REVIEW / SYNTHÈSE

Mistletoe ecophysiology: host–parasite interactions[1]

G. Glatzel and B.W. Geils

Abstract: Mistletoes are highly specialized perennial flowering plants adapted to parasitic life on aerial parts of their hosts. In our discussion on the physiological interactions between parasite and host, we focus on water relations, mineral nutrition, and the effect of host vigour. When host photosynthesis is greatest, the xylem water potential of the host is most negative. To maintain a flux gradient and avoid stomatal closure and wilting, the mistletoe must tolerate a more negative water potential than the host. Succulent leaves enhance water storage and allow mistletoes to rehydrate before their hosts rehydrate. Mistletoe infections may disrupt the host stomatal control system, causing early and oscillating closure of host stomata, thereby diminishing host photosynthetic gain. Mistletoes lack the active uptake of minerals of a typical plant root system and rely upon the haustorium to connect with the host for the essentially one-way flow of photosynthates and nutrients from host to parasite. Modest growth rates, tolerance, succulence, and rapid leaf turnover are some means by which mistletoes avoid mineral deficiency or excess. We propose high concentrations of some mobile elements in the mistletoe by comparison with the host result not from active uptake, but from the inevitable accumulation by a parasite that utilizes host phloem sap. The relationship between host condition and mistletoe performance varies by situation and over time. In some cases, the host can outgrow the mistletoe, but favorable host status can also accelerate mistletoe growth. A better understanding of the mistletoe–host interaction can be utilized in improved management of infested forest plantations for resource production as well as for conservation of biodiversity and endangered species.

Key words: water relations, mineral nutrition, host–parasite interaction.

Résumé : Les faux-guis sont des plantes à fleurs pérennes adaptées à la vie parasitaire sur les parties aériennes de leurs hôtes. Dans cette discussion sur les interactions physiologiques entre le parasite et l'hôte, les auteurs mettent l'accent sur les relations hydriques, la nutrition minérale et l'effet sur la vigueur de l'hôte. Lorsque la photosynthèse de l'hôte est la plus élevée, le potentiel hydrique de l'hôte est le plus négatif. Pour maintenir un gradient de flux et éviter la fermeture des stomates et la flétrissure, le faux-gui doit tolérer un potentiel hydrique plus négatif que celui de l'hôte. Les feuilles succulentes favorisent l'accumulation de l'eau et permettent au faux-gui de se réhydrater avant que l'hôte ne le fasse. L'infection par le faux-gui peut perturber le système de contrôle stomatique de l'hôte, diminuant ainsi les gains photosynthétiques de l'hôte. Le faux-gui ne possède pas d'absorption active des minéraux par un système racinaire typique et repose sur l'haustérie pour se connecter avec l'hôte; le flux est essentiellement unidirectionnel transportant à la fois les photosynthétats et les nutriments, de l'hôte vers le parasite. Les taux de croissance modestes, la tolérance, la succulence, et le cyclage rapide des feuilles constituent des moyens par lesquels le faux-gui évite la déficience ou l'excès de minéraux. Les auteurs suggèrent que de fortes concentrations de certains éléments mobiles chez le faux-gui comparativement à l'hôte, proviennent non pas d'une absorption active, mais plutôt d'une accumulation inévitable par le parasite qui utilise la sève du phloème de l'hôte. La relation entre la condition de l'hôte et la performance du faux-gui varie selon les situations et le temps. Dans certains cas l'hôte peut surpasser la croissance du faux-gui; mais un état favorable de l'hôte peut également accélérer la croissance du faux-gui. Une meilleure compréhension de l'interaction du faux-gui avec son hôte peut être utilisée pour améliorer l'aménagement des plantations forestières aux prises avec le faux-gui, pour la production de la ressource aussi bien que pour la conservation de la biodiversité et des espèces menacées.

Mots-clés : relations hydriques, nutrition minérale, relation hôte–parasite.

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G. Glatzel. Institute of Forest Ecology, UNI BOKU Vienna, Peter Jordan-Strasse 82, A-1190 Vienna, Austria.
B. Geils.[2] USDA Forest Service, Rocky Mountain Research Station, Southwest Forest Science Complex, 2500 South Pine Knoll Drive, Flagstaff, AZ 86001, USA.

[1]This review is one of a collection of papers based on a presentation from the *Stem and Shoot Fungal Pathogens and Parasitic Plants: the Values of Biological Diversity* session of the XXII International Union of Forestry Research Organization World Congress meeting held in Brisbane, Queensland, Australia, in 2005.
[2]Corresponding author (e-mail: bgeils@fs.fed.us).

Introduction

Mistletoes, as perennial flowering plants and aerial parasites of trees, face several interesting physiological challenges. Mistletoe seeds must firmly attach to a host branch and the seedlings must overcome host defenses and secure access to organic and inorganic resources of the host (see Rödl and Ward 2002). To grow and reproduce, mistletoes must successfully compete for a share of the host's water, avoid mineral deficiencies, tolerate differences in host xylem sap chemistry and, over time, flower and seed within the host canopy. Mistletoes are a diverse group of plants that meet these challenges in various environments and with a variety of physiological mechanisms. The approximately 1300 species of mistletoes are distributed among four plant families and range in size of their aerial shoots from small (e.g., *Arceuthobium minutissimum* Hook. f., < 4 mm) to large (e.g., *Viscum album* L. and many Loranths > 1 m). Mistletoe flowers of different groups include the inconspicuous (usually in temperate regions) and the showy (usually tropical). Although most mistletoes have viscous seeds, dispersal may be by birds (typical of Loranthaceae), by wind (Misodendraceae), or hydraulic–explosive (*Arceuthobium*). All mistletoes are parasites — they form a long-lasting, intimate physiological connection with a host that generates phenotypic (and ultimately genetic) consequences for both symbionts (see Combes 2001). A mistletoe plant may appear as another branch (in cases with strong mimicry); but a mistletoe infection is functionally very different in its photosynthetic contribution to the host and nonpruning persistence. The diversity of mistletoes represents a range of physiological dependence on host photosynthesis from photo-autotrophic hemiparasites parasitizing the xylem system of their host for water and inorganic nutrients, to holoparasites, which depend not only on water and inorganic solutes, but also on photosynthate from their host.

Few general and physiological reviews of mistletoe parasitism are recently published (see Calder and Bernhardt 1983; Hawksworth and Wiens 1996; Kolb 2002; and online sites Parasitic Plant Connection (www.parasiticplants.siu.edu) and Mistletoe Center (www.rmrs.nau.edu/mistletoe)). A main topic of this review is to present various aspects of mistletoe–host ecological interactions. Watson (2001) reviews aspects of mistletoe biotic interactions from the perspective of community ecology and the keystone importance of mistletoes on biodiversity. Here, we consider key features of mistletoe parasitism from an ecophysiology perspective and offer hypotheses for the mechanisms by which mistletoes meet various physical and biotic challenges. In particular, we discuss (*i*) how stomatal control, succulence, and host–parasite conflicts might affect water relations, (*ii*) possible mistletoe strategies for balancing mineral nutrition, and (*iii*) that host condition can have differential influences on mistletoe performance.

Water relations

Upon infection, the developing mistletoe begins to utilize water from the host transpiration system. The extent of the diversion depends on whether the mistletoe is a holoparasite that taps both xylem and phloem and depends on photosynthates from the host, or a photosynthetically activ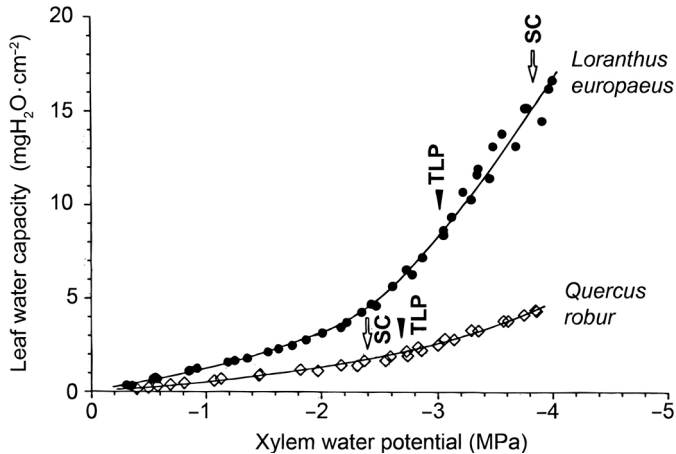e hemiparasite that taps mainly the xylem of its host. Holo-parasitism is common among the Viscaceae, but some species in the Loranthaceae have been demonstrated to be capable of tapping the host's phloem for carbon and inorganic nutrients (Bowie and Ward 2004). Even within a single genus, extreme differences may occur. In *Tristerix* (Loranthaceae), typical hemiparasitic species with good-sized green leaves are the rule; but a single species, *Tristerix aphyllus* Tiegh. ex Barlow & Wiens, parasitizing *Echinopsis chiloensis* (Colla) H. Friedrich & G.D. Rowley, has no vegetative aerial parts and sprouts flowers from an endophyte growing within the cactus (Mauseth 1990). For hemiparasitic xylem-tapping mistletoes, photosynthesis by the parasite is significant and the ratios of diffusive water loss to CO_2 gain are similar for host and parasite leaves (see review by Kolb 2002). Although photosynthesis by holoparasitic phloem-tapping mistletoes contributes negligible photosynthate gain, transpiration flux by the mistletoe may be high enough to exceed that of host leaves (see Hawksworth and Wiens 1996, p. 91). In the case of *Tristerix aphyllus*, transpiration flux cannot play any role; as an endophyte it is embedded in host tissue and lacks epidermis and stomata. Considering the amazing diversity among the mistletoes, there are exceptions to any generalization. Nonetheless, for many hemi- and holoparasitic mistletoes the following, general concepts on water relations and inorganic nutrition are applicable.

Stomatal control

Movement of the xylem sap from the host to the parasite requires a gradient in water potential. Water potential (ψ) is a measure of the energy status or tension of the xylem water relative to free water. Cellular osmotic potential is affected by solute concentration and is important for water storage and phloem activity. When water is moving from the soil to the leaves and to the atmosphere, frictional resistance adds to the xylem water tension (which under static conditions is related to height). Should water potential fall below osmotic potential, first wilt, and then beyond the tolerable threshold potential, physiological damage can occur. Within a feedback system, xylem water potential affects stomatal opening, gas exchange, and photosynthesis. This homeostatic feedback system balances evapotranspiration and photosynthesis (limited water versus limited CO_2). Three relevant components of the host–mistletoe system are (*i*) the mistletoe shoots, leaves, and seeds (transpiration and photosynthesis), (*ii*) the haustorium connecting mistletoe and host (adds frictional resistance), and (*iii*) the endophytic systems, epicortical runners, and secondary haustoria (may reduce frictional resistance; Kuijt 1991).

When host photosynthesis is greatest, the xylem water potential of the host is most negative. To maintain a flux gradient and avoid stomatal closure and wilting, the mistletoe must tolerate a more negative water potential than the host. Glatzel (1983) illustrates differences in stomatal closure and wilting for the *Loranthus europaeus* Jacq. and *Quercus robur* L. pathosystem (Fig. 1). By tolerating lower water potential, the hemiparasite is capable of extracting water from the host and delay stomatal closure to much lower host xylem water potential compared to the host. For holoparasites, maintaining a high transpiration flux provides continued flow of photosynthate-rich phloem sap from host to parasite.

Fig. 1. The transpiration control system in the hemiparasitic 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.

Fig. 2. Phosphorus concentration of *Loranthus europaeus* leaves closely reflects the foliar phosphorus concentration of host *Quercus petraea* leaves (40 mistletoes sampled from 11 host trees in the same stand; Hochleithenwald, Lower Austria, August 2003).
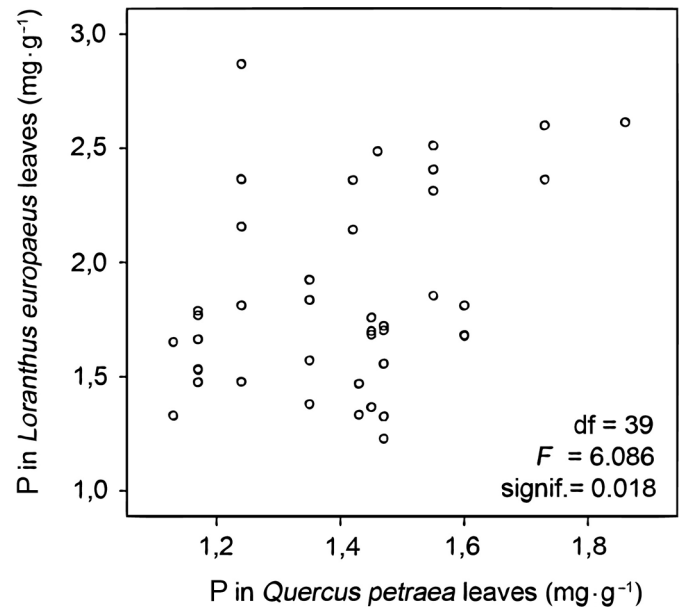

Succulence

Besides a higher physiological tolerance to wilting, the aerial portions of many mistletoe species are succulent (Fig. 1). Fleshy leaves and high concentrations of osmotically active organic solutes enhance mistletoe water storage (Popp 1987; Popp et al. 1995). When xylem water tension eases, mistletoes rehydrate from available water until the storage capacity of the succulent leaves is met and ahead of the host's rehydration (see Fig. 1).

Disruption of the host's homeostatic water control system

All branches of a tree and, in fact, all leaves of a tree compete for the water transported from the roots to the canopy. Because mistletoes enter this competition, it is reasonable to ask "why can't a mistletoe infection be considered just another branch that competes for water like other branches?" Most trees satisfactorily tolerate a fluctuating water supply: on dry sites, trees are often just smaller versions of similar trees found on mesic sites. In part, mistletoes are not just additional branches because they do not contribute significantly to the photosynthetic gain of the host tree. They do not contribute to the production of necessary absorbing, conducting and supporting structures such as roots and stems (they also affect the host's mycorrhizal community, see Cullings et al. 2005). In addition, mistletoes introduce a second, conflicting, water control system.

The opening and closing of stomates is homeostatically controlled by leaf-xylem water potential: when more water is lost than supplied by host xylem, water potential drops which triggers stomatal closure (Brodribb and Holbrook 2003; Brodribb et al. 2003). Essentially, the mistletoe bypasses the homeostatic control of water by the host. Because the host cannot control the water lost by the mistletoe, mistletoe water use reduces host xylem water potential, triggers host stomatal closure, and potentially reduces host carbon assimilation. Engineering systems theory predict an overshoot response when two, competing control systems attempt to regulate one process (here, host and parasite attempt to regulate transpiration water loss). Härtel (1937) and Vareschi and Pannier (1953) report erratic changes in transpiration rates of mistletoes but attribute these oscillations to "poor stomatal control" by the mistletoe. Subsequently, Glatzel (1983) suggests an alternative explanation for *Quercus robur* under water-stress and infected by *Loranthus europaeus*, whereby parasite transpiration continues and the host overshoots its stomatal reaction. Disruption of the host homeostatic stomatal control system appears to be due to mistletoe diversion of water provoking an overshoot of stomatal closure and resulting in diminished photosynthetic gain for the host. This may explain at least partially why trees seem to accommodate fluctuations in soil moisture well, but mistletoe-induced water competition poorly.

Mineral nutrition

Mistletoes lack a usual plant–root system capable of active uptake; they rely upon a host connection through the haustorium for nitrogen and mineral nutrients. The best correlation for predicting the concentrations of elements in mistletoe is often (but not always) the concentration of elements in the host (e.g., Fig. 2). This is not really surprising, as both host leaves and mistletoe leaves draw from the same xylem sap. Hemiparasitic mistletoes lack specific mechanisms for discrimination and active uptake of nitrogen and mineral nutrients beyond that of simple diversion of host xylem sap. Holoparasitic and partially holoparasitic mistletoes have the additional phloem contact (Kuijt 1991) that permits nutrient grain from phloem sap as well as xylem sap. For mistletoes in general, the flow of nutrients is predominantly one-way, from host to parasite. Although host plants cycle such nutrients as potassium and phosphorus between xylem and phloem (Ernst 1990), parasites do not share their nutrients with the host so very little of their phloem sap joins the

host's xylem–phloem cycle. The challenges for the parasite are to avoid mineral deficiency and cope with excess and imbalance, especially of potassium. Variation among mistletoes in their physiological capability to meet these challenges has ecological and evolutionary significance which is reflected in community and phylogenetic diversity.

Avoiding mineral deficiency

An obvious strategy to avoid mineral deficiency is to not outgrow the supply. Hemiparasitic mistletoes draw from the same xylem sap as their host, and therefore they should have the same limits on supply at the leaf level. To avoid deficiency, water-use efficiency (ratio of carbon gain to water use) should be lower in the mistletoe than in the host. Even though mistletoes produce masses of flowers and fruits that are significant carbon sinks, host trees must support the growth and respiration of their extensive root systems (with mycorrhiza), massive trunks and crowns, requiring large amounts of carbon. Experiments confirm that at least for some species, mistletoes do have low photosynthetic efficiency (Schulze and Ehleringer 1984; Schulze et al. 1984; Strong et al. 2000). Small size, therefore, not only reduces the likelihood a mistletoe aerial plant breaks off its host branch but also helps to avoid mineral deficiency. Holoparasitic mistletoes obviously can draw mineral nutrients from both the xylem and phloem of their hosts and have no need for their own photosynthetic foliage. They can afford to be small, needing their aerial parts only to support reproductive organs and to maintain a water gradient from the host to the parasite.

Coping with excess and imbalance

Excess and imbalanced nutrition are the other challenges encountered by mistletoes as a consequence of their parasitism. Although many mistletoe species have a very small host range (one to few), numerous mistletoe species are parasitic on a large number of host species (dozens) growing on many different soils from acidic to alkaline and ultramafic. These hosts vary greatly in their mineral composition and physiology, and they include hosts that are hyper-accumulators of sulfur or metals and may be extremely tolerant of salts.

Chemical analyses of mistletoes from a large sample of host species provide evidence that these parasites can cope well with many difference nutrient sources (Glatzel and Balasubramaniam 1987). Some elements may vary by one or two orders of magnitude in samples from the same mistletoe species on different host trees and species. High concentrations of sulfur, chloride, or manganese in the leaves of specialized hosts are carried into the mistletoe leaves without noticeable damage to the parasite.

An example of salt tolerance is provided by *Amyema mackayense* (Blakely) Danser growing on *Avicennia marina* (Forssk.) Vierh., a salt-excreting mangrove. The xylem sap of the mangrove transports sodium chloride to its leaves where the salt is excreted by special glands. *Amyema mackayense* grows on hosts other than mangrove; it lacks salt glands and does not excrete salt but does have succulent leaves. Where the mistletoe infects salt-tolerant mangrove, its leaves bloat and sequester the salty xylem sap within a tolerable level of osmotic potential. When the mistletoe's

leaf capacity for salt is reached, mobile nutrients are translocated to emerging leaves, and the leaf is shed (Glatzel 1996). Succulence and rapid leaf turnover thus enable the mistletoe to grow under these very extreme conditions.

Potassium accumulation in mistletoes

Chemical analysis of mistletoe leaves shows rather striking enrichments of potassium and phosphorus by comparison with to their host. An explanation for the accumulation of potassium has been the active uptake of an element important for osmosis and stomatal control (Lamont and Southall 1982; Lamont 1985). An alternative hypothesis proposed by one of us (Glatzel 1983) is that elements such as potassium and phosphorus merely accompany sugars in the phloem sap. The phloem sap of many plants is usually rich in potassium and phosphorus (Davis and Johnson 1987). Even though there is an active phloem connection between host and parasite, photosynthate transfer is almost exclusively to the mistletoe: elements gained are elements held. Because holoparasites use both phloem and xylem sap, they have two sources for mobile elements. The accumulation of potassium may not be the result of active uptake to satisfy a metabolic requirement, but may be just the inevitable consequence of parasitic nutrition ("shades of the spandrels of San Marco", Gould and Lewontin 1979).

### Host condition and mistletoe performance

Host condition may, in various ways, affect mistletoe parasites. Neighboring host trees of the same species frequently show very different infestation by parasites. Failure of the establishment of mistletoes may be due to different attractiveness of the neighboring host tress to dispersers or owing to differences in seed attachment and penetration of the bark by the germinant. As mistletoe seeds must strongly adhere to the bark to allow the germinant to penetrate the bark, small differences in the physical or chemical properties of the bark obviously can make a large difference in establishment. In dwarf mistletoes (*Arceuthobium*), the biochemical properties of the host's xylem and phloem have a direct influence on the physiological performance and ultimately the survival of the mistletoe (Snyder et al. 1996; Linhart et al. 2003).

Once a mistletoe has established on its host, sufficient water, mineral nutrients, and light are needed to complete its life cycle, but its performance also appears to be influenced by or along with that of its host. Just as there are differences in growth and reproduction for host populations on different sites or in response to different treatments, there are also differences in the growth and reproduction of the associated mistletoe population. Although the cumulative impacts of a long infestation and large mistletoe load can result in severe pathogenic effects to the host, the relationship between host condition and mistletoe performance can vary by situation and over time. We consider here two apparently contrasting examples.

For the hemiparasitic *Loranthus europaeus* on *Quercus,* better host condition reduces mistletoe performance. In a favorable moisture and nutrient environment, the host tree grows well and can even shade out the mistletoe; but on droughty, infertile sites the oak grows more slowly, the mis-

Fig. 3. Mistletoe shoot regrowth was higher on trees in the thinned stand than the unthinned stand in two studies (regrowth did not differ significantly between studies, but differences between thinned and unthinned were consistent within studies). Means represent least square means and bars represent one SE (modified from Bickford et al. 2005).

Mistletoe shoot regrowth
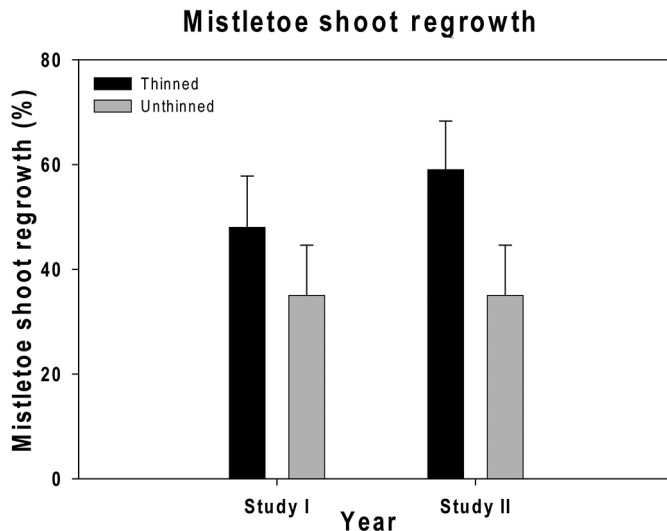
tletoe increases, and eventually severe disease impacts develop (Mayer 1982).

Hawksworth and Wiens (1996) review the ecological relationships of the holoparasitic dwarf mistletoes and cite various reports where these mistletoes are more abundant or more damaging on host quality sites that are either better, poorer, or both. To better understand the physiological relation between host condition and dwarf mistletoe performance, Bickford et al. (2005) examined the shoot growth of *Arceuthobium vaginatum* subsp. *cryptopodum* (Engelm.) Hawksw. & Wiens on two similar sites of *Pinus ponderosa* Dougl. ex P. Laws. & C. Laws., one of which was manipulated by forest thinning to improve host water and nutrient status. Relative to the control, trees in the thinned areas increased uptake of water and carbon. Co-incident with improved host condition, dwarf mistletoe shoot re-growth was higher relative to the control (Fig. 3). Although these are only two short experiments in a single forest type and pathosystem, they do suggest that one measure of dwarf mistletoe performance (production of reproductive shoots) can respond positively to better host condition (measured by water status and photosynthetic gain).

Conclusion

Considering the biological and ecological diversity of some 1300 mistletoe species, we can only present some general concepts of parasite–host ecophysiology. Other topics which deserve attention include the roles of the endophytic system in nutrition and plant growth regulation, the physiological mechanisms of host resistance to mistletoe infection, and coevolutionary biology (adaptive traits in local populations and their distribution across metapopulations). Most of the better studied mistletoe species are classified by foresters as pests, and the focus of research has often been on finding ways to fight these pests. Mistletoes are, however, not just

pests but they also contribute directly and indirectly to biodiversity (Watson 2001). With increasing replacement of these ecosystems by managed plantations, mistletoes may become as endangered as the forest they dwell within.

Acknowledgements

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