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Exploring sexual dimorphism in *Viscum album*: Fewer, smaller, and more yellow males

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Abstract: Mistletoe (*Viscum album*) shrubs exhibit a yellowish hue during host dormancy, a trait that is more pronounced in male individuals. Moreover, in populations of this hemiparasite, a female-biased sex ratio is commonly observed. In the present study, we raised the question of the physiological basis and consequences of these between-sex differences. We hypothesized that males might be more impacted by host dormancy and restricted resource acquisition. Furthermore, we considered the possibility that females could be more efficient at acquiring resources from host tissues compared to males.

The population of *V. album* subsp. *album* growing on *Malus* sp. within the collection of the Institute of Dendrology, Polish Academy of Sciences in Kórnik, was studied during the host's (*Malus* sp.) dormant period. Measurements included number, location and size of shrubs, chlorophyll fluorescence, chlorophyll and carotenoid contents, water contents, leaf morphology, and the content of selected elements.

We observed a female-biased sex ratio in the mistletoe population, and females were larger than males. The females had a lower chlorophyll *a* / *b* ratio due to the greater concentration of chlorophyll *b*, higher chlorophyll to carotenoid (chl / car) ratio and potassium concentration in leaves. Moreover, a slightly stronger correlation was observed between the nitrogen concentration and the chl / car ratio in females than in males. No significant differences between sexes were observed in other parameters, including specific leaf area, relative water content, magnesium, phosphorus, calcium concentrations, or chlorophyll fluorescence parameters. Our results showed that *V. album* males were more yellowish during host dormancy than females because they had a lower chl / car ratio. The disparities in pigment concentrations, coupled with the smaller size and fewer male individuals in populations, suggest that male individuals are in an overall weaker condition than females.

Keywords: mistletoe, reproductive effort, sex ratio, chemical elements, chlorophyll, chl / car ratio

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Introduction

In the past century, it has been observed that shrubs of mistletoe (*Viscum album* L.) become more yellow during winter. Tubeuf et al. (1923) noted that this yellowing was more intense in individuals and branches exposed to full sunlight. Moreover, some differences in colouration between males and females have been observed; in particular, males tend to be more yellow than females (Tubeuf et al., 1923). During winter, ultrastructure analyses of *V. album* chloroplasts revealed a transition between chloro- and chromoplasts (Hudak & Lux 1986). This indicates a lower chlorophyll to carotenoid ratio during this period compared to the rest of the year. This ratio can also differ depending on light exposure, as chlorophyll is required for light capture and carotenoids have photoprotective properties. Under low light conditions, the chlorophyll to carotenoid ratio is higher, while it is lower under intense irradiance (Young, 1991; Rosevear et al., 2001; Lichtenthaler, 2007).

Mistletoe is unable to grow in soil and relies on host branches for its survival. It was suggested that mistletoe derives not only water and nutrients from its host tissues but also up to 43% of its carbon (C) content (Richter & Popp, 1992; Escher & Rennenberg, 2006). However, recent studies challenge this claim (Wang et al., 2022), while others (e.g. Schröder et al., 2022) propose that mistletoe significantly harvests carbon from its host.

Nevertheless, a physiological link exists between the host and hemiparasite (Su et al., 2024; Teixeira-Costa et al., 2025). Changes in deciduous tree tissues throughout the year are considerable, affecting mistletoe growing on their branches (Escher et al., 2004; Thomas et al., 2023; Cocoletzi et al., 2020). Mistletoe and their host trees exhibit asynchronous flowering, with mistletoe blooming in late winter or early spring, while most hosts remain dormant (Thomas et al., 2023; Li & Zhang, 2020). *Viscum album* is dioecious, and differences in reproductive requirements and allocation strategies between the sexes have been observed in dioecious species (e.g. Barrett & Hough, 2013; Tonnabel et al., 2017). Moreover, physiological differences between sexes in relation to their environments are very common (Obeso, 2002).

Individual male flowers of *V. album* are larger than female flowers, and the amount of pollen they produce can reach the amount produced by some wind-pollinated species (Noryśkiewicz & Noryśkiewicz, 2017). Pollen production is a resource-consuming process, requiring a significant amount of nitrogen (N) (Harris & Pannell, 2008; Van Drunen & Dorken, 2012). In the case of mistletoe, this process coincides with the dormancy period of its host.

During dormancy of trees, water and solute transport is stopped because of the loss of leaves and the consequent loss of negative water potential pressure (Fadón et al., 2020). However, the presence of mistletoe on host branches forces the negative water potential to be maintained by the high transpiration rates of the hemiparasite (Ziegler et al., 2009; Huang et al., 2025). Conditions associated with water deficiency may affect the content of elements used by the plant in the mechanisms of coping with stress (Hosseini & Hosseini, 2022). Mistletoe acquires a wide range of elements from host tissues, and in most cases, its concentration is higher in mistletoe tissues than in the host, with the difference being greatest between the parasite and infected branches (Lamont, 1983). Resources acquired from host tissues are not required exclusively for reproduction but also for photosynthetic pigment synthesis and hemiparasite photosynthesis (Těšitel et al., 2015; Speetjens & Jacobs, 2023). Mistletoe virulence may differ between sexes, and females can be more burdensome for host plants (Burns, 2021).

In dioecious species, a biased sex ratio is commonly observed (Munné-Bosch, 2015). A male-biased sex ratio has been reported most often (Delph, 1999; Field et al., 2013) but not for *V. album*, where female-biased sex ratios are observed (Barlow et al., 1978). Mistletoe is a hemiparasitic species, and biased sex ratios in parasitic species (not only plants) have been observed in relation to host quality. More numerous female individuals grow on hosts of better quality (e.g. Werren, 1983; Adam et al., 2017). Moreover, females of mistletoe *Phoradendron tomentosum* [(DC.) Engelm. ex A. Gray] have shown greater bias on trees with heavier infestation (Nixon & Todzia, 1985). If one sex is more likely to survive and reproduce in the future, parental plants produce more individuals of that sex (Lloyd, 1974a, b). Nevertheless, in long-leaving dioecious plants, male individuals are often larger because of lower reproductive effort (Obeso, 2002). Consequently, being larger, they can produce more flowers and greater amounts of pollen, and they can increase their reproductive success by winning the competition with other males (Willson, 1994; Emms et al., 1997). However, the sex ratio can be considered the degree of investment to reproduction on a population scale, not only as the ratio of the number of female to male individuals (Lloyd, 1980).

In our study, we aimed to answer the question of how male and female mistletoe differ in physiological performance and morphology at the beginning of the host vegetative period. Additionally, we investigated potential physiological factors contributing to the evolutionary stability of the female-biased sex ratio.

We put forward the following hypotheses:

1. *Viscum album* females' greater chlorophyll concentration and smaller carotenoid concentration ex-

plain why males have more yellow leaves during host dormancy.
2. *Viscum album* males occur in the upper part of the crown of the host tree compared to females growing in the lower and inner parts of the crown. High-intensity sunlight induces leaf yellowing in male *V. album* plants, whereas female plants develop deeply green leaves in shaded conditions.
3. Male individuals are more depleted of N because of their limited acquisition during host dormancy and allocation to pollen production.
4. *Viscum album* males show element deficiencies and lower photosynthetic activity in connection with pigments deficiencies.
5. *Viscum album* females are more numerous and better adapted to intraspecific competition than males on larger hosts.

Material and Methods

Plant material and morphological measurements

In the present study, we analysed the *Viscum album* subsp. *album* population growing on the *Malus* sp. collection (with 357 apple trees) (Fig. 1). The research took place in the Arboretum of the Institute of Dendrology, Polish Academy of Sciences in Kórnik, Poland (52°14'N, 17°05'E), which lies in a temperate climate zone, characterized by moderate precipitation (659 mm annually) and cold winters, with mean annual temperatures ranging from 8 to 9 °C. The genus *Malus* is a typical host for *V. album* subsp. *album*. Employing a single genus that grows in homogeneous environmental conditions, such as: size and age of host tree, consistent light exposure, presents a significant advantage for these studies. Additionally, the accessibility of mistletoe for research, particularly due to its growth at relatively low heights above ground, is also a crucial factor. All 357 apple trees were measured, and their previously determined age was retrieved from existing records. They were 52 to 97 years old, with heights ranging from 1.7 to 8.8 m. The sum of cross-sectional areas at breast height ranged from 2.0 to 1294.4 cm^2, calculated based on stem diameters. In most cases, this value corresponded to a single stem, but for multi-stemmed individuals, the total area of all stems was used.

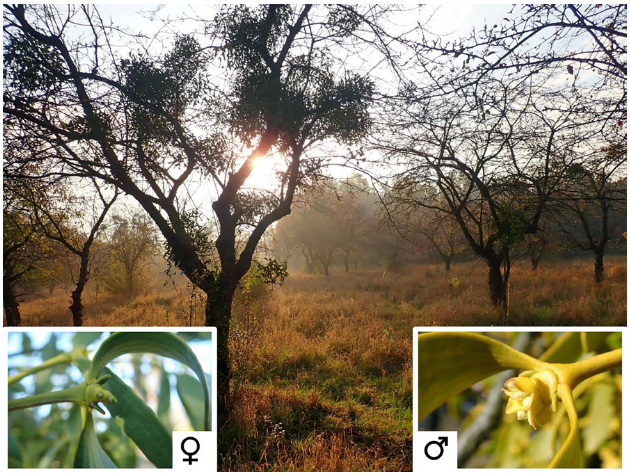

Fig. 1. Apple trees covered with mistletoe in the study area. Two smaller images in the bottom corners of the main photo show close-ups of mistletoe shrubs: the female plant on the left and the male plant on the right, each marked with the appropriate gender symbol (photo: D. Adamczyk)

For our analysis, we counted how many individuals of *V. album* were on each of the 357 *Malus* sp. individuals. Additionally, we chose 101 *Malus* sp. trees on which we not only counted mistletoe individuals but also identified their sex and age. For the mistletoe individuals growing on these trees, we measured the height and width of the *V. album* clump, length of the longest shoot and the height above the ground. The age of individuals was determined according to Zuber (2004) by counting the number of internodes and adding two years. The height of the clump was measured perpendicular to the ground surface, and the width of the clump was measured parallel to the ground surface and perpendicular to the base of the *V. album* shrub. The height above the ground was measured as the distance from the ground surface to the base of the shrub. We also determined the distance of the clump to the treetop. Moreover, we checked if the sex of mistletoe was connected to tree (host) height, diameter of the trunk at 5 cm above the root collar and sum of the intersection trunk area counted from the tree's diameter at breast height (DBH). We chose this last parameter instead of simple DBH, as measured apple trees have multiple trunks at breast height.

We considered mistletoe individuals to belong to the same clump if they grew on the same branch, were no more than 10 cm apart, and their shoots were touching. Based on this spatial criterion, we recorded the number of individuals in each clump. We then investigated whether male and female individuals differed in their tendency to grow in association with others, as reflected by the number of individuals sharing the same clump. We also calculated the mistletoe sex ratio for each apple tree, expressed as the percentage of female individuals among all mature mistletoe individuals. We then tested whether this ratio was correlated with the total number of mistletoe shrubs present on each tree, including both mature and immature individuals.

Assessment of chlorophyll fluorescence and photosynthetic pigments

In early spring (25 March 2022), chlorophyll *a* fluorescence parameters were measured in 50 individuals (25 males and 25 females) using a Fluorometer OS1p (Opti-Sciences, Hudson, New Hampshire, USA). Leaves were collected at about 9 a.m., wrapped in moist paper, placed in sealed bags and immediately transported to the laboratory. They were left in complete darkness for about 30 minutes at room temperature before the measurements were conducted. The leaves of male and female individuals were randomly measured. Parameters connected with chlorophyll *a* fluorescence, namely minimal (F_0) and maximal (F_m) fluorescence, were measured, and the maximum quantum efficiency of PSII photochemistry (F_v / F_m) and basal quantum yield (F_v / F_0) were calculated.

The leaf chlorophyll content of 50 individuals chosen previously for chlorophyll *a* fluorescence measurements was determined in early spring (29 March 2022) according to the method of Barnes et al. (1992). Five leaves from each individual were collected and placed in sealed bags on ice. They were placed in a refrigerator, and the next day, they were cut into small pieces (about 1 mm^2). Tissue samples with a fresh weight of 0.020 to 0.025 g were placed in a glass vessel fitted with a lid. Four millilitres of dimethylosulphoxide (DMSO) saturated with $CaCO_3$ was added to each vessel and placed in an incubator heated to 60 °C for 4 hours until complete discolouration of the leaves. Subsequently, the absorbance was measured on a Cary 60 UV–Vis spectrophotometer (Agilent Technologies) at 665, 648 and 470 nm wavelengths, and DMSO solution was used as a blank. Chlorophyll *a* and *b* contents were calculated on a dry weight basis according to Barnes et al. (1992), and carotenoids were calculated according to Lichtenthaler and Wellburn (1983). From these results total chlorophyll to carotenoid ratio (chl / car) and chlorophyll *a* to chlorophyll *b* ratio (chl *a* / *b*) were calculated.

Leaf functional traits: SLA and RWC

Branches (three-year internodes) of 50 individuals designated earlier for F_v / F_m measurements were collected and placed in leakproof bags on ice and immediately transported to the laboratory. Leaves were then detached from shoots and immediately weighed to obtain fresh weight (M_f). Subsequently, they were placed in bags filled with distilled water and left at room temperature for about 24 hours. They were then taken out of the bags and placed on dry paper towels to remove excess water from the surface of the leaves. They were weighed to obtain the turgid weight (M_t). Thereafter, they were placed in bags again and stored in a freezer. When they were defrosted, the surface of the leaves was scanned using an Epson Perfection V700 Photo scanner. They were then placed in envelopes and dried at 40 °C for 72 h, and the dry weight (M_d) was obtained.

Leaf traits were determined as follows:

- area
- specific leaf area (SLA):

$$SLA = \text{leaf area} / M_d;$$

- relative water content (RWC):

$$RWC = 100\% \times [(M_f - M_d) / (M_t - M_d)$$

(Slatyer & Shmueli, 1967).

Elemental analysis

C and N concentrations were obtained from leaves dried previously for SLA and RWC analysis (on average, about 40 leaves per sample). They were ground to fine powder, and 4 mg was used. The percentages of N and C in the dry weight were obtained using an elemental analyser (CHNS-/2400 Series II Perkin-Elmer, Waltham, MA, USA). Concentrations of P, K, Ca and Mg were obtained using an inductively coupled plasma time-of-flight mass spectroscope (ICP-TOF-MS; GBC Scientific Equipment; Braeside, Australia). Nitric acid was used to mineralise the samples prior to analysis. Standard PN-EN ISO 11885:2009 was used as the external standard method for calibration (ISO 11885:2007; Water Quality. Determination of Selected Elements by Inductively Coupled Plasma Optical Emission Spectrometry (ICP-OES); Warsaw, Poland, 2009). Additionally, calculations of the element ratios were conducted after the analysis.

Statistical analysis

JMP® 16.1 Pro software (SAS Institute Inc., Cary, NC, 1989–2022) was used for most statistical analysis. The results obtained as a percentage were transformed with Bliss correction for further analysis (Bliss, 1938). The methods described by Dean et al. (2017) were used to identify outliers. The homogeneity of variances was checked using Levene's test. When the data did not have equal variances, Welch's test was applied. All data were tested for normality using the Shapiro–Wilk test. Logarythmisation was applied when the data did not have a normal distribution. For data with a distribution deviating from normal, the Wilcoxon test was applied.

Data were analysed using analysis of variance or Welch's test. Sex was used as a source of fixed effects. For the age of shrubs and the number of individuals in one clump, Pearson and Mann–Whitney U tests were conducted in JMP and R packages (R Core Team, 2021). To compare the values of percent of females per tree with the total number of mistletoe shrubs per tree, we used the nonparametric Spearman's correlation. For the other relationships, Pearson's coefficient of correlation was used. The data are presented as the means ± standard errors (SE). Differences between means were considered statistically significant at $P < 0.05$.

Results

A total of 899 mistletoe individuals were recorded on the entire *Malus* sp. collection including 357 apple trees. From these, we selected 101 apple trees for detailed analysis, on which 394 mistletoe shrubs were growing. We identified the sex of these 394 individuals, which included 110 males, 174 females, and 110 immature individuals. Females accounted for 61% of mature individuals (chi^2 = 14.42, $p<0.001$). This indicates a female-biased sex ratio for this population. There were no significant differences between sexes based on age (Mann–Whitney U test, $p = 0.3648$; female 5.15±0.07, male 5.05±0.11), and the age structure for both sexes was similar.

We observed significant differences between sexes in the height of the *V. album* clump, with females exhibiting greater values than males (Table 1). Similarly, the width of the clump was significantly larger in female individuals (Table 1). Females also had a significantly longer main shoot compared to males. In contrast, no significant differences were found

Table 1. Mean and standard error for parameters describing morphology of the clump, its location and ecophysiological parameters of the leaves of male and female individuals of *Viscum album*. The table also contains the results of the analysis of variance. Significant differences are marked in bold

Parameter	Female		Male				
	mean	SE	mean	SE	F	DF	P
clump width (cm)	34.15	1.10	27.66	1.66	19.0500	1	**<0.0001**
clump height (cm)	32.72	1.16	25.64	1.34	18.6900	1	**<0.0001**
the longest shoot (cm)	20.97	0.59	18.26	0.91	13.0200	1	**0.0004**
distance from the ground (cm)	317.80	7.97	309.4	9.30	0.5400	1	0.4612
distance from the treetop (cm)	51.38	1.09	50.66	1.27	0.1300	1	0.7187
leaf area (mm^2)	53.03	1.60	53.93	1.87	0.1334	1	0.7166
RWC (%)	90.27	0.36	90.78	0.24	1.3917	1	0.2442
SLA (cm^2 g^{-1})	347.86	18.21	368.45	19.16	0.6072	1	0.4397
chlorophyll *a* mg g^{-1} DW)	2.05	0.17	1.71	0.11	2.4245	1	0.1262
chlorophyll *b* (mg g^{-1} DW)	0.32	0.03	0.23	0.02	7.3665	1	**0.0093**
chlorophyll total (mg g^{-1} DW)	2.37	0.19	1.94	0.13	3.0464	1	0.0875
chlorophyll *a* / *b*	6.41	0.18	7.44	0.23	12.2144	1	**0.0011**
carotenoids (mg g^{-1} DW)	0.93	0.05	0.86	0.03	1.4378	1	0.2373
chlorophyll / carotenoids	2.58	0.11	2.16	0.07	10.7842	1	**0.0019**
carbon (%)	46.51	0.28	46.59	0.23	0.0385	1	0.8453
nitrogen (%)	1.97	0.07	2.01	0.06	0.2337	1	0.631
C / N	28.47	1.14	27.59	0.85	0.3782	1	0.5417
magnesium (mg / g)	1.78	0.06	1.80	0.05	0.0661	1	0.7982
phosphorus (mg / g)	4.95	0.23	4.97	0.19	0.0036	1	0.9527
potassium (mg / g)	22.46	1.08	19.70	0.78	4.3416	1	**0.0427**
calcium (mg / g)	7.12	0.33	7.40	0.41	0.2792	1	0.5996
N / Mg	10.85	0.47	11.35	0.40	0.6524	1	0.4233
N / P	3.88	0.17	4.07	0.17	0.6014	1	0.4421
N / K	0.88	0.04	1.03	0.05	5.5458	1	**0.0229**
N / Ca	2.77	0.11	2.68	0.11	0.3723	1	0.5448
K / Mg	11.72	0.57	10.86	0.46	1.3915	1	0.2443
K / P	4.52	0.18	4.10	0.09	3.8372	1	0.0578
K / Ca	3.12	0.19	2.49	0.13	7.5213	1	**0.0091**
F_v / F_m	0.53	0.02	0.53	0.02	0.0442	1	0.8345
F_0	432.36	14.41	434.16	16.42	0.0068	1	0.9347
F_m	983.60	73.50	991.72	68.31	0.0065	1	0.9358
F_v / F_0	1.23	0.11	1.23	0.09	0.0256	1	0.8736

SE – standard error, F – results of statistic F, DF – degrees of freedom, P – probability, RWC – relative water content, SLA – specific leaf area, F_v / F_m – maximum quantum efficiency of PSII photochemistry, F_0 – minimal fluorescence, F_m – maximal fluorescence, F_v / F_0 – basal quantum yield.

between sexes in the height of the clump above the ground or in its distance from the treetop (Table 1). Male and female mistletoe individuals did not differ in the height of the host tree colonised by them (p = 0.7904), the diameter of the trunk of the host tree at 5 cm above the root collar (p = 0.6945) or the sum of the intersection trunk area counted from the tree's DBH (p = 0.6734). At the same time, sex did not influence the occurrence in association with other mistletoe individuals (sharing the same clump) (p = 0.6341) and the Spearman's coefficient of correlation values of percent of females per each tree with the total number of mistletoes per tree was negative (−0.16; ρ = 0.007).

There were no statistically significant differences between sexes in leaf area, RWC, SLA, or chlorophyll *a* content (Table 1), although the mean chlorophyll *a* concentration was numerically higher in females.

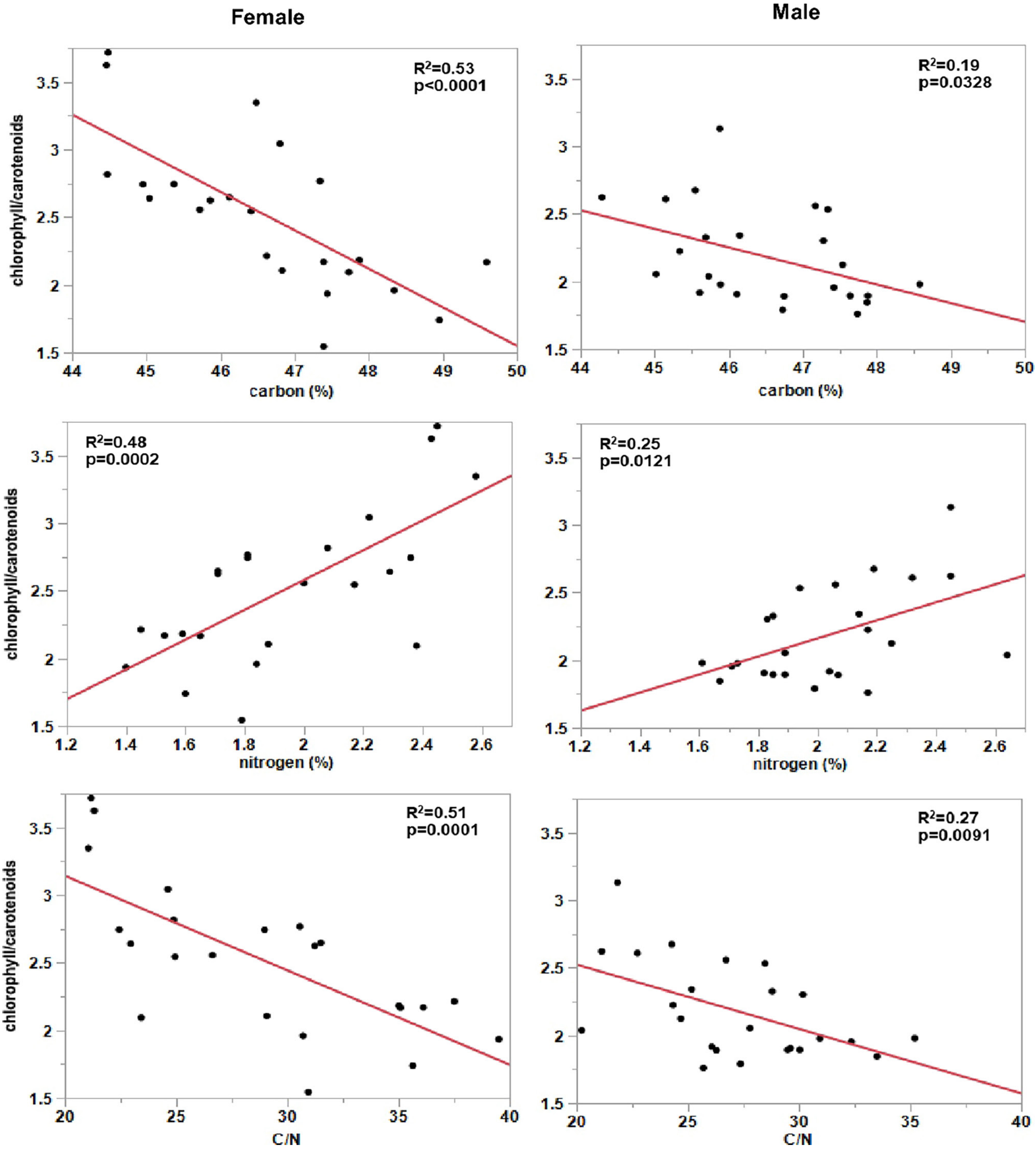

Fig. 2. Pearson's correlation analyses between chlorophyll / carotenoid ratio and carbon (%), nitrogen (%) and C / N ratio in leaves of male and female individuals of *Viscum album*

In contrast, chlorophyll *b* content was significantly higher in females than in males. Despite these differences, the total chlorophyll content (*a* + *b*) did not differ significantly between sexes. However, the chlorophyll *a* / *b* ratio was significantly higher in male individuals, reflecting the proportionally lower chlorophyll *b* content in this group.

Male and female individuals did not differ in carotenoid content, but the ratio of total chlorophyll to carotenoids (chl / car) was significantly higher in females (Table 1). This ratio was negatively correlated with both carbon concentration and the C / N ratio, and positively correlated with nitrogen concentration. In all cases, these correlations were stronger in females than in males (Fig. 2).

Nitrogen and carbon concentrations, as well as the C / N ratio, did not differ significantly between sexes. Similarly, no sex-related differences were observed in the concentrations of magnesium, phosphorus, or calcium. However, potassium (K) concentration was significantly higher in females. Consequently, females also exhibited a higher K / Ca ratio and a lower N / K ratio compared to males (Table 1). Chlorophyll *a* fluorescence parameters showed no significant differences between sexes (Table 1).

Discussion

After a century, the observations of Tubeuf et al. (1923) have been verified for the first time in terms of photosynthetic pigment concentrations. In line with hypothesis (1), our findings suggest that males invest more in photoprotective pigments, whereas females allocate more resources to chlorophyll. This explains the significantly yellower leaves of males during host dormancy, as previously noted by Tubeuf et al. (1923). This raises the question of whether the observed sex-based differences result from light conditions or differential stress responses.

The lower chlorophyll *a* / *b* ratio, higher chlorophyll *b* concentration, and higher chlorophyll / carotenoid (chl / car) ratio in females may indicate better shade adaptation or more efficient light absorption (Rosevear et al., 2001; Simova-Stoilova et al., 2001; Lichtenthaler & Babani, 2004; Willows, 2004; Lambers et al., 2008; Filimon et al., 2016). Although it might be assumed that males are more frequently exposed to light–particularly when the host is leafless–due to their positioning in the upper, more open crown areas, this seems unlikely. Contrary to hypothesis (2), no significant sex-based differences were found in specific leaf area (SLA), a parameter associated with light availability (Ackerly et al., 2002; Burns, 2004), or in vertical position within the host tree.

Another, not necessarily mutually exclusive, explanation for intersexual differences in photosynthetic pigment parameters relates to stress or senescence. An increased chlorophyll *a* / *b* ratio may indicate preferential chlorophyll *b* degradation under stress or during leaf aging (Hörtensteiner, 2006; Cunha Neto et al., 2020), while a reduced chl / car ratio shows a similar trend (Trifunović-Momčilov et al., 2021; Song & Wang, 2022; Miettinen et al., 2025). These patterns may reflect greater stress exposure or faster senescence in males, independent of leaf developmental timing, while the opposite in females suggests lower stress levels.

Differences in photosynthetic pigments may relate to sex-specific reproductive roles in *V. album* during early spring flowering. Males may allocate more resources to reproduction, reflected by reduced chlorophyll *b* concentration, prioritizing pollen production over photosynthesis. Male flowers are larger, with about 50 pollen sacs producing 35 × 60 μm pollen grains (Becker, 2000). In the related dioecious *V. capense*, pollen-to-ovule ratios are relatively high (12,012:1) for zoophilous plants (House, 1989; Cruden, 1977). Since *V. album* is partially anemophilous (Zuber, 2004), a similar or even greater ratio likely exists, indicating significant male reproductive investment. Thus, lower photosynthetic pigment levels in males may reflect a trade-off prioritizing reproduction over photosynthesis during flowering.

Despite potentially higher male reproductive effort early in the host's vegetative period, our results did not support hypothesis (3). No significant sex differences in nitrogen (N) concentrations were found. Although males had visibly yellower leaves and N availability correlates with pigment content in other species (Bayar, 2022), there was no evidence of reduced N acquisition or depletion in males during host dormancy compared to females. While N is vital for pollen production and photosynthesis (Rabie et al., 1983; Hikosaka, 2004), lower pigment concentrations in males were not directly linked to N deficiency. Both sexes may experience N depletion during dormancy but differ in N allocation, as suggested by correlations between N and the chl / car ratio.

Although nitrogen (N) and carbon (C) concentrations did not differ significantly between sexes, the strength of their correlations with the chl / car ratio differed markedly. The relationship between chl / car ratio and N was notably stronger in females, suggesting that females allocate more nitrogen to photosynthetic pigment synthesis, while males may use nitrogen for other metabolic processes.

The negative correlation between the chl / car ratio and carbon concentration in both sexes was unexpected and, to our knowledge, first documented in mistletoe. Typically, higher carbon content correlates with increased chlorophyll and indicates good physiological condition (Lorenzen, 1968). If *V. album* acquired carbon from the host, this could explain the pattern via its mixotrophic lifestyle, through a mechanism similar to that found in algae, where external carbon lowers chl / car ratio (Kong et al., 2020). However, evidence suggests *V. album* does not obtain host carbon (Wang et al., 2022). Thus, the pattern may reflect endogenous carbon metabolism or resource allocation over the course of the year, possibly indicating increased carotenoid production and energy reserve accumulation–strategies important for winter survival as seen in conifers (Huang et al., 2021). Moreover, this pattern might differ in stems, which contribute significantly to photosynthesis in winter (Míguez et al., 2015).

Despite significant differences in photosynthetic pigments, fluorescence parameters showed low photosynthetic efficiency with no sex differences contrary to hypothesis (4). The relatively low F_v / F_m ratio in March, compared to Chen et al. (2011), indicates strong physiological stress likely due to low temperatures and high light, causing photoinhibition typical of evergreens in winter or early spring (Skillman et al., 1996; Neuner et al., 1999; Yan & Hu, 2025).

Despite these constraints, transpiration in mistletoe leaves is maintained throughout the year, even at low temperatures, though it reaches a minimum in winter (Sapozhnikova, 2012), and under such conditions, water availability may be further limited by host dormancy – a potential source of additional stress for a parasitic species like *V. album*. The relative water content (RWC) did not differ between sexes, suggesting no major water status disparity (González & González-Vilar, 2001). Although water loss in mistletoe can be substantial (Escher et al., 2008; Zweifel et al., 2012; Zhang et al., 2025), water availability is generally not limiting for this hemiparasite (Skrypnik et al., 2020). Interestingly, Hultine et al. (2016) linked higher water availability to a greater proportion of females in population.

However, the physiology of *V. album* during host dormancy remains unclear. As the host reduces water uptake and increases cell sap viscosity to prevent freezing, water and nutrient transport may be restricted, potentially limiting element availability to the parasite (Fadón et al., 2020). Reduced transport capacity during host dormancy may explain sex-related differences in mineral concentrations. Significant differences in potassium (K) levels – supporting hypothesis 4 – could reflect male K deficiency during limited uptake, as K is a major element absorbed from the host (Horak, 1974; González de Andrés et al., 2024). While nitrogen (N) and calcium (Ca) levels did not differ between sexes, females showed higher K / Ca and lower N / K ratios. Mistletoe shows a preference for potassium uptake from host tissues over other elements (Horak, 1974; González de Andrés et al., 2024), with concentrations measured in this study consistent with previous findings (Horak, 1974; Lamont, 1983) and K / Ca ratios slightly higher than those reported by Horak (1974). In uninfested *Malus* sp., K levels in leaves, stems, and roots (Li et al., 2016) are comparable to those in mistletoe leaves, supporting the idea that mistletoe actively acquires K from the host, although the previously proposed phloem transport pathway (Horak, 1974; Lamont & Southall, 1982) now seems unlikely (Dołkin-Lewko et al., 2025). Because K is crucial for reproductive processes and mistletoe diverts it toward reproduction, males may face greater K limitation during host dormancy. This difference may reflect sex-specific variation in resource acquisition, with females potentially being more efficient at extracting nutrients from the host.

The biased sex ratio in *V. album* is linked to a cytogenetic mechanism–permanent translocation heterozygosity related to sex determination (Barlow & Wiens, 1976). However, the exact stage at which this bias phenotypically arises remains unclear (Showler, 1974; Wiens et al., 1996). It is also not fully understood why this female-biased system persists evolutionarily, especially since, according to our findings, females are not only more numerous but also larger in size.

Nevertheless, the female-biased sex ratio in *V. album* is consistent with findings for other parasitic species (e.g., Li et al., 2017; Cochard et al., 2019; Schneider & Reece, 2021). This phenomenon has also been documented in numerous previous studies on mistletoe from the genus *Viscum* (e.g., Barlow & Wiens, 1976; Barlow et al., 1978; Stanton et al., 2010; Zamora & Mellado, 2019). The persistent and universal female-biased sex ratio should be analysed in the context of mistletoe parasitism and the potential for secondary sexual dimorphism.

Chewyreuv (1913) reported that parasite sex ratios were influenced by host quality, with larger hosts supporting a higher proportion of females and smaller hosts a higher proportion of males. Subsequent research has confirmed this pattern (Seyrig, 1935; Werren, 1983; Harvey & Gols, 1998; Szentiványi et al., 2017). However, our study found no link between mistletoe colonization and host growth parameters, contrary to hypothesis (5). Nonetheless, it is conceivable that female shrubs are situated on branches or in areas of the crown that are of higher quality, though this hypothesis warrants further investigation.

Poulin (1997) suggested that female-biased parasite populations are most common in small or highly isolated populations–a pattern supported by some studies (Mullens & Luhring, 2023), but not all (Harvey & Gols, 1998; Szentiványi et al., 2017). Another explanation, Hamilton's (1967) local mate competition (LMC) theory, links female bias to sibling mating in isolated populations (e.g. Du et al., 2021). However, this does not apply to *V. album* subsp. *album*, which is widespread in Central Europe; the studied population was neither small nor isolated.

Sex biases in parasitic plants may relate to the degree of host colonization, as seen in *Phoradendron tomentosum* (female-biased in heavily infested trees) and *P. juniperinum* (male-biased) (Nixon & Todzia, 1985; Dawson et al., 1990). In our study, contrary to hypothesis (5), we found only a weak but significant negative correlation between the proportion of female mistletoes per tree and total mistletoe abundance on the host (Spearman's $\rho = -0.16$; $p = 0.007$). While this does not confirm male dominance in crowded conditions, it challenges the idea of female prevalence. Despite the overall dominance of females and their larger size in sexually mature stages, this pattern did not extend to trees with more shrubs. Early female growth advantages seen in other dioecious species (Nicotra, 1999; Cipollini et al., 2020; Nowak et al., 2021) may not translate into higher female abundance in clustered seed deposition zones created by birds (Thomas et al., 2023). The causes of this pattern remain unclear and require further study.

In *V. album*, resource availability for reproduction may be lower in males than in females, as males flower and produce pollen during the host's dormancy, when resource uptake is limited. Although females also flower at this time, their flowers are smaller and do not produce pollen (Becker, 1986; House, 1989). Differences in floral traits and pollen production have been discussed earlier in relation to pigment composition. The main reproductive costs for females occur during seed development and maturation, when the host is active and environmental conditions favour photosynthesis. As a result, female physiology may be more closely aligned with the host's vegetative cycle.

Females tend to be larger than males in some parasitic species (e.g., Harvey & Gols, 1998; Mullens & Luhring, 2023), and similar patterns have been observed in plant *Misodendrum quadrifolium* (Burns, 2021). Our study confirms this trend in *V. album*. Since age structure did not differ between sexes, size differences are unlikely due to age. A female-biased sex ratio can persist when pollen is abundant (Lloyd, 1974a; Stehlik et al., 2008), suggesting males may invest more in reproduction, leading to a stronger growth-reproduction trade-off – contrary to our original hypothesis. Recent studies show that survival and reproduction in *V. album* is dependent on plants size and trade- off between growth and reproduction is significant (Spacey et al., 2025). Secondary sexual dimorphism may give females a growth advantage, contributing to their larger size and the female-biased sex ratio.

Conclusions

In this study, we demonstrated for the first time that female *Viscum album* individuals outperformed males in several aspects. Not only was their frequency of occurrence higher, but they also attained greater size. Females allocated more resources to chlorophyll production, while males invested more in photoprotective pigments, resulting in a more yellowish appearance in males observed in early spring. This difference suggests that females may acquire resources more efficiently than males, as indicated by leaf discoloration. These variations in resource allocation and physiological responses might reflect adaptations to distinct sexual functions, potentially leading to differences in growth rates between the sexes. It is likely that female-biased sex ratios in *V. album* persist due to secondary sexual dimorphism favouring greater growth in females and possibly higher reproductive investment in males, which together create a trade-off that maintains this imbalance despite the absence of clear ecological advantages favouring females.

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