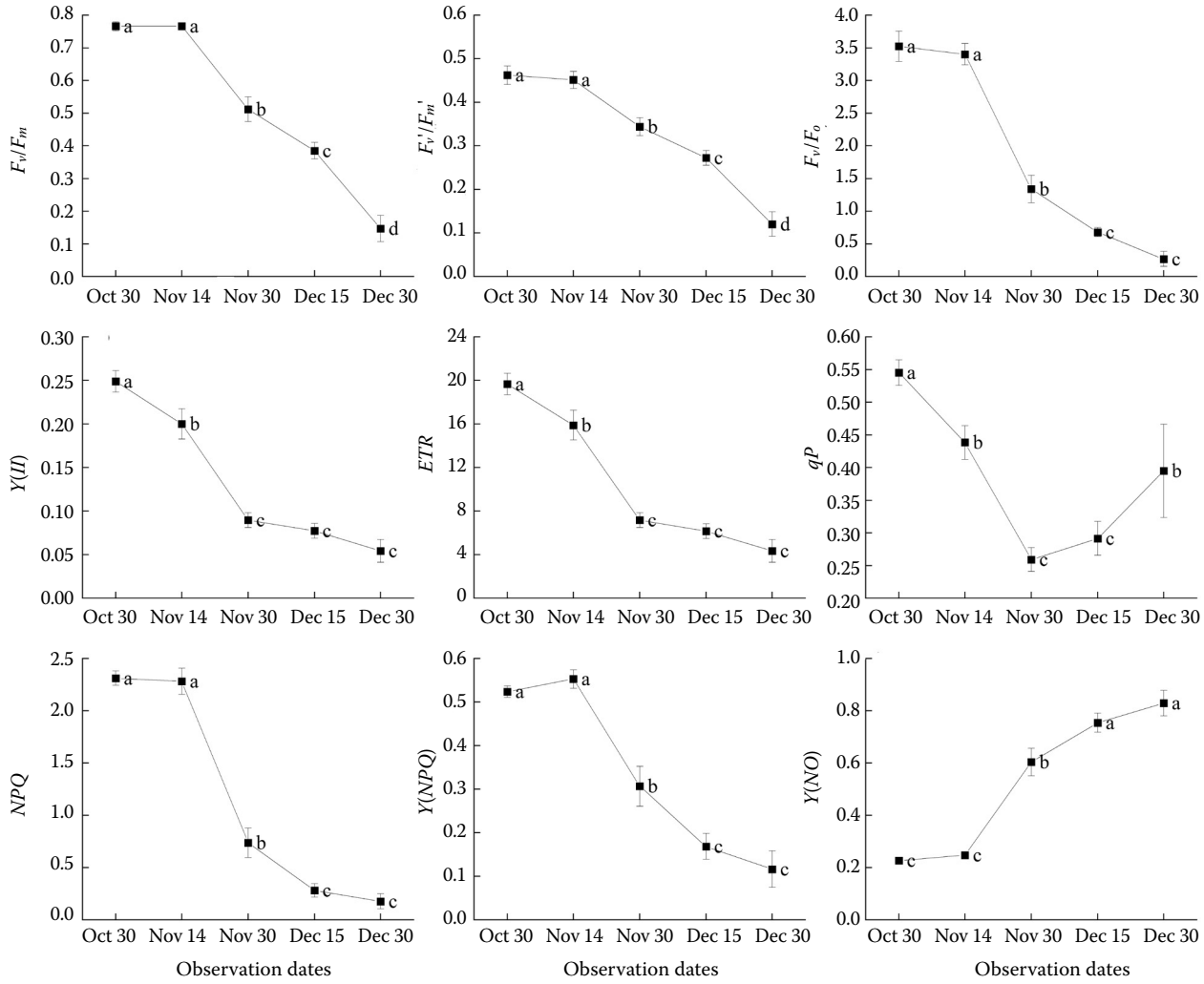

Figure 2. Chlorophyll fluorescence parameters of *Elaeocarpus sylvestris* leaves at different sampling time points

F_v/F_m – maximum photochemical efficiency of photosystem II (PSII); F_v'/F_m' – effective quantum yield; F_v/F_o – potential activity of PSII; *Y*(*II*) – actual photochemical quantum yield of PSII; *ETR* – electron transfer rate; *qP* – photochemical quenching coefficient; *NPQ* – non-photochemical quenching coefficient; *Y*(*NPQ*) – regulated energy-dissipation quantum yield; *Y*(*NO*) – non-regulated energy-dissipation quantum yield; data are means ± standard error (SE); different lowercase letters indicate significant differences among sampling timepoints ($P < 0.05$)

in F_v/F_m and an increase in non-regulated energy-dissipation quantum yield (*Y*(*NO*)). We speculate that the decrease in temperature during autumn and winter may affect the fluorescence parameters during leaf colour changes in *E. sylvestris* trees. Thus, the decreases in F_v/F_m, F_v'/F_m', and F_v/F_o were attributed to the decrease in photovoltaic use efficiency as a result of chlorophyll degradation and leaf senescence due to seasonal low-temperature stress.

The light energy absorbed by PSII is predominantly allocated to three pathways for use and dissipation: actual photochemical quantum yield of PSII (*Y*(*II*)), regulated energy-dissipation quantum yield (*Y*(*NPQ*)), and non-regulated energy-dissipation quantum yield (*Y*(*NO*)) (Kono et al. 2022). In this study, mean *Y*(*II*) values showed a significant decline from 0.25 on October 30 to 0.09 on November 30 (approximately 64.00% lower) and remained relatively low thereafter. The non-photochemical quenching coefficient (*NPQ*) and *Y*(*NPQ*) values followed similar trends and decreased stepwise on the later observation dates. Conversely, non-regulated energy-dissipation

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quantum yield (*Y*(*NO*)) increased over time, with higher values observed during the final period, suggesting that the reddening of *E. sylvestris* leaves reduced the allocation of light energy to regulatory energy-dissipation pathways, such as photochemical reactions and heat dissipation, while reducing the ability of PSII to dissipate excess light energy, which led to photodamage to PSII.

Chlorophyll absorbs light and maximises the use of light energy for photosynthetic electron transport. Additionally, it protects chloroplasts from excess light by dissipating it in the form of heat or fluorescence radiation (Nishio 2000). During leaf colour changes in *E. sylvestris*, Chl *a*, Chl *b*, Chl *a*/*b*, Chl (*a* + *b*), and Car all decreased significantly with time. Furthermore, correlation analysis revealed that, except for *Y*(*NO*), all fluorescence parameters significantly and positively correlated with pigment contents (Table 4). Thus, during leaf reddening, the significantly reduced chlorophyll and carotenoid contents were not conducive to proper PSII functions, partly reflecting that fluorescence characteristics, pigment content, and photosynthetic characteristics of *E. sylvestris* leaves are complementary. Additionally, correlation analysis revealed that chlorophyll content affected electron transfer rate (*ETR*) and *NPQ*. These results are consistent with those of Tian (2020), who reported a decrease in leaf *ETR* with decreasing chlorophyll content, directly affecting photosynthetic rate and leading to a decrease in *NPQ*.

Leaf gas exchange parameters and pigment contents. Leaf photosynthesis is reduced by stomatal closure, low intracellular CO_2 concentration, and other non-stomatal variables (Li 2016). Between October 30 and November 14, photosynthetic rate (P_n) and intercellular CO_2 concentration (C_i) decreased significantly, while imiting value of stomata (L_s) increased significantly (Figure 3). Then, from November 14, P_n and L_s further decreased significantly. Specifically, P_n fell from 4.28 to 0.38 μmol $CO_2/(m^2 \cdot s)$, a reduction

Table 4. Correlation analysis for leaf pigment contents and various physiological indicators in reddening leaves of *Elaeocarpus sylvestris* trees

Group	Index	Chl *a*	Chl *b*	Chl *a*/*b*	Chl (*a* + *b*)	Car	Ant	Ant/Chl	Ant/Car	Car/Chl
Chlorophyll fluorescence parameters	F_v/F_m	0.84**	0.79**	0.87**	0.84**	0.73**	−0.63**	−0.64**	−0.72**	−0.74**
	F_v'/F_m'	0.80**	0.77**	0.79**	0.80**	0.70**	−0.59**	−0.61**	−0.68**	−0.70**
	F_v/F_o	0.91**	0.85**	0.82**	0.90**	0.83**	−0.46**	−0.50**	−0.57**	−0.63**
	Y(*II*)	0.76**	0.77**	0.64**	0.77**	0.76**	−0.36**	−0.39**	−0.50**	−0.51**
	ETR	0.76**	0.77**	0.64**	0.77**	0.76**	−0.36**	−0.39**	−0.50**	−0.51**
	qP	0.40**	0.43**	0.28**	0.41**	0.45**	−0.11	−0.14	−0.17	−0.20
	NPQ	0.79**	0.72**	0.79**	0.78**	0.73**	−0.36**	−0.40**	−0.52**	−0.56**
	Y(*NO*)	−0.79**	−0.74**	−0.79**	−0.79**	−0.74**	0.40**	0.41**	0.55**	0.57**
	Y(*NPQ*)	0.72**	0.64**	0.76**	0.70**	0.65**	−0.37**	−0.37**	−0.51**	−0.53**
Gas exchange parameters	P_n	0.88**	0.85**	0.82**	0.88**	0.78**	−0.53**	−0.58**	−0.63**	−0.70**
	g_s	0.79**	0.76**	0.71**	0.79**	0.69**	−0.46**	−0.49**	−0.53**	−0.60**
	C_i	−0.48**	−0.45**	−0.60**	−0.47**	−0.37**	0.54**	0.56**	0.59**	0.61**
	T_r	0.81**	0.79**	0.75**	0.81**	0.72**	−0.48**	−0.52**	−0.56**	−0.64**
	WUE	0.02	−0.00	0.15	0.02	−0.06	−0.29**	−0.29**	−0.28**	−0.24*
	L_s	0.46**	0.44**	0.58**	0.46**	0.36**	−0.54**	−0.56**	−0.58**	−0.60**
	CUE	0.80**	0.80**	0.75**	0.81**	0.74**	−0.50**	−0.54**	−0.59**	−0.66**

F_v/F_m – maximum photochemical efficiency of photosystem II (PSII); F_v'/F_m' – effective quantum yield; F_v/F_o – potential activity of PSII; *Y*(*II*) – actual photochemical quantum yield of PSII; *ETR* – electron transfer rate; *qP* – photochemical quenching coefficient; *NPQ* – non-photochemical quenching coefficient; *Y*(*NPQ*) – regulated energy-dissipation quantum yield; *Y*(*NO*) – non-regulated energy-dissipation quantum yield; P_n – photosynthetic rate; g_s – stomatal conductance; C_i – intercellular CO_2 concentration; T_r – transpiration rate; *WUE* – water use efficiency; L_s – limiting value of stomata; *CUE* – apparent CO_2 use efficiency; *,**significant ($P < 0.05$) and highly significant ($P < 0.01$) correlations, respectively

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of approximately 91.12%. Meanwhile, L_s declined by 55.00%, from 0.60 to 0.27. In contrast, C_i increased significantly over the observation period, rising from 157.41 to 291.56 μmolCO_2/mol. These results suggest that the decrease in photosynthetic rate in *E. sylvestris* leaves during the first period was due to stomatal limitations. Stomatal closure restricted gas exchange, limiting intercellular CO_2 availability, and altering leaf biochemistry. Altogether, these changes affected photosynthetic efficiency and caused physiological damage, ultimately reducing growth and hindering development. However, with the gradual reddening of *E. sylvestris* leaves, P_n was also affected by non-stomatal limitations, presumably, senescence-related processes caused by seasonal low-temperature stress.

During the green to red colour change in *E. sylvestris* leaves, C_i showed an initially decreasing and then increasing trend. This may be because the photosynthetic pigments (chlorophyll and carotenoids) started to change during the pre-colour-change period, and the chloroplasts were able to maintain normal photosynthesis through self-regulation; thus, the change in C_i was not significant before November 14. In the middle and late stages of colour change, as the photosynthetic pigment content continued to decrease significantly, the photosynthetic rate was reduced, and CO_2 could not be fully utilised or accumulated in cells. This trend is reflected in the increasing C_i and decreasing *CUE*.

Numerous studies have suggested that the photosynthetic properties of plants with coloured foliage are primarily influenced by changes in pigment content during leaf colour changes (Yang 2020). In this study, the Chl (*a* + *b*) and Car contents of *E. sylvestris* leaves showed highly significant positive correlations with P_n (Table 4). During the colour change, these pigments decreased significantly, while Ant increased significantly. Moreover, Ant, Ant/Chl, and Ant/Car showed a highly significant negative correlation with P_n but a highly significant positive correlation with C_i. These observations are consistent with the findings of Yang (2020) for *Liquidambar formosana*. Thus, the decrease in photosynthetic pigments and an increase in non-photosynthetic pigments (anthocyanins) were inferred to represent the primary non-stomatal limiting factors underlying the

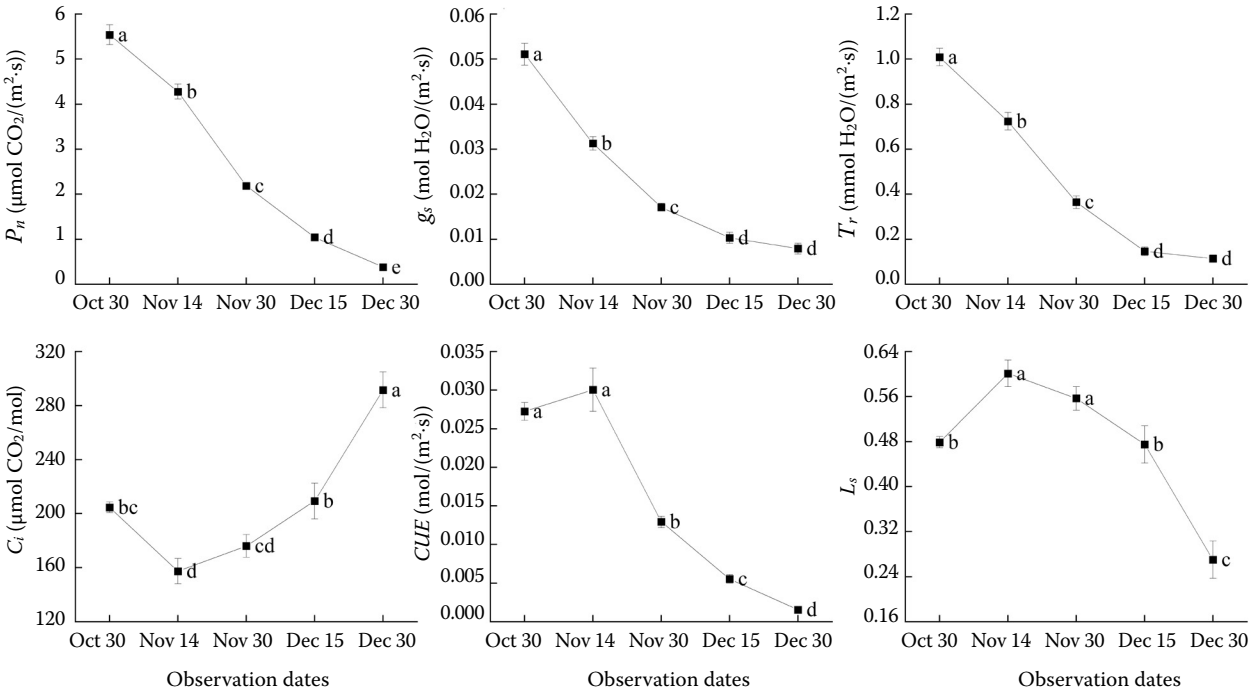

Figure 3. Gas exchange parameters for *Elaeocarpus sylvestris* leaves on different observation dates

P_n – photosynthetic rate; g_s – stomatal conductance; T_r – transpiration rate; C_i – intercellular CO_2 concentration; *CUE* – apparent CO_2 use efficiency; L_s – limiting value of stomata; data are presented as the mean ± standard error (SE), and different lowercase letters indicate significant differences among observation dates ($P < 0.05$)

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decreased photosynthetic capacity of chloroplasts and decreased P_n during the colour-change period.

CONCLUSION

During the pre-colour-change stage of *E. sylvestris* leaves, the green colour gradually lightens, and the leaf margins and tips begin to appear red. During the later stages, the green colour completely fades while the red colour develops into a bright red. This transition is likely accelerated by temperature reduction and leaf senescence, which exacerbate chlorophyll degradation and inhibit the accumulation of chlorophyll and carotenoids, whereas substantial synthesis and accumulation of anthocyanins occur. The results indicate that significant increases in the Ant content as well as Ant/Chl and Ant/Car ratios are the primary determinants of the red leaf colour. Throughout this colour shift, the chlorophyll content was significantly reduced, and light energy allocation from *E. sylvestris* leaves to photochemical reactions, heat dissipation, and other regulatory energy dissipation pathways was reduced. Consequently, light use efficiency gradually declines, photosynthetic rate drop, and environmental conditions become less favourable for leaf growth. Our findings on the relationship between leaf colour change, pigment content, and fluorescence and photosynthetic characteristics in *E. sylvestris* establish a framework that could be tested in other horticulturally or ecologically important evergreens.

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