Transpiration and stomatal conductance of mistletoe (Loranthus europaeus) and its host plant, downy oak (Quercus pubescens)

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Abstract: Sap flow rate was measured in the crown of a solitary specimen of downy oak (Quercus pubescens) infested by mistletoe (Loranthus europaeus). Five oak branches and two mistletoe plants were selected for analysis. The seasonal sum of transpired water expressed per leaf area unit was five times higher in the mistletoe than in the oak. In addition, the diurnal curves of sap flow were different between the plants. In the morning, the sap flow measured in the mistletoe lagged one hour behind the sap flow measured in an oak branch unencumbered by mistletoe. In contrast, no time lag was observed in the evening. The proportion of water transpired at night relative to the total transpiration was 7% in both species. The stomatal conductances derived from the inverted Penman-Monteith equation and their dependence on global radiation and the vapour pressure deficit (D) revealed that D exerts a different behaviour in stomatal control of transpiration in the mistletoe. We also determined that the concentration of calcium in the leaf mass could serve as a proxy for transpiration rate, however the relationship was not proportional.

Key words: sap flow; Penman-Monteith; hemiparasitic plant; nighttime transpiration; calcium concentration

Abbreviations: \( R_g \), global radiation (W m\(^{-2}\)); \( D \), vapour pressure deficit (Pa); PET, potential evapotranspiration (mm); \( L_{df} \), leaf development factor; P-M equation, Penman-Monteith equation

Introduction

The Loranthaceae are a group of hemiparasitic plants that usually tap the xylem and sometimes even the phloem of a host plant to acquire water and mineral nutrients (Bowie 2004). The haustorium of Loranthus europaeus consists of a single cone-shaped sinker. New layers of mistletoe tissue are laid down radially and synchronously with ring growth in the oak. There are very few phloem elements in the haustorium, and they terminate well before the host-mistletoe interface (Buchleitner 1982). Therefore Loranthus is rather a photosynthetic mistletoe (Těšítel et al. 2010) and is only water and nutrient parasite (Eliáš 1987).

Mistletoe cannot be considered as only another branch of a tree. It has specific reactions to external factors that are different from those of the host plant. Only a few studies have investigated the relationship between the hemiparasite Loranthus europaeus and Quercus sp. Schulze et al. (1984) found rates of assimilation that were similar in the host and its parasite, whereas the rates of transpiration and leaf conductance in Loranthus were approximately three times greater than in Quercus. During the day, Loranthus also operated at a lower water potential and higher internal mesophyll CO\(_2\) concentration than the oak, reflecting greater water-use efficiency in Quercus than in Loranthus. A higher transpiration rate in mistletoe than in the host plant was found in many previous studies (Ullmann et al. 1985; Escher et al. 2004; Glatzel & Geils 2009), although the opposite has also been found (Fischer 1983; Küppers et al. 1992). To maintain high rates of photosynthesis, the mistletoe continues to extract water and minerals from the host even during drought and can therefore cause severe stress to the host (Garkoti et al. 2002). It has been proposed that Loranthus has relatively little stomatal control over water loss (Vareschi & Pannier 1953; Hellmuth 1971). However, several studies have provided evidence for stomatal control over transpiration in mistletoe, but its reaction to an increasing vapour pressure deficit (D) is less pronounced (Glatzel 1983; Schulze et al. 1984; Ullmann et al. 1985; Strong & Bannister 2002). The minimum water potential in the parasite is approximately 1.0–1.5 MPa below that of the host plant (Schulze et al. 1984). This behaviour effectively supplies the mistletoe with water and nutrients; however, it also jeopardises the life of the host plant. As, given the climatic change, oak is more susceptible to infestation (Kumbasli et al. 2011) and as Loranthus is spreading northwards and to higher al-

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attitudes (Kubiček et al. 2008), more oaks are threatened.

The transpiration rate is coupled with the uptake of ions. Calcium (Ca) is a nutrient that is only transported acropetally in xylem vessels. Its immobility in the phloem has been well documented (Marschner 1974; Fink 1991). This transportation pattern means that larger quantities of calcium accumulate in trees with higher transpiration rates. Because mistletoe has direct connections to the xylem sap of its host, we expected that a higher transpiration rate in mistletoe would result in a higher Ca concentration in mistletoe leaves. Therefore, we measured leaf calcium content in this study.

The few studies performed on the transpiration and stomatal conductance of mistletoe and its host plant were mostly based on diurnal observations (Glatzel 1983; Ullmann et al. 1985). There has been no comprehensive study comparing the seasonal courses of transpiration and stomatal conductance during an entire growing season as well as at night. Therefore, the aim of this study was to describe and compare the water use of the deciduous mistletoe (Loranthus europaeus) and its host plant, downy oak (Quercus pubescens), during the growing season. The second aim was to describe the stomatal conductance responses of these two plants to environmental variables. The third aim was to determine whether the concentration of calcium in the leaf mass could serve as a proxy for transpiration rate.

**Material and methods**

Our study site was the “Pouzdrany steppe” near Brno, Czech Republic (48°56'52.46" N and 16°38'41.28" E; 278–295 m a.s.l.). This site was heavily infested with mistletoe (Loranthus europaeus) growing on several species of oak, Quercus petraea, Q. pubescens, and Q. robur. The mean annual temperature at the site was 9.5°C, and the annual precipitation was between 450 and 500 mm (Quitt 1971). The trees were growing solitarily (in average 15–20 trees per ha) with an average height of 6 m. The average crown projected area was 23.7 m², and the average diameter at breast height was 22.4 cm. There were frequently more than 4 mistletoe plants per oak tree. There were 18 mistletoe parasites growing on the most infested tree. The oldest living hemi-parasite was 24 years old (the age was estimated with respect to the regular branching patterns). The soil was loessy, and the sediment depth was several metres (Vandenberghe & Czudek 2008). A steep slope of 15° was oriented to the south.

We chose one solitary specimen of downy oak (Quercus pubescens) for detailed study. This tree was approximately 45 years old. The diameter at breast height was 30.9 cm, and its height was 7 m. The mistletoe plants were predominantly attached to the topmost branches of the crown. There were a total of 8 plants on the measured tree.

**Field methods**

**Meteorology and soil**

Meteorological variables were measured approximately 20 m from the measured tree. The global radiation, air temperature at a height of 2 m and air humidity were measured by a Minikin TRH (EMS Inc., Brno, Czech Republic) at 1-minute intervals. Fifteen-minute means were downloaded to the datalogger, and these data were used to calculate the potential evapotranspiration (PET) as previously described (Penman 1948). Soil water potential was monitored by two gypsum block sensors (GB2, Delmhorst Inc., USA). The sensors were attached to the datalogger (Microlog SP, EMS Inc., Brno, Czech Republic) and buried at a distance of three metres from the tree at depths of 15 cm. Data were collected every hour.

**Sap flow**

Five oak branches and two male mistletoe plants were selected for sap flow measurements using the heat field deformation (HFD) method (Nadezdina et al. 1998; Cermák et al. 2004; Steppe et al. 2010), which accounts for the size and overall distribution of the branches in the crown. Given the small size of the oak and mistletoe branches, the sap flow rate was only measured at one depth, 2-3 mm below the cambium, by single-point HFD sensors (Dendronet, Inc. Brno, Czech Republic). The sap flow sensors were installed on 5 oak branches and the bases of 2 mistletoe plants (Fig. 1). The biometric parameters of the branches are presented in Table 1. After installation, the sensor needles were thermally insulated with foam and covered by a radiation shield (0.5 mm-thick aluminium foil), the upper borders of which were sealed with silicone to protect against rain. The voltage outputs of the sensors were registered by the datalogger (Midi12, EMS Inc., Brno, Czech Republic) at 1-minute intervals, and fifteen-minute averages were stored in the memory. Sap flow was measured for 201 days from 15 April 2009 (i.e., the beginning of leaf flush) to 3 November 2009. Some gaps in the measurements occurred when the...