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Current knowledge on hemi-parasitic yellow mistletoe (*Loranthus europaeus* Jacq.)

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Abstract

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In spite of marked economical impact on forest timber production, more aspects of yellow mistletoe (*Loranthus europaeus* Jacq.) performance remain unknown and can inspire further research. This review comprehences current knowledge on taxonomical classification of this hemi-parasite, anatomy and morphology of its organs, its biological cycle and population ecology, effects on host-tree performance as well as its pharmaceutical potential. Based on it, gaps in the knowledge, particularly those with potential to be applied in management of this species, were outlined

Keywords

biology, impact on host trees, medicinal applications, morphology, population ecology, taxonomy, yellow mistletoe

Introduction

A recent unique project of the state enterprise Forests of the Slovak Republic and Forest Protection Service of the National Forest Centre on determination of hemi-parasitic yellow mistletoe (*Loranthus europaeus* Jacq.) effects on oak timber production and quality revealed significant decrease in height and bulk growth in infested oaks, which mirrored in timber volume loss of 0.117 m^3 calculated for a decade (economical loss of almost 12%). Furthermore, yellow mistletoe contributed to tree weakening and mortality, and lower oak branching caused by the parasite moves the production quality to lower categories. In spite of expensiveness, mechanical eradication in the tree crowns remains the only effective way of its regulation (Galko et al., 2022; Rozkošný et al., 2020). These results are a sufficient reason to know more about this economically important woody plant hemi-parasite. Thus, here we review the current knowledge on it, published in the past 50 years and outline gaps needing to be filled in order to prevent further damage in oak forests significantly affected by climate change.

Taxonomy, morphology and organ anatomy of *Loranthus europaeus* Jacq.

Yellow mistletoe is the only one European species of genus *Loranthus* Jacq. (Krasylenko et al., 2019). Classification of *L. europaeus* according to GBIF Backbone Taxonomy (2023): kingdom: Plantae → phylum: Tracheophyta → class: Magnoliopsida → order: Santalales → family: Loranthaceae → genus: *Loranthus* → species: *Loranthus europaeus* Jacq. Authors of older works stated that genus *Loranthus* Jacq. comprises about 600 species (Krüssmann, 1977) or 450–500 species (Hegi, 1981), but more recent papers based on nucleotide sequence data fundamentally revised phylogenetic classification of Santalales and assert that the genus consists of only about 10 species (Nickrent et al., 2010). Kuijt and Hansen (2015) even mentioned just two species. Most of *Loranthus* Jacq. species are semi-parasites on dicotyledonous angiosperms, a smaller number on gymnosperms (Zebec and Idžojtić, 2006). *Loranthus europaeus* (Fig. 1) is dioecious

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hemi-parasitic shrub, 40–100 cm tall, with a rounded shape, richly branched (Hoskovec, 2007). The branches are smooth, fragile, round, black-grey, with pseudo-dichotomous branching, divided at their base by ring-shaped furrows on which the rests of bud scales can be seen. Shoot is flexible, multi-nodal, with chestnut-brown paraepidermis (Bartha, 2014). The leaves are deciduous, nearly opposite, elongated or oval, simple, entire, 1–5 cm long, 1–2 cm wide, dark green, with short petioles (Záhradníková, 1984; Kubát, 1997; Hoskovec, 2007). There is no autumnal foliage colouring, leaves fall of green (Bartha, 2014). Inflorescence is simple, sessile, with or without terminal flower, male flowers are organized in racemes and female flowers in short spikes, species is entomogamous. Four to six petals are small, yellowish-green and flowering is dated to May–June (Hoskovec, 2007; Kuijt and Hansen, 2015). Male individuals are more vigorous and have a less drooping habitus, compared to female individuals. The flowers are not fragrant. The most common pollinators are bees from genus *Halictus* (Bartha, 2014). Fruits are yellow pear-shaped to round drupes, up to 1 cm in diameter, which ripen from mid-September to the end of November and remain on the trees during the winter months. Due to their development, fruits are called false berries. Seed inside is brown, rough in surface, 3–4 mm long, conical, bluntly hexagonal, rounded at the base and sunken at the tip. They are surrounded by a thick, mucous layer and are produced only by female shrubs, from the age of three years (Hoskovec, 2007; Bartha, 2014; Kuijt and Hansen, 2015; Bampali et al., 2024).

Fig. 1. *Loranthus europaeus* Jacq. on its host (Ouercus sp.): A – staminate ♂ and pistilate ♀ flowers, B – fruits. C – seed. Graphical design by Kateřina Janošiková (published by Krasylenko, 2019).

Several authors paid attention to anatomical and micro-morphological studies of *Loranthus europaeus* Jacq. – Andronache et al. (2006) investigated the structure of two vegetative organs (stem and leaf); Shahi Shavvon et al. (2012) published a complex work on anatomical and micro-morphological features of stem, leaf, petiole, fruit and seed; Glatzel et al. (2016) compared the wood structure of the hemi-parasite and its host, and Gebauer et al. (2019) introduced a comparative xylem study of petioles and twigs of mistletoe and host.

<u>*Stem:*</u> Cross section of stem is circular (Shahi Shavvon et al., 2012), but Andronache et al. (2006) described also elliptical contour in case of young stems. Epidermal cells are elliptic and covered with thick layer of cuticle. Stem shows a secondary growth and complete cambium ring is formed. Phellogen produces a thin cork zone (1–2 layers) and phelloderm is similar to the external cortical parenchyma. Numerous open collateral vascular bundles are present in the central cylinder. The pith is parenchymatic, with groups of sclereids containing cubical crystals of calcium oxalate. In lower parts of the stem, epidermis can be exfoliated, the cork layer is thicker and phelloderm collenchymatic (Fig. 2). Differently sized sclerenchyma bands are visible at the periphery of the vascular bundle (Andronache et al., 2006; Shahi Shavvon et al., 2012).

<u>*Leaf:*</u> In cross section, the leaf is quadrangular and epidermal cells are elliptic. Cuticle is present on the epidermis. Mesophyll is undifferentiated, of spongy type, with large, isodiametric or slightly elongated cells and involves only few intracellular spaces. The veins are not prominent. Vascular bundles are collateral. Paracytic stomata are arranged irregularly (Andronache at al., 2006; Shahi Shavvon et al., 2012).

<u>*Petiole:*</u> Usually, it is elliptic in cross section, epidermal cells also elliptic. Cuticle is on both sides of the epidermis. Mesophyll is undifferentiated with large intercellular spaces. Main vascular bundle is located in the central part, vascular bundles are of collateral type (Shahi Shavvon et al., 2012).

<u>*Wood structure:*</u> This species forms ring-porous wood with large-diameter early wood vessels (Glatzel et al., 2016).

Geographical distribution and host preferences

Loranthus europaeus is widely distributed in south-eastern and central Europe (Fig. 3), the eastern distribution border reaches Romania and Dnieper river in Ukraine, southern border of distribution includes areas to Sicily and Balkan peninsula, northern distribution border probably crosses Slovakia and extends to the Saxon region in Germany. Several isolated populations have been noted in Crimea and southern Turkey (Kubát, 1997; Eliáš, 2014; Krasylenko et al., 2019). The limit for the occurrence of *L. europaeus* at the northern border of its distribution are probably the climatic conditions, primarily the occurrence of frosts during the winter and spring months. Late spring frosts are causing increased shrub mortality. It is believed that climate change is responsible for expansion of yellow mistletoe into oak stands at higher elevations (Eliáš,

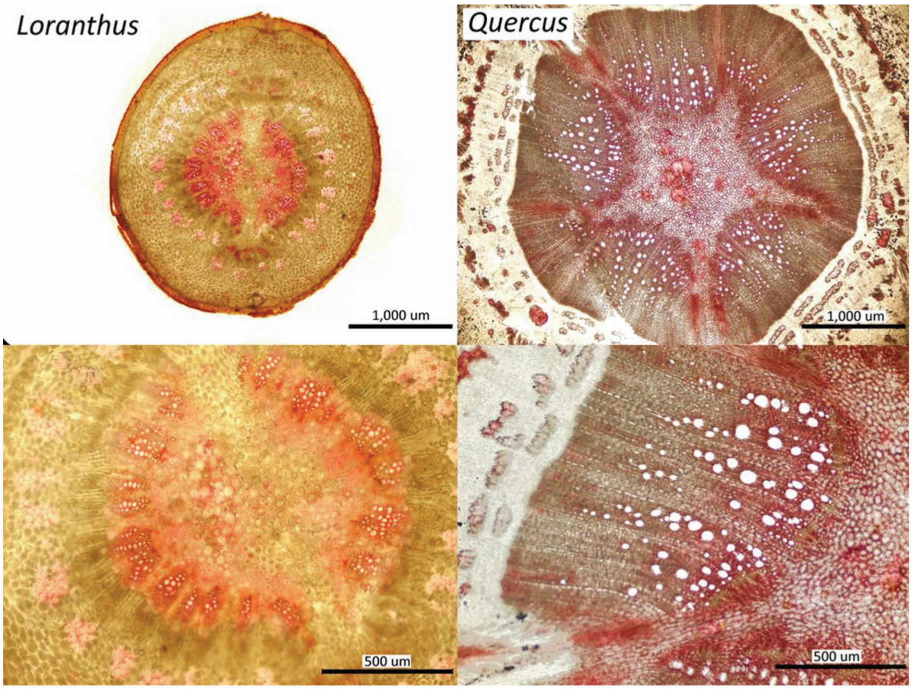

Fig. 2. Micrographs of *Loranthus europaeus* and *Quercus pubescens* cross sections of current-year twig (Gebauer et al., 2019).

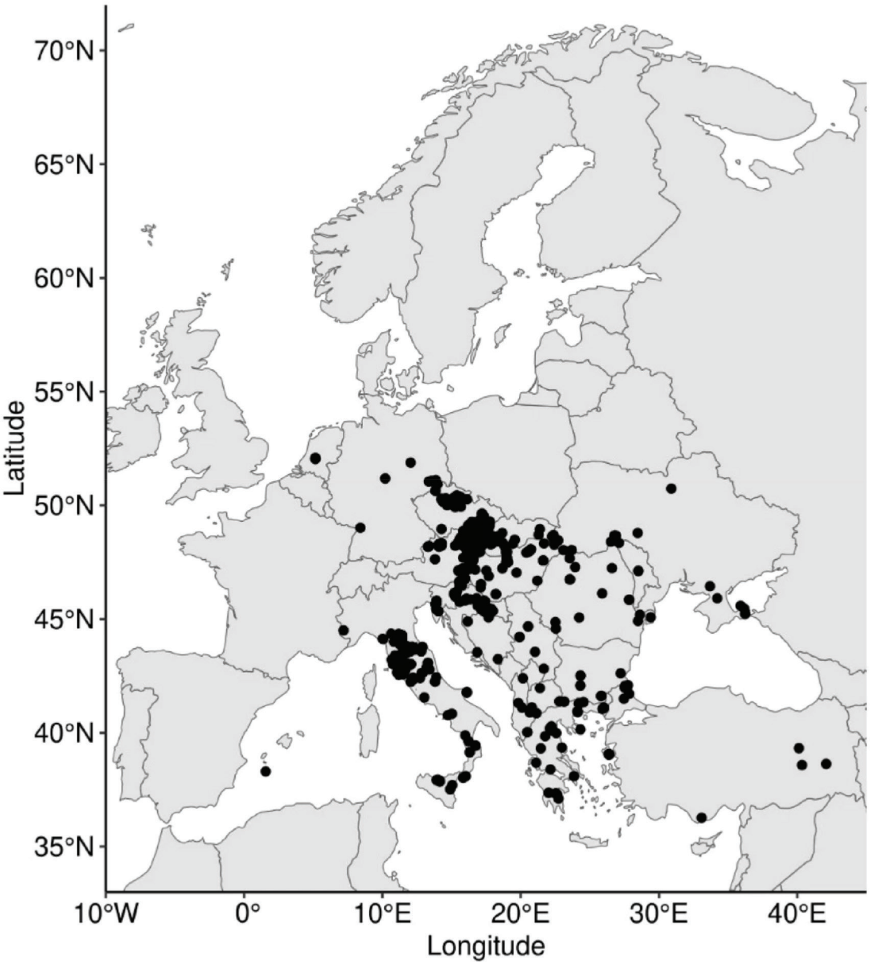

Fig. 3. Distribution of *Loranthus europaeus* Jacq. in Europe – retrieved from Global Biodiversity Observation Facility (GBIF. org, 2024), field surveys, herbarium and literature records (Baranowska et al., 2025).

2007; Galko et al., 2018). Birds are the main vector of yellow mistletoe, especially species of family Turdideae (Bartha, 2014).

The yellow mistletoe host trees are primary oaks (Fagaceae), such as *Quercus pubescens* Willd., *Q. cerris* L., *Q. robur* L. and *Q. petraea* /Matt./Liebl., though it can also appear on *Olea europaea* L. (Oleaceae) and *Castanea sativa* Mill. (Fagaceae) (Krüssmann, 1977; Hegi, 1981). In Slovakia, *L. europaeus* was confirmed on *Quercus pubescens*, *Q. cerris*, *Q. petraea*, *Q. robur*, *Q. dalechampii* Ten., *Q. virgiliana* (Ten.) Ten., *Q. rubra* L., *Q. acutissima* Carruth. (in the Mlyňany Arboretum SAS) (Eliáš, 2002; Eliáš, 2020) and *Betula pendula* Roth. (Betulaceae) (Kovaříková and Procházka, 2001). Eliáš (2002) also mentions *Acer campestre* L. (Sapindaceae), *Castanea sativa*, *Carpinus betulus* L. (Betulaceae) and *Crataegus monogyna* Jacq. (Rosaceae), but without additional confirmation. In the Czech Republic, *L. europaeus* grows on *Quercus robur*, *Q. petraea*, *Q. pubescens*, *Q. rubra* and *Q. cerris*, very rarely it was observed on *Carpinus betulus*, *Prunus spinosa* L. (*Rosaceae*) and *Acer campestre* (Kubát, 1997; Hoskovec, 2007). In Slovenia, yellow mistletoe was reported on three autochthonous oaks – *Quercus petraea*, *Q. pubescens*, *Q. robur* and *Castanea sativa* (Kogelnik, 2002). In Croatia, *L. europaeus* was found on 10 species, 5 autochthonous oaks – *Quercus robur*, *Q. petraea*, *Q. cerris*, *Q. pubescens*, *Q. frainetto* Ten., 2 allochthonous oaks – *Q. rubra*, *Q. palustris* Münchh, *Castanea sativa* and *Carpinus betulus* (Zebec and Idžojtić, 2006). In Ukraine, *L. europaeus* was confirmed on *Quercus petraea*, *Q. robur* and *Q. rubra* (Krasylenko et al., 2019). In Austria, it was observed on *Q. robur* and *Q. petraea* in Styria (Aprent, 2017) and on *Q. cerris*, *Q. macrocarpa* Michx., *Q. petraea*, *Q. robur*, *Q. rubra* and *Q. pubescens* in Vienna and in the surrounding forests (Tokarieva et al., 2025).Kumbasli et al. (2011) observed the greatest infection rate on *Quercus petraea*, lower on *Q. frainetto* and no infection on *Q. cerris* in Turkey. In contrast, *L. europaeus* itself can be a host of *Viscum album* L. subsp. *album* (hyper-parasitism), as referred by Grazi and Urech (1985) and Kubát (1997).

Host tree – hemi-parasite interaction and infestation process

Seed germination and establishment of the connection to host tissues represents the critical point in the life cycle of a parasitic plant (Těšitel, 2016). Hemi-parasitic mistletoes have evolved photosynthesis in the endosperm (Nickrent and García, 2009), which is very rare in angiosperms. This adaptation helps the seedling to penetrate thick host bark, what may require a large amount of energy. Mistletoes seeds must firmly attach to the host branch and then the seedlings must overcome host defence mechanisms and establish the connection (Glatzel and Geils, 2009). It is easier in places, where the primary dermal tissues of the branches are under tension, disturbed and replaced by secondary dermal tissues – this exchange occurs in oak branches between the 4th and 6th year of growth (Kubíček et al., 2011). Sargent (1995) mention that mistletoe seedlings more frequently died on larger branches than on smaller twigs, probably because they are unable to penetrate the thicker bark of larger stem diameter branches. The haustorium of *L. europaeus* is relatively small and cone shaped (Fig. 4). This haustorium grows simultaneously with the xylem of its host. The tip of the cone has its origin at the annual growth ring of the host, where the germinating *Loranthus* seed firstly penetrated the bark and came into contact with the cambium of the host (Glatzel et al., 2016).

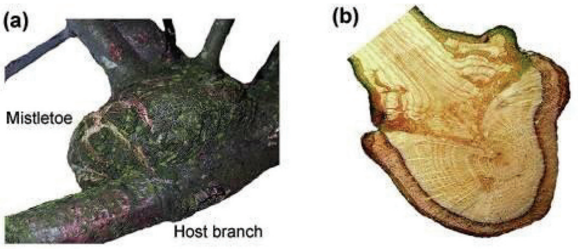

Fig. 4. Haustorium of *Loranthus europaeus*: a – general view of haustorium; b – transverse section (Glatzel et al., 2016).

Ecology and spatial distribution of the hemi-parasite

Importance of host suitability and habitat conditions for mistletoe distribution was confirmed in several studies (Press and Phoenix, 2005; Rist et al., 2011; Matula et al., 2015; Ramon et al., 2016; Sayad et al., 2017). Mistletoes show a low host preference in heterogeneous tropical rain forests and high host preference in less diverse temperate forests because in such systems is the abundance in favour of distribution and infection (Press and Phoenix, 2005). The presence and abundance of mistletoes at the habitat scale are regulated by a range of abiotic and biotic factors (Gairola et al., 2013), the distribution of suitable host, vector and pollinator species (Norton and Reid, 1997; Rist et al., 2011; Ramon et al., 2016), behaviour of avian vectors (Aukema and Martínez del Rio, 2002), habitat fragmentation (Lavorel et al., 1999), herbivory (Reid and Yan, 2000) and topographical parameters (Aukema, 2004).

Most studies confirm a higher abundance of yellow mistletoe in less dense habitats, solitary trees or trees closer to the edge of the stand (Sterba et al., 1993; Lopez de Buen et al., 2002; Kubíček and Martinková, 2010; Kumbasli et al., 2011). Watson (2008) has suggested that parasitic plants are more likely to establish and grow on host plants with better access to resources. The probability of mistletoe infection decreased with neighbouring host abundance (Sasal et al., 2021). Matula et al. (2015) found that competition among host trees has important negative effect on probability of *L. europaeus* occurrence as well as on its abundance on a tree. Competition also changes resource allocation within individual trees available for mistletoes. However, the number of mistletoe seeds is usually limited, so the decrease in the probability of mistletoe infection with an increase in competition from neighbouring trees may arise not from the changes in availability of resources, but simply from a decreasing probability of receiving mistletoe seed due to the increased number of neighbouring host trees (Matula et al., 2015; Sasal et al., 2021). On the other hand, Matula et al. (2015) stated, that distance to an infested tree affects the probability of mistletoe infection at short distance (less than 5 m), but does not affect the severity of infection.

On the individual host scale, most studies state that mistletoe infection is positively related to tree size (height, diameter), age, occurrence of branches with certain diameter and previous infection of host tree or stand (Aukema and Martínez del Rio, 2002; Ward, 2005; Kubíček and Martinková, 2010; Matula et al., 2015; Kubíček et al., 2018). Probability and intensity of yellow mistletoe infection increase with host size and age (Matula et al., 2015; Sayad et al., 2017; Kubíček et al., 2018; Kubov et al., 2020; Rozkošný et al., 2020). However, some studies suggest that large trees are more likely to be infected because they receive more mistletoe seeds than smaller trees due to the higher number of bird visits (Aukema and Martínez del Rio, 2002; Lopez de Buen et al., 2002). In addition, it is also likely that larger trees have greater surface area of the small twigs on which yellow mistletoe seed are able to establish successfully (twig diameter less than 6 cm) (Kubát, 1997). Eliáš (2020) summarized that the majority of *L. europaeus* (86.1%) grew on branches 5 cm in diameter at a height of 16 m. Matula et al. (2015) observed that the probability of infection on a whole tree level increased significantly with an increase in mean stem diameter but decreased with growth of Hegyi competition index (Hegyi, 1974) for trees (the whole infection rate was 14.8% (105 infected trees of 710 monitored trees)) and the probability of mistletoe infection at the stem level significantly increased with increasing stem diameter but decreased with increasing distance from the nearest infected stem (infection rate of oak stems was 12.9% (131 infected stems of 1015 monitored stems)). Sayad et al. (2017) suggest, that the mistletoes first establish in the middle crown part and then develop downward into the lower crown.

Population structure and dynamics

The populations of *Loranthus europaeus* can be considered as host-specialized to a few related host species (Atsatt, 1983). It shows contagious dispersion associated with oaks monitored a half century ago at the territory of Czechoslovakia. More than a third of all oaks in the research area in Slovakia (34%) was infected (*Q. cerris* 38.2%, *Q. petraea* 24.1%) (Eliáš, 1987; 1988; 2004; 2020). The infection with *L. europaeus* has been considered to proceed more or less centrifugally from a „founding“ infected host plant to the neighbouring hosts (Alfaro et al., 1985). In forest stands occupied solely by tall oaks, „founding“ individuals of infection were identified as heavily infected dominant trees. Their upper crown portions above the main canopy layer, which was formed predominantly by e.g. crowns of Carpinus betulus and *Acer campestre* (Eliáš, 1987).

A considerable part of *L. europaeus* populations does not participate in the reproductive process (currently expressed only by metapopulation dynamics (Eliáš, 1996; 2020), but not by individual reproductive success in population), fruit production, and on the infection process due to dioecy and demographic structure of population (Eliáš, 1987; 2004a). Eliáš (1989) mentioned that male mistletoe shrubs accounted 69.2% of all living *L. europaeus* individuals in the host-tree population, but in subsequent publications (Eliáš, 1997; 2004b; 2020) author noted that the sex ratio was either male-biased or approached parity. Only 25.6% of whole coenopopulation (collective term for the sum of individuals of a species in a plant community (Rabotnov, 1985)) in the oak-hornbeam forest were fruiting (Eliáš, 1988). Frequency and density of the fruiting mistletoe shrub coenopopulation as well as sex ratio were low in the *Q. petraea* host in both the oak-hornbeam forest and within-host-tree population in southwestern Slovakia (Eliáš, 1997; 2020).

When interpreting estimates of sex ratio, several caveats appear. First, sex ratios were obtained from reproductive individuals because of the inability to identify the gender of non-reproductive plants. The sex ratio is underestimated because young female mistletoes unable to produce fruits were not distinguished from male plants (Eliáš, 1987; Barrett et al., 2010). Second, many dioecious species are clonal and in these cases sex ratios were based on samples of ramets rather than genets (Barrett et al., 2010). *L. europaeus* is considered subdioecious, i.e. populations have pistillate plants, staminate plants, and some individuals with both staminate and bisexual flowers (Fig. 5) (Sakai and Weller,

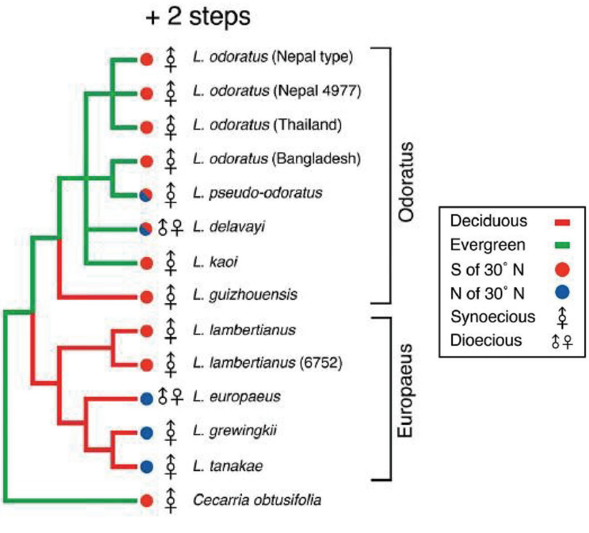

Fig. 5. Relationships among *Loranthus* species determined by cladistic (maximum parsimony) analysis of morphological characters. The topology of the tree adds two steps for *L. lambertianus* and *L. europaeus*, thus making a Europaeus clade monophyletic. Foliar habit (deciduous vs. evergreen), geographic distribution, and plant sexual mode are plotted on this tree (Nickrent et al., 2021).

1999). Subdioecy was first described in *L. europaeus* by Von Jacquin (1762) who used the term "hermaphroditus sterilis" for plants with female sterile plus bisexual flowers (Nickrent et al., 2021). The trade-off between female and male fitness reflecting the gender plasticity (including ecological, life history and demographic factors) might lessen and help maintain subdioecy (Ehlers and Bataillon, 2007). The subdioecy may persist at the metapopulation level as a result of selection during colonization/recolonization (hermaphrodites), and in established colonies (unisexuals) due to inbreeding avoidance (Pannell, 2006).

The host-hemiparasite interaction intensified for last 50 years, leading to higher within-tree population in oaks, and this trend is observed not only in eastern Austria (Tokarieva et al., 2025). In the period from 1978 to 1987 metapopulation of *L. europaeus* in southwestern Slovakia increased by about 10%, the number of infested trees (oaks) increased by approximately 10%. The population density reached 6.8 shrubs per infested tree, and the mean density was approximately 1.9 shrubs per branch (Eliáš, 2020). Matula et al. (2015) found from 1 to 7 mistletoes shrubs per stem, but most of the infected stems had only 1 mistletoe shrub. Currently, there is an absence of up-to-date information regarding the *L. europaeus* populations, metapopulations, and coenopopulations.

Impact on the host tree performance

Loranthus europaeus, as a hemi-parasitic mistletoe plant, lacks the typical root system and is dependent on the formation of a xylem connection with host plants through the haustorium to obtain water and mineral nutrients (Watson, 2001; Glatzel and Geils, 2009). In the case of hemi-parasitic *Loranthus europaeus* on *Quercus* spp., better host fitness reduces mistletoe performance. In a sufficient moisture and nutrient environment, the host grows well and can even shade out the mistletoe; but on dry sites with the lack of nutrients oaks grow more slowly and the mistletoe infestation increases, eventually impacts of severe disease may develop (Mayer, 1982; Glatzel and Geils, 2009). Thus, yellow mistletoe is particularly dangerous for oaks exposed to water deficit. Drought progressively impairs tree water relations and physiological performance (Ayaz et al., 2025), making host trees more susceptible to infection under climate change (Sanguesa-Barreda et al., 2012).

Mistletoes divert xylem sap from the host through direct xylem connections, altering the host tree's water status (Glatzel, 1983). The movement of xylem sap requires a gradient in water potential. When photosynthesis of host is greatest, its water potential in the xylem becomes most negative. To maintain this gradient and avoid stomatal closure, mistletoe has to tolerate even lower water potential (Glatzel and Geils, 2009). The parasite's narrower xylem conduits may be adapted to withstand a higher water potential gradient without cavitation (Gebauer et al., 2019).

Schulze et al. (1984) report that a minimum water potential of the parasite is 1.0–1.5 MPa lower of that of the host (*Q. robur*). According to Eliáš and Huzulák (1978) the water potential of mistletoe branches during the midday hours throughout the whole vegetation season was 1.6–4.9 MPa lower than the water potential of its host (*Q. cerris*) leaves on the nearest branch above the attachment site. This behaviour supplies the mistletoe with water and nutrients, but at the same time puts the host plant's life at risk (Urban et al., 2012). During drought conditions, infested *Q. petraea* trees exhibit a more negative leaf water potential (−2.5 MPa) compared to non-infested trees (−1.58 MPa) (Kubov et al., 2020), approaching the xylem embolism threshold for this species (Cochard et al., 1996). The host tree cannot control the water lost by the mistletoe, leading to a reduction in its xylem water potential, which triggers stomatal closure and reduces carbon assimilation (Glatzel and Geils, 2009). During stomatal closure at critical leaf water content levels, water depletion by the parasite is likely to seriously disrupt the feedback loops (Glatzel, 1983).

Transpiration of *Loranthus europaeus* may even increase initially at constant low water potential (Fig. 6), however cannot endure over prolonged periods of time since transpiration would deplete any water stored. Transpiration is reduced before reaching maximum vapor pressure deficit in the air (Schulze et al., 1984). During the season of growth, mistletoe transpired five times more water (per unit of leaf area) than its host *Q. pubescens*. In addition, the two plants also exhibited differences in the shapes of their diurnal sap flow curves. Typically, the mistletoe's sap flow lagged by roughly one hour compared to that of the oak. Therefore, mistletoe not only transpired a greater amount of water per unit of leaf area but also accomplished this over a shorter duration (Urban et al., 2012). Schulze et al. (1984) observed about 3 times higher transpiration and leaf conductance in mistletoe than in

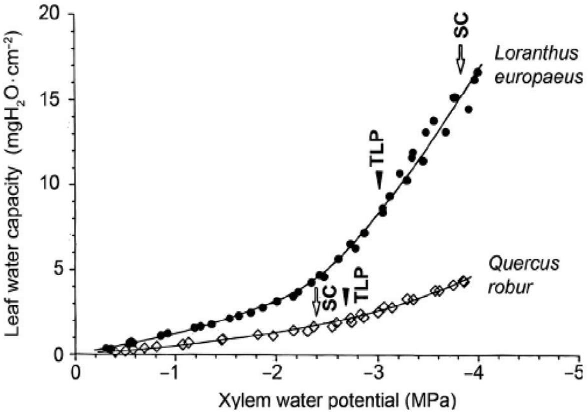

Fig. 6. The transpiration control system in the hemi-parasitic mistletoe *Loranthus europaeus* and its host *Quercus robur*. The host closes its stomata at less negative water potential well before wilting, the parasite tolerates wilting and closes it stomata only at much more negative water potential. Mistletoe leaves are succulent and store more water per unit leaf area than host leaves (modified from Glatzel, 1983). TLP, turgor loss point (wilting); SC, stomata closed (Glatzel and Geils, 2009).

its host (*Q. robur)*. KUBOV et al. (2020) similarly reported higher average transpiration rate and also stomatal conductance in mistletoe than in infested oaks (3.3 and 4 times higher) or non-infested oaks (2.2 and 2.5 times higher).

Assimilation rates in non-infested trees were almost twice as high as in infested trees. However, there was a little or no significant difference in assimilation rates between hosts and their parasites. In addition to reducing the CO_2 assimilation rate of the host tree, yellow mistletoe may also extract carbon from the host xylem sap, as no direct phloem connection exists between the host tree and the hemiparasite (TENNAKOON and PATE, 1996; KUBOV et al., 2020). Considering transpiration and assimilation rates, water-use efficiency was the lowest in mistletoe, what generally means that more water is required for carbon fixation (SCHULZE et al., 1984; KUBOV et al., 2020).

Despite lower stomatal conductance in infested trees, higher intercellular CO_2 (Ci) concentrations were observed compared to non-infested trees, while mistletoe maintained Ci concentrations close to ambient levels (KUBOV et al., 2020). FLEXAS and MEDRANO (2002) identified an inflection point beyond which Ci increases as stomatal conductance declines. This suggests that photoinhibition may have occurred in infested trees (KUBOV et al., 2020). Photosystem II in infested trees showed no significant damage compared to non-infested trees, suggesting a high drought resistance of PS II photochemistry. Nevertheless, infested trees exhibited significantly reduced electron transport rates, while upregulating non-photochemical quenching (dissipation excess energy as heat) to prevent ROS overproduction (KUBOV et al., 2020).

Nitrogen and mineral nutrient uptake of mistletoes also rely upon the connection through the haustorium. Hemi-parasitic mistletoes lack specific mechanisms for selective nutrient uptake and depend only on simple diversion of host xylem sap. Nutrient flow is predominantly one-way as parasites do not share nutrients with their hosts (GLATZEL and GEILS, 2009). The concentration of minerals in mistletoes is generally higher than in branches of the host, with average differences between the two decreasing in the following order: K (up to 20.6 times), P, Mg, Mn, Na, Ca, N, and Fe (up to 1.4 times) (LAMONT, 1983). The study by GEBAUER et al. (2018) confirmed this general trend for S, P and Mg, however nutrient ratios varied greatly during the growing season, especially in leaves during leaf expansion and senescence.

Compared with their host, mistletoes show very high levels of potassium enrichment (GLATZEL, 1983; SCHULZE, 1984; GEBAUER et al., 2012). SCHULZE et al. (1984) reported potassium concentrations of 0.23 mmol g^{-1} in the leaves of *Q. robur* and 1.5 mmol g^{-1} in *L. europaeus*. Several hypotheses have been proposed to explain this phenomenon. Potassium usually accompanies sugars in phloem sap, moves to the sites of photosynthate utilization, and then can freely enter xylem sap and ascend into leaves. The absence of retranslocation between the parasite and the host makes this a passive process, where mistletoe acts as a potassium trap, diverting this element from the xylem-phloem cycle of the host. The hypothesis of active uptake of potassium, as an important element for osmosis and transpiration, was also suggested. However, this would require very high flux densities of potassium in haustorial boundary layer (GLATZEL, 1983; GLATZEL and GEILS, 2009).

Accumulation of calcium in the trees increases with higher transpiration rates. Due to the fact that mistletoe is directly connected to the same xylem sap as its host, it is expected that the higher transpiration of mistletoe will cause higher calcium concentration in mistletoe leaves (GEBAUER et al., 2012). URBAN et al. (2012) found that mistletoe had higher calcium content per leaf area compared to its host, with 3.04 g m^{-2} for *L. europaeus* and 1.79 g m^{-2} for *Q. pubescens*. However, calcium accumulation was not proportional to the transpiration rate. This could be attributed to calcium leaching through mistletoe foliage by rain, dew and mist.

Nitrogen is much more mobile than calcium but leaf growth is a strong sink for nitrogen, as it is utilized in proteins and other cell components, resulting in minimal retranslocation before senescence. A seasonal nitrogen uptake ratio of 1.31 in *L. europaeus*/*Q. petraea* is described by GLATZEL (1983b). GEBAUER et al. (2012) found higher nitrogen concentrations in *L. europaeus* leaves during spring and autumn, while *Quercus* showed higher concentrations in summer, but the values were quite similar. Nitrogen is suggested to be a limiting element for *L. europaeus* growth. Considering the high transpiration of the *L. europaeus*, it is likely that in early stages of leaf development, the host may receive nitrogen not only from the xylem (which would be the same for host and mistletoe), but also from a source inaccessible to the parasite, perhaps the phloem (SCHULZE, 1984).

Mistletoes can tolerate extreme excesses of certain elements and variability in nutrient balance, enabling them to occupy a wide range of sites with different soil characteristics. Regarding mineral deficiencies, no symptoms have been detected in mistletoes. This may be explained by their ability to produce less biomass for a given amount of xylem sap than their host, allowing them to concentrate solutes, as well as by higher transpiration rates of yellow mistletoes (GLATZEL and BALASUBRAMANIAM, 1987).

L. europaeus should be considered as an indicator of habitat health or, in the case of heavy infestation, as a sign of landscape disturbance (WATSON, 2001). DAKSKOBLER (2014) indicates, that frequent occurrence of *L. europaeus* points out to poor state of the oak population. KUMBASLI et al. (2011) state that *L. europaeus* is one of the biological parameters contributing to the decline of oak stands. Heavily affected hosts respond with accelerated aging and crown dieback, which can lead to losses in the economic value of oak timber mass and a reduction in the increment (NOVÁČEK, 1985). In infested oaks, lower branches become thicker, what alters the entire tree habitus. Accelerated growth of lower branches is an effort of the tree to maintain the physiological performance as the upper part of the crown is more severely affected. However, this defence mechanism is effective only when the infection is not spread and has a small extent (KUBÍČEK et al., 2011; KUBOV et al., 2020). Heavy infestation by yellow mistletoe leads to a loss of wood quality (Eliáš, 1988). Rozkošný et al. (2019) conducted a study on two sites in Slovakia and stated, that *L. europaeus* negatively affects the growth of oaks, as infected trees were on average 1.9 meters lower than uninfected trees, and the annual diameter increment was 0.9 cm lower per year. The growth of haustoria leads to branch malformations in the host trees, disruption of their dermal tissues, occurrence of wood rot, dieback and breakage of branches (Kubíček et al., 2011). Trees infected by yellow mistletoe are more susceptible to secondary abiotic and biotic factors (insects, fungi, etc.) (Treštić, 2006) and are easily infected through dead or broken branches (Ogris et al., 2010).

Medicinal applications

The Loranthaceae family, comprising various species, has been the subject of several chemical studies, which have revealed presence of important phytochemical compounds. Recent research has resulted in identification of numerous secondary metabolites, including alkaloids, flavonoids, phenolic compounds, lignans, neolignans, and triterpenes (Muhammad, 2024). *L. europaeus*, like many other species of mistletoe, has a long history of use in folk medicine for a variety of therapeutic purposes (Jawad et al., 2006; Vitasović Kosić et al., 2017). Leaves and fruits of *Loranthus europaeus* were used in Iraq traditional medicine for treatment of inflammation, tumours and antimicrobial infection (Harvvey 1993). In several regions of central Italy, the whole plant macerated in wine or grappa was used to cure atherosclerosis and hypertension (Leporatti and Corradi, 2001), whereas in Calabria region (southern Italy) leaves were also topically applied to cure wounds (Leporatti and Pavesi, 1989). Ambrosio et al. (2020) reported the antibacterial properties of methanolic and ethanolic extracts of *L. europaeus* berries against a range of microorganisms, including *Listeria monocytogenes*, *Staphylococcus aureus*, *Salmonella typhimurium* and *Escherichia coli*. In an animal study employing a methanolic extract of *L. europaeus* leaves, anaesthetic and analgesic properties were observed (Nasrin et al., 2015). The antimicrobial and cytotoxic activities attributed to *L. europaeus* could be also due to the presence of so-called defense peptides, more recently known as plant defensins, largely occurring in different genera of parasitic members of Santalaceae and Loranthaceae (Parisi et al., 2019). Recently, an anti-leishmaniasic effect has been attributed to the presence of a high concentrations of quercetin in the whole plant extract (Sharquie et al., 2017).

The medicinal properties of *L. europaeus* are closely linked to the content of bioactive compounds, whose concentration/abundance may vary depending on various factors. These include the stage of development of the plant, the organ analysed (leaves, flowers, stems, fruits or seeds), the habitat of the plant or the extraction method used. For example, Benabderrahim et al. (2019) reported that the highest total phenolic content (TPC) was detected in the fruits and stems of *L. europaeus*, whereas the leaves exhibited lower levels. The total flavonoid content (TFC) was highest in the fruits, with concentrations being twice as high as those found in the stems and leaves. Similarly, in the study by Katsarou et al. (2012), TPC and TFC varied significantly between different parts of the plant. TPC was significantly higher in fruits (83.98 ± 0.30 mg GAEs g^{-1} extract) and stems (83.25 ± 1.43 mg GAEs g^{-1} extract) than in leaves (72.59 ± 0.20 mg GAEs g^{-1} extract). In the case of TFC, fruits had approximately 2-fold higher values (139.73 ± 1.80 mg QEs g^{-1} extract) than those found in stems and leaves (63.61 ± 1.33 mg QEs g^{-1} extract). The research conducted by Najjarsadeghi et al. (2024) indicated that the dried fruits of *L. europaeus* contained 12.78 g of phenolics and 3.61 g of flavonoids per 100 g of dry weight. Furthermore, Çömlekçioğlu et al. (2024) found that ethanol extracts of the entire *L. europaeus* plant from Turkey contained 34.49 mg g^{-1} of total phenolics and 55.82 mg g^{-1} of flavonoids. In contrast, methanol extracts had higher phenolic content (46.10 mg g^{-1}) but slightly lower flavonoid content (55.49 mg g^{-1}). Rajab et al. (2024) reported a significantly lower flavonoid content (2.545 mg g^{-1}) in methanolic extracts of *L. europaeus* fruits collected in Iraq. A study conducted in Tunisia revealed that the total phenolic content in methanol extracts of *L. europaeus* ranged from 72.59 to 83.98 mg GAEs g^{-1}, while the total flavonoid content ranged from 63.61 to 139.73 mg QEs g^{-1} (Benabderrahim et al., 2019). Meanwhile, research in Greece indicated even greater variability in total phenolic content of different aerial plant parts (stems, twigs, leaves, flowers, fruit): the methanol extract of *L. europaeus* contained 94 to 320 mg g^{-1} of total phenolics. Additionally, the ethyl acetate extract showed a phenolic content between 61 and 313 mg g^{-1} (Katsarou et al., 2012).

A comprehensive screening of phenolic compounds in the methanolic extracts of diverse plant parts (Benabderrahim et al., 2019) revealed the presence of 22 distinct compounds. The predominant compounds were identified as chlorogenic acid and hyperoside, which were found to be present mainly in the leaves, while the predominant compounds in the stems of *L. europaeus* were identified as (+)-catechin and (-)-epicatechin (Fig. 7). High concentrations of pinoresinol (a lignan) were exclusively observed in the stems of the yellow mistletoe. The dominance of (+)-catechin and (-)-epicatechin in the stems of *L. europaeus* was also confirmed by Bampali et al. (2024). In a study by Hamad et al. (2013), the presence of kaempferol, quercetin and rutin in methanolic and ethyl acetate extracts was observed in the seeds. The aglycones of quercetin have been identified in the leaves of *L. europaeus* (Aljeboory and Al-Zubaidi, 2020), as well as derivatives of kaempferol and quercetin, namely rhamnocitrin-3-*O*-rhamnoside, rhamnetin-3-*O*-glucoside, rhamnetin-3-*O*-rhamnoside, and quercetin-3-*O*-rutinoside were identified (Harvala et al., 1984; Aidy et al., 2022). The presence of quercitrin was documented in the stems (Bampali et al., 2024) and leaves of *L. europaeus* (Aljeboory and Al-Zubaidi, 2020). Conversely, smaller quantities of apigenin and luteolin were identified exclusively in the fruits, as reported by Benabderrahim et al. (2019).

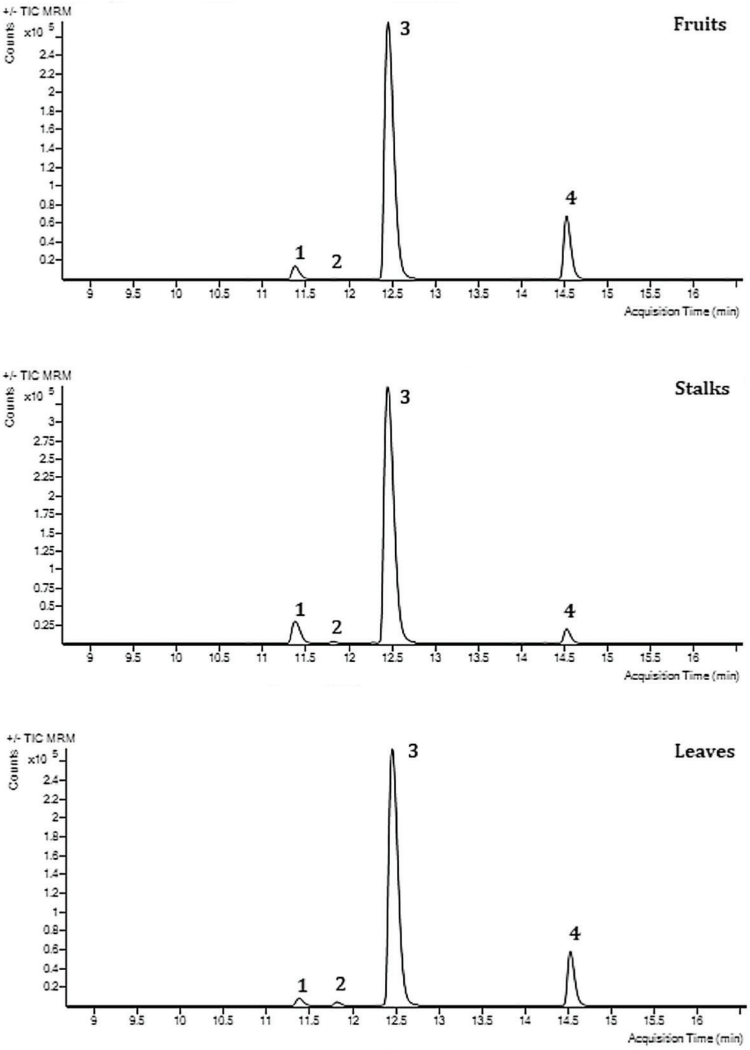

Fig. 7. LC–ESI–MS/MS chromatograms of the methanolic extracts from fruits, stalks and leaves of *L. europaeus*. 1: (+)-catechin, 2: chlorogenic acid, 3: (−)-epicatechin, and 4: hyperoside (Benabderrahim et al., 2019).

In addition to the previously identified phenolic compounds, Bampali et al. (2024) observed that *L. europaeus* twigs accumulate unsaturated fatty acids, including lycanic, linolenic and linoleic acids. The analysis of *L. europaeus* seed extract revealed the presence of carbohydrates, aldehydes and ketones, triterpenoid groups, proteins, saponins and alkaloids (Jawad et al., 2006; Al-Fartosy and Al-Rikaby, 2007). Furthermore, the essential oil of *L. europaeus* leaves was found to contain notable quantities of phytol (18.91%), dodecane (10.30%), and trans-caryophyllene (5.86%), which serves to illustrate the diversity and value of the essential oils of this plant (Aidy et al., 2022). These findings underscore the importance of continued research into *L. europaeus*, which holds promise for the development of novel medicinal applications.

Further research prospects

As seen, many aspects of the yellow mistletoe biology, ecology and medicinal usage have been widely investigated. However, there is almost no available information on its population genetics, interactions with pollinators, as well as its pests and diseases. What is crucial, publications concerning yellow mistletoe regulation methods are nearly impossible to find (Galko et al., 2018). Of course, it is possible to weaken the *L. europaeus* by optimizing the soil environment of the host trees through addition of potassium salts and irrigation. These interventions must be combined with the continuous removal of the hemi-parasite shrub (Kubíček et al., 2011). Rozkošný et al. (2020) saw the potential in mechanical treatment of oaks, which had an accelerating effect on the tree diameter increment in the first year and likely influenced crown regeneration in the second year. They also suggest that during thinning, it will be necessary to select primarily individuals that are weakened, damaged or affected by other harmful factors. Species composition in the stand is also important, as mixed stands are more resistant and less frequently attacked by mistletoe. Kubíček et al. (2018) point to proper management focused primarily on preventing young trees from drought stress (planting of drought tolerant species, increased species diversity, coppicing). Removing mistletoes by pruning of infected branches revealed promising results for management of mistletoes depending on scientific understanding of their ecology (Ramon et al., 2016; Sayad et al., 2017), but needs more research in this area.

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