REVIEW

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Biology and resource acquisition of mistletoes, and the defense responses of host plants

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Abstract

Background: Mistletoes are the most successful group of obligatory hemi-parasitic flowering plants that attach to the host via haustorium for obtaining water and minerals. This review aims to assess the current knowledge on mistletoes host plant recognition, haustorium formation, water/minerals acquisition, and host plants' defense signaling and responses against mistletoe attack.

Results: Some mistletoes are host-specific while others are generalists occurring on a wide range of vascular plants. The host nitrogen (N) content, parasite–host chemical interactions, compatibility, and dispersal agents are the main determinant factors for host specificity. Mistletoes take up substantial amounts of water and minerals passively via apoplastic routes, and most are xylem feeders, but could shift to phloem-feeding during the physiological stress of the host plants. Current evidence highlighted that cell wall loosening and modification are critical during the development of the haustorium in the host tissue. This is made possible by the application of physical pressures by the developing haustorium and cell wall degradation using enzymes (xyloglucan endotransglycosylases, glucanase, expansins, etc.) produced by the mistletoe. Host plants defend against mistletoe infection mechanically by producing spines, lignin, suberin, etc., which discourages dispersers, and chemically defend by killing the infector or inhibiting the establishment of the haustorium using their secondary metabolites such as terpenes, phenolics, and N-containing compounds. Although the host plants' response to mistletoe attack resembles the response to other biotic stresses, unlike short-term stressors, the effect of mistletoe attack is long-term and depends on the parasite load. Infection by mistletoe leads to water and nutrient stress of the host plant and deteriorates its healthy establishment and survival.

Conclusion: Mistletoes are heterogeneous group in the order Santalales which have versatile mechanisms for pollination, seed dispersal and nutrient acquisition from host plants. Infection by mistletoes triggers host plant responses, varying from mechanical to chemical mechanisms which are analogous to herbivory defences, and negatively impacts host plant growth and reproduction.

Keywords: Biotic stress, Haustorium, Host defense, Mistletoes, Mimicry, Resource procurement

Introduction

Mistletoes are the most successful group of parasitic flowering plants in the order Santalales (Nickrent 2011; Glatzel and Geils 2009) that parasitize the aerial parts of a wide range of host plants (Amico et al. 2007; Glatzel and Geils 2009). They are true perennial parasites that can grow on plants over a wide range of habitats and environmental conditions (Lüttge et al. 1998; Escher et al. 2004; Ornelas et al. 2016). They occur ubiquitously in the temperate zone, arid regions, and wet tropics (Lüttge 2008), but are absent in extremely cold regions (Ornelas et al. 2016). Mistletoes are small evergreen shrubby plant species that infect diverse types of host plants (generalists)

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and a few are specialists that infect only specific species (Gibson 1967; Glatzel and Geils 2009; Okubamichael et al. 2016). The generalists are more abundant and they have the greatest chance for survival compared with the specialists (Nickrent and Musselman 2004). In terms of diversity, mistletoes evolved through five separate times in sandalwood order (Santalales). This polyphyletic group of aerial stem obligate hemi-parasites are represented by five Santalales families (Misodendronaceae, Eremolepidaceae, Santalaceae, Loranthaceae, and Viscaceae), 88 genera, and nearly 1600 species (Vidal-Russell and Nickrent 2008; Nickrent 2011). Loranthaceae (1000 species) and Viscaceae (550 species) have the highest species diversity (Nickrent 2011). Mistletoes are attached to the host via a modified root called the haustorium (Press and Phoenix 2005; Vidal-Russell and Nickrent 2008; Nickrent 2011), which distinguishes them from epiphytic or myco-heterotrophic plants (Nickrent and Musselman 2004).

Most mistletoes range from hemi-parasites (e.g., *Viscum album* L.) that are capable of photosynthesizing their organic matter, but rely on the host xylem for water and mineral nutrients (Table 1) to holoparasites (e.g., *Tristerix aphyllus* G.Don), which completely absorb water, nutrients, and carbohydrates (Medel et al. 2004; Devkota et al. 2010). Some species of mistletoes can even grow on other mistletoes and their interaction is mistletoe–mistletoe parasitism (epiparasitism) (Nickrent and Musselman 2004; Mathiasen et al. 2008). Growth and development of mistletoes essentially depend on nutrients and water availability of the host (Zweifel et al. 2012), haustorium-inducing factors (Amico et al. 2007; Glatzel and Geils 2009; Ornelas et al. 2016), and parasite–host chemical bindings (Ko et al. 2014). In addition, climatic conditions are key drivers that affect mistletoe growth, distribution, and host preference (Bach et al. 2005). Structure and heterogeneity of habitat may influence the mistletoe vectors whereby the birds are the principal seed dispersal agents although some are dispersed by wind or hydraulic explosives (Glatzel and Geils 2009; Nickrent 2011; Okubamichael et al. 2011; Rist et al. 2011).

Mistletoe infection does not directly lead to the death of host species, but it triggers water stress and strongly reduces carbon assimilation under stressful occasions (Zweifel et al. 2012). Various studies have been conducted on the water–minerals relationship and absorption mechanisms of the mistletoes (e.g., Lamont 1983; Hosseini et al. 2007; Glatzel and Geils 2009; Zweifel et al. 2012). These parasitic flowering plants lack the active uptake of minerals of a typical plant root system (Glatzel and Geils 2009) and, thus, obtain nutrients by a

Table 1 The host–parasites ranges and specificity of stem hemi-parasite mistletoes based on global studies

No.	Mistletoes	Family	Most preferred hosts	SHR	Country	References
1	*Dendrophthoe falcata* var. *pubescens* (Hook.f.)	Loranthaceae	*Morus alba, Murraya paniculata*	401	USA	Hawksworth and Wiens (1996)
2	*Amyema pendula* Tiegh	Loranthaceae	*Eucalyptus* spp., *Acacia* spp.	107	Australia	Clark et al. (2020)
3	*Amyema conspicua* Danser	Loranthaceae	*Eucalyptus* spp., *Acacia* spp.	44	Australia	Clark et al. (2020)
4	*Scurrula elata* Danser	Loranthaceae	*Lilium nepalense, Gossia fragrantissima*	22	Central Himalaya	Devkota et al. (2010)
5	*Taxillus tomentosus* (B. Heyne ex Roth) Tiegh	Loranthaceae	*Phyllanthus emblica, Phyllanthus indofischeri*	14	India	Rist et al. (2011)
6	*Erianthemum dregei* Tiegh	Loranthaceae	*Sesbania sesban, Jacaranda mimosifolia*	11	Ethiopia	Hishe and Abraha (2013)
7	*Tapinanthus globifer* (A.Rich.) Tiegh	Loranthaceae	*S. sesban, J. mimosifolia*	9	Ethiopia	Hishe and Abraha (2013)
8	*Viscum rotundifolium* Eckl. & Zeyh	Santalaceae	*Euphorbia rigida, Ziziphus mucronata*	9	South Africa	Okubamichael et al. (2011)
9	*Psittacanthus robustus* Mart	Loranthaceae	*Quararibea cordata*	8	Brazil	Guerra et al. (2018)
10	*Englerina woodfordioides* (Schweinf. ex Engel.) Balle	Loranthaceae	*Coffea arabica, Acacia abyssinica*	6	Ethiopia	Yirgu (2014)
11	*Dendrophthoe curvata* (Blume) Miq	Loranthaceae	*Andira inermis, Mangifera indica*	3	Brunei	Le et al. (2016)
12	*Viscum congolense* De Wild. & T. Durand	Viscaceae	*C. arabica, Croton macrostachyus*	3	Ethiopia	Yirgu (2014)
13	*Viscum combreticola* Engl	Viscaceae	*Combretum erythrophyllum*	1	South Africa	Okubamichael et al. (2016)
14	*Tristerix aphyllus* G.Don	Loranthaceae	*Echinopsis chiloensis*	1	Chile, Patagonia	Amico and Nickrent (2009)
15	*Tapinanthus rubromarginatus* (Engl.) Danser	Loranthaceae	*Protea caffra*	1	South Africa	Okubamichael et al. (2016)
16	*Korthalsella arthroclada* Cranfield	Santalaceae	–	1	Australia	Clark et al. (2020)

SHR, Species host range

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passive pathway where the transport of nutrients occurs with water flow from the host to the parasite (Lamont 1983), and via haustorium (Glatzel and Geils 2009). Because of parasitism, the nitrogen (N) concentration in leaves of mistletoes was four times higher than the hosts (Schulze et al. 1994) and causes N to become the most limiting macronutrient in host plants (Okubamichael et al. 2011; Yan et al. 2016). For example, nitrogen extracted from dwarf mistletoes was found to be 20% more than the host *Acacia nilotica* (Gibson 1967). Glatzel and Geils (2009) further reviewed that the leaves of mistletoe showed higher calcium, potassium, and phosphorus contents and a lower C/N ratio compared with their host. In terms of productivity, mistletoes infected Alma tree (*Phyllanthus emblica*) reduce fruit productivity by over 40% compared with the uninfected tree (Rist et al. 2011). The acquisition of host resources by mistletoe often severely reduces host biomass, reproduction, and physiology (Glatzel and Geils 2009; Bell and Adams 2011). Also, mistletoe infections alter host allocation patterns, modify plant community structure and dynamics, and mediate interactions between host plants, and other organisms (Pennings and Callaway 2002). However, host plants have evolved to possess a myriad of defensive mechanisms to detect such attacks and counteract the effect of parasitism by mistletoes (Medel et al. 2004; Anselmo-Moreira et al. 2019). Such scenarios, therefore, initiated us to review the current knowledge on the mechanisms of mistletoes' host recognition, nutrient acquisition, and the host plants' responses against the infection.

Review methodology

The methodological approach in this review was carried out based on the broader literature search and synthesis of peer-reviewed articles, theories, and empirical findings, extracted from international databases for scientific studies through a comprehensive search of Scopus, Google Scholar, Web of Science, and University repositories using the following search terms for English articles: "Mistletoes," "Parasitic flowering plants," "Mistletoes-host attachment," "Plants defense responses," "Ecophysiology of mistletoes," and "Haustorium formation". Hence, searched articles were imported to EndNote X7 software (Thompson Reuter, CA, USA), and then, in this review, 90 relevant peer-reviewed articles were assessed. Based on the empirical data sources, the authors made endeavors to synthesize and review a wide array of scientific evidence on the biology of mistletoes, their nutrient procurement mechanisms, and defense responses of the host plants against mistletoes attacks. Finally, concluding remarks were drawn.

Biology of mistletoes

Reproduction, seed dispersal, and germination of mistletoes

Mistletoes are highly specialized perennial shrubby flowering plants, dense, and evergreen clumps of semi-succulent foliage adapted to parasitic life on aerial parts of their hosts (Glatzel and Geils 2009; Mathiasen et al. 2008; Bell and Adams 2011; Clarke et al. 2019). Due to high diversity in the host range, a high variation in morphology such as the leaf, internodes length, fruit size, fruit pigmentation, and leaf architecture have been documented within mistletoe species (Medel et al. 2004). Most mistletoes produce either showy (usually tropical) or cryptic and actinomorphic flowers with large amounts of sugar-rich nectar (Mathiasen et al. 2008). Biotic agents (e.g., avian, insects, and bats) and wind have been described as mistletoes pollinators (Zuber 2004; Mathiasen et al. 2008; Wiesenborn 2016). The flowers may be hermaphroditic, conspicuous, and bright in color (e.g., Loranthaceae) and are mainly pollinated by avians (Kuijt 1969; Watson 2001; Vidal-Russell and Nickrent 2008). For instance, birds pry open the fused corollas to reach their nectar reward, upon which the pollen "explodes" onto the bird's head, and thereby affecting pollination (Mathiasen et al. 2008). In Viscaceae, the flowers are narrow, tubular, dioecious with or without corolla, and thus pollinated by insects and wind (Gill and Hawksworth 1961; Kuijt 1969; Aparicio et al. 1995). Mistletoes usually start sexual reproduction when they reach four to five years of age (Szmidla et al. 2019). Reproduction can also occur vegetatively through the production of adventitious shoots, especially when the plant is damaged mechanically (e.g., by breaking, pruning, or freezing) (Gill and Hawksworth 1961).

Mistletoes have unique seeds coated with mucilaginous viscin which glues seeds to woody branches after dispersers such as the generalist birds defecate or regurgitate (Gill and Hawksworth 1961; Kuijt 1969). Besides, in some cases, marsupial (*Dromiciops australis*), wind (Misodendraceae, Viscaceae), and hydraulic explosive (*Arceuthobium* spp.) mechanisms can also be seed dispersal vectors and agents (Gill and Hawksworth 1961; Kuijt 1969; Aparicio et al. 1995; Amico and Aizen 2000; Glatzel and Geils 2009). In addition, the low nutritional value of mistletoe berries necessitates that birds eat large quantities of seed to meet their calorific needs (e.g., up to 100 berries per day) which is a vital strategy in survival and spread of the mistletoes (Szmidla et al. 2019). This dependency of seed dispersal by birds shows the high degree of coevolution between mistletoes and birds (Medel et al. 2004), as well as plays a significant role in their pollination and dispersal (Devkota 2005). A study by Yan (1993) has shown that *Turdus viscivorus* L., *T. pilaris* L., *Bombycilla garrulus* L., and *Sylvia atricapilla*

L., are among the most common avian dispersers. During unfavorable conditions such as winter, the seeds of mistletoes are in a resting state (no cell division or DNA synthesis), which lasts on average for 5–6 months (Szmidla et al. 2019), because their berry needs optimal temperature to grow (Mathiasen et al. 2008). Yan (1993) further observed that *Amyema preissii* and *Lysiana exocarpi* (both Loranthaceae) had adequate reservoir food to grow for up to a year before attaching to the host vasculature. Seeds of Viscaceae have a chlorophyllous endosperm and embryo, and so are capable of producing simple sugars as an energy source after germination and persist for several years until the establishment of the host–parasite connection (Lamont 1983). Mistletoe embryos germinate while still in the fruit, but are unable to break through the tough exocarp without the help of an animal (Ko et al. 2014). The hypocotyl then extends and bends towards the host plant and swells to form suckers (Figs. 1C, 2 D, E) which complete the short non-parasitic part of the mistletoe life cycle (Mathiasen et al. 2008). Similar to other higher flowering plants, seed germination is influenced by temperature, moisture, and light, and thus, mistletoes can germinate with an optimum temperature of 15–20 °C (Mathiasen et al. 2008). However, *Viscum album* can grow in areas with up to temperature ranges of 8 to 10 °C (Lamont 1983), and their lethal temperature is even lower (between − 15 and − 19 °C) (Tikkanen et al. 2021).

Ecophysiology of mistletoes

Parasitic plants share cellular structures inherited from autotrophic ancestors including distinctive features of plants such as plastids and cell walls (Clarke et al. 2019). However, the remarkable differences from the normal autotrophs is found in the carbon economy (Scalon and Wright 2015), as they access resources from their host plants (Mathiasen et al. 2008) and a modified root that taps into host tissues replaces (reduced or absent) root
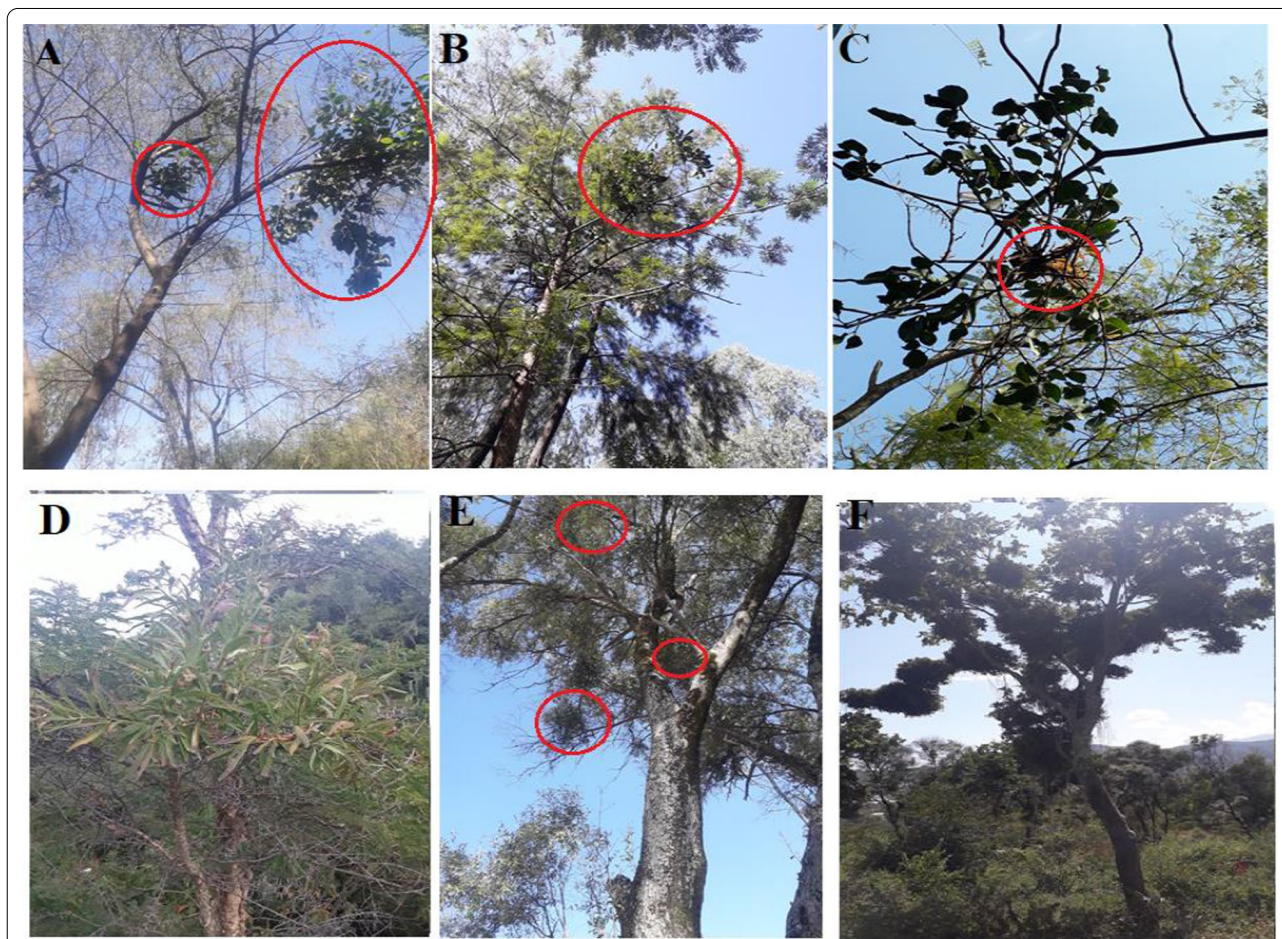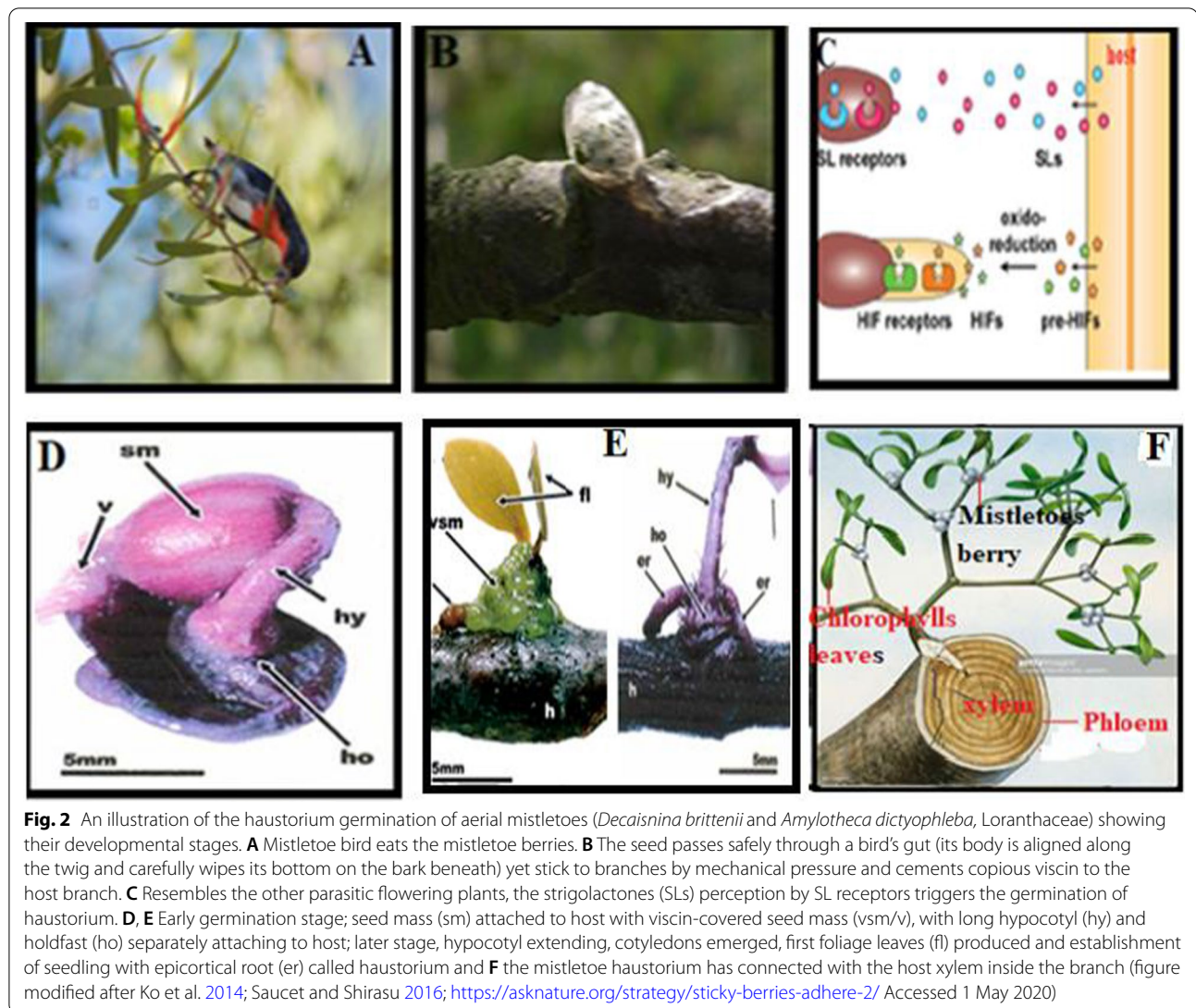

Fig. 1 The potential host adaptive ranges and specificity of mistletoes. *Erianthemum dregei* (hairy mistletoe) infecting **A** *Sesbania sesban* and **B** *Grevillea robusta*; *Tapinanthus globiferus* subsp. *apodanthus* parasitizing **C** *Jacaranda mimosifolia*; *Amyema pendula* infecting **D** *Acacia abyssinica*; and *Viscum album* growing on **E** *Olea europaea* subspec. *cuspidata* and **F** *Cordia myxa* (Photo by Meseret Muche 2021)

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Fig. 2 An illustration of the haustorium germination of aerial mistletoes (*Decaisnina brittenii* and *Amylotheca dictyophleba,* Loranthaceae) showing their developmental stages. **A** Mistletoe bird eats the mistletoe berries. **B** The seed passes safely through a bird's gut (its body is aligned along the twig and carefully wipes its bottom on the bark beneath) yet stick to branches by mechanical pressure and cements copious viscin to the host branch. **C** Resembles the other parasitic flowering plants, the strigolactones (SLs) perception by SL receptors triggers the germination of haustorium. **D**, **E** Early germination stage; seed mass (sm) attached to host with viscin-covered seed mass (vsm/v), with long hypocotyl (hy) and holdfast (ho) separately attaching to host; later stage, hypocotyl extending, cotyledons emerged, first foliage leaves (fl) produced and establishment of seedling with epicortical root (er) called haustorium and **F** the mistletoe haustorium has connected with the host xylem inside the branch (figure modified after Ko et al. 2014; Saucet and Shirasu 2016; https://asknature.org/strategy/sticky-berries-adhere-2/ Accessed 1 May 2020)

systems. They have functional leaves, but often show some level of heterotrophy (obtain carbon and nitrogen directly from their hosts' xylem in the form of amino acids) (Marshall et al. 1994; Okubamichael et al. 2011; Scalon and Wright 2015). The prevailing view that mistletoes exclusively are parasites for water and nutrients needs to be modified since the carbon gain of mistletoes from the host can be significant (Escher et al. 2004). Studies on the partitioning of dry matter and minerals using carbon-isotope ratios showed that 24% to 62% of the mistletoe carbon is obtained heterotrophically from the host and even the value tabulate up to 87% (Marshall et al. 1994; Lüttge et al. 1998). Despite their taxonomical diversity, the plant–water relations of different mistletoe species are remarkably similar (Le et al. 2016). Yet, the net CO_2 uptake and assimilation rates are generally lower in mistletoes than their hosts (Maes et al. 2018) and even

among C_3 plants (Lüttge et al. 1998; Escher et al. 2004, 2008; Lüttge 2008). This implies that the mistletoes may have considerably lower water-use efficiencies (WUE, the ratio of photosynthesis to transpiration) (Lüttge 2008) and low electron transport rates or hill reaction activities in thylakoids than the host (Le et al. 2016) and thus behave as shade plants (Strong and Bannister 2002).

Mistletoes generally transpire more water and have less sensitivity of stomata to water deficit than the associated hosts (Escher et al. 2008; Glatzel and Geils 2009; Scalon et al. 2016). The higher transpiration rate and stomatal conductance in mistletoes have been suggested to ease access to the limiting nutrients like nitrogen from the host xylem (Schulze and Ehleringer 1984), and the adoption of a more negative water potential due to greater accumulation of nutrients helps the mistletoes to attach with the host plants and then grow and reproduce

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(Strong and Bannister 2002; Shen et al. 2006; Maes et al. 2018). In addition, in response to defense against vector-borne macroparasites, mistletoes absorb the host defense chemical compounds (secondary metabolites and hormones) and use them for their defense (Pennings and Callaway 2002; Glatzel and Geils 2009).

Host preferences of mistletoes

Host specificity and recognition

Parasitic flowering plants are a successful and specialized group of plants that can potentially parasitize a large number of different co-occurring plant species, ranging from herbaceous annuals and perennials to trees and shrubs (Nickrent and Musselman 2004; Press and Phoenix 2005; Bell and Adams 2011). Mistletoes can be generalists, which can parasitize many different species or extremely host-specific (Okubamichael et al. 2011; Kokla and Melnyk 2018; Fig. 1; Table 1). For example, *Dendrophthoe falcata*, *Amyema benthamii*, *Dendrophthoe curvata* and *Amyema pendula* can parasitize wide ranges of host plants and are generalists (Nickrent and Musselman 2004; Zhang et al. 2013; Le et al. 2016; Clarke et al. 2019; Table 1). However, *Tapinanthus rubromarginatus* and *Korthalsella emersa* occur on a limited host range or specialist that can infect only *Protea caffra* and *Eucalyptus* sp., respectively (Nickrent and Musselman 2004; Okubamichael et al. 2016; Clark et al. 2020).

Host specificity is an overall consequence of the ability of a parasitic plant to recognize and attack a particular host plant. The fusion or specificity of mistletoes onto vascular plants could be related to morphological and physiological adaptation or phenotypic plasticity (Glatzel and Geils 2009; Guerra et al. 2018) that allow seeds to overcome hosts' chemical and mechanical defenses (Okubamichael et al. 2016; Guerra et al. 2018). Successful parasitism depends on one or more factors, which include the quality of the host in terms of nitrogen content (Schulze et al. 1994; Yan et al. 2016), compatibility (Okubamichael et al. 2011), the strength of the parasite (parasite load) at the stage of development and parasite–host chemical interactions (Saucet and Shirasu 2016; Fig. 2B, C). The dispersal agent plays a role for mistletoes–host fusion, in which birds are potentially effective by depositing mistletoe seeds (Medel et al. 2004). Similarly, the host twigs diameter regulates mistletoes population (Arruda et al. 2013), in which the host plants without suitable branches are less likely to host mistletoes because their seeds are merely washed away (Okubamichael et al. 2011). Host preference may also depend on the diversity of available potential hosts; mistletoes of the Loranthaceae show a low host preference in heterogeneous tropical rain forests and high host preference in less diverse temperate forests (Press and Phoenix 2005).

So far, almost all the host specificity factors identified and the attachment to the host plants are largely influenced by the induction of chemical molecular signals, germination stimulants (nucleophilic protein receptor and ethylene generation), and haustoria-inducing factors (HIFs) (Okubamichael et al. 2016; Yoshida et al. 2016). These haustoria-inducing factors (HIFs) initiate a signal transduction cascade leading to reactive oxygen species (ROS) accumulation in the parasitic root and the formation of the haustorium (Kokla and Melnyk 2018; Fig. 2). Following formation, host invasion, the establishment of host–parasite vascular continuity, and the creation of a parasitic sink will happen (Saucet and Shirasu 2016; Fig. 2).

Formation of mistletoe haustorium

The multicellular invasive organ named haustoria plays an important role in the attachment and penetration of the vasculature to extract water, nutrients, and even macromolecules (Kokla and Melnyk 2018; Table 2). Once mistletoe-eating birds or marsupial attach the berries to tree branches, the epidermal cells on the haustorium tip secrete a viscous fluid (Amico and Aizen 2000; Wiesenborn 2016; Clarke et al. 2019), which enables close contact with the bark and helps to affix the embryo directly to the host (Fig. 2B). By this time, cell division starts and a typical apical meristem develops (Ko et al. 2014). In mistletoes (e.g., *Viscum album*), cell wall loosening and modification is critical for haustorium development and establishment (Sallé 1983; Chang and Lynn 1986; Ko et al. 2014). By exerting mechanical forces and chemical signals released from the mistletoes' haustoria probably help to weaken the process, cleave the backbone of major matrix polymers, and open up the host tissues (Sallé 1983). Interestingly, transcriptome analysis showed that enzymes including xyloglucan endotransglycosylases (XETs), glucanase, expansins, and other cell wall hydrolases are expressed in mistletoe (*Viscum album*) during the stages of host–mistletoes connection (Ko et al. 2014). For instance, xyloglucan plays a role in the formation of secondary walls in vascular tissues, however, breakage of these critical linkages using XETs may be an essential feature of cell wall loosening and progression (Chang and Lynn 1986). The haustorium, having entered the host bark, grows along the longitudinal axis of the host branch in the phloem and develops into the cortical haustorium or primary haustorium (Yan 1993).

All parasitic angiosperms (including mistletoes) may require chemicals (haustorium-inducing factors, HIF) such as strigolactones (SLs), flavonoids, quinones, and mucilaginous substances to disrupt dormancy and initiate haustorium formation (Joel et al. 2013; Okubamichael et al. 2016; Saucet and Shirasu 2016; Kokla and

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Table 2 Variation in the average values of growth rates, nutrient, and organic compound contents of mistletoes parasitized hosts (MPH) and mistletoes non-parasitized hosts (MNPH)

No.	Host	Mistletoes	Par	MNPH	MPH	Δ	References
1	*Pinus sylvestris*	*Viscum album* L.	SLI	3.9	3.0	0.9	Yan et al. (2016)
2	*Pinus sylvestris*	*Viscum album* L.	TN	0.9	0.8	0.1	Yan et al. (2016)
3	*Tapirira guianensis*	*Phoradendron perrottetii* (DC.) Eichler	C/N	38.4	36.7	1.7	Anselmo-Moreira et al. (2019)
4	*Acacia karroo*	*Agelanthus natalitius* (Meisn.)	WP	− 1.8	− 2.3	0.5	Okubamichael et al. (2016)
5	*Pseudotsuga menziesii*	*Arceuthobium sichuanense* (H.S.Kiu)	XPP	− 1.6	− 1.8	0.2	Pennings & Callaway (2002)
6	*Quercus deserticola*	*Psittacanthus calyculatus* G.Don	SP	2.8	3.1	− 0.3	Cuevas-Reyes et al. (2017)
7	*Quercus deserticola*	*Psittacanthus calyculatus* G.Don	TF	0.4	0.9	− 0.5	Cuevas-Reyes et al. (2017)
8	*Quercus deserticola*	*Psittacanthus calyculatus* G.Don	TT	1.4	1.9	− 0.5	Cuevas-Reyes et al. (2017)
9	*Pinus sylvestris*	*Viscum album* L.	TR	4.2	11.1	3.1	Rigling et al. (2010)
10	*Pinus sylvestris*	*Viscum album* L.	NDW	26.6	6.2	20.4	Rigling et al. (2010)
11	*Tapirira guianensis*	*Phoradendron crassifolium* Trel	FVD	78.2	67.8	10.4	Teixeira-costa and Ceccantin (2015)
12	*Tapirira guianensis*	*Phoradendron crassifolium* Trel	RD	25.1	24.4	0.7	Teixeira-costa and Ceccantin (2015)

Par, parameters; Δ, change in differences in MNPH and MPH; SIL, shoot length increment (cm); TN, total nitrogen (%); C/N, carbon-to-nitrogen ratio; WP, water potential (MPa); XPP, xylem pressure potential (MPa); SP, soluble phenolics; TF, total flavonoids; TT, total tannins; TR, tree rings (count); NDW, needle dry weight (g); FVD, function vessel diameter (μm); RD, rays diameter (rays/mm^2)

Melnyk 2018). For example, the genes involved in SLs biosynthesis, reported from all green plants, are the best-characterized class of germination stimulants for members of parasitic plants (Saucet and Shirasu 2016; Clarke et al. 2019). Thus cross-talk with auxin, SLs initiate the establishment of the holdfast, and subsequently, collar-like, fully encircling haustorium is developed around the stem branches of a host containing a sclerenchymatous `prong' or `horn-like device' (Calladine and Pate 2000; Fig. 2D–G). Similarly, parasites encoded chemicals (peroxidases and hydrogen peroxide) are together produced at the parasite radicle tip that is active in oxidative degradation and alteration of the host cell wall lignin into active HIFs (Keyes et al. 2007). Once the intrusive cells of parasites with HIF penetrate the host cells (Fig. 2B), the haustorium establishes and connects with the vasculature through a way of the host epidermis and cortex, and cell wall-degrading enzymes may assist in the penetration process (Hibberd and Jeschke 2001). Upon germination, seeds form a hypocotyl that elongates until it forms a holdfast that attaches firmly to the host branch (Mathiasen et al. 2008; Fig. 2), enabling the parasite to acquire water and nutrients and to modulate host physiology (Hibberd and Jeschke 2001; Saucet and Shirasu 2016). Ultimately, the parasitic plants develop special morphological structures (haustoria) and physiological characteristics, such as high transpiration rates, high leaf conductance, and low water potentials in hemi-parasites, for nutrient transfer and resource acquisition from their hosts (Calladine and Pate 2000; Figs. 1C, 2 E, F).

Mistletoes–host resource acquisition mechanisms

Mistletoes represent a widespread group of parasitic plants that establish long-lasting relationships with a diverse range of host plant species (Griebel et al. 2017). They are often green and have unique strategies to obtain water, minerals, and a substantial amount of carbon from their host plants (Těšitel et al. 2010; Scalon and Wright 2015; Clarke et al. 2019; Table 2). Under optimal conditions when water and nutrients are available for the host tree, the mistletoe may be able to obtain nutrients directly from the host xylem (one-way) to their vessels through the haustorium, which is a passive nutrient uptake mechanism (Bowie and Ward 2004; Scalon and Wright 2015). In mistletoes, the transfer of solutes and water is typical via apoplastic flow, but the possibility of symplastic transfer cannot yet be ruled out (Bell and Adams 2011). However, if there is lumen-to-lumen continuity between the xylem of the host and parasite, compounds would be essentially unchanged in form and quantity and would move by mass flow into the transpiring parasite (Irving and Cameron 2009). In this case, the composition and concentration of compounds in the xylem sap of the parasite should match that of the host (Bell and Adams 2011). On the contrary, if the host experiences physiological stress, the mistletoe can avoid the stress through taking water and nutrients actively from the host phloem (Bowie and Ward 2004).

In terms of acquiring significant amounts of water and minerals (e.g., K, N, P, Ca, and Mg), mistletoes often have high transpiration rates, which they achieve by having a lower water potential (more negative) than the host (Bowie and Ward 2004), opening their stomata, and experiencing a high water loss (Bowie and Ward 2004; Press

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and Phoenix 2005; Glatzel and Geils 2009; Table 2). Accumulation of osmotically active solutes in mistletoe tissue also promotes lower xylem water potential in their tissue compared with the host (Mathiasen et al. 2008), and thus the gradient in water potential between the host and mistletoes facilitating flux of water and solutes imported via the xylem (Escher et al. 2004). Okubamichael et al. (2011) confirmed that the more negative the water potential of the host trees (*Ziziphus mucronata*), the more the mistletoe (*Viscum rotundifolium*) needs to exceed their water potential to access nutrient passively. Concerning nitrogen and carbon dependence, most parasitic angiosperms lie between complete heterotrophic xylem- and phloem-feeders and complete autotrophic xylem feeders (Bell and Adams 2011). Various hypotheses have been proposed to explain this pattern (Scalon and Wright 2015). The most recognized one is the 'N-parasitism hypothesis', which posits N to be the most limiting resource for mistletoes, hence they use their faster transpiration rates to acquire sufficient N from the host xylem (Schulze and Ehleringer 1984). Bowie and Ward (2004) and Okubamichael et al. (2011) also compared nutrient accumulation and derives in mistletoe tissues either from the host xylem or phloem by examining the N:Ca ratio and hence reasoned that a N:Ca ratio of ≤ 1 indicates nutrients were obtained from the host xylem (passive nutrient uptake), but obtained from the host phloem (active nutrient uptake) if the ratio is > 1. In contrast to the N-parasitism hypothesis, they found that the mistletoes had N:Ca ratio > 1, indicating active uptake from the host phloem. So, mistletoes procure N in both active and passive to acclimatize nutrient-limited environments. The other hypothesis is the 'mimicry hypothesis' that suggested some mistletoe mimic the morphology of host leaves to deploy higher-N leaves (Barlow and Wiens 1977), and the 'C-parasitism hypothesis' revealed the partial heterotrophy, in which a part of the carbon in the mistletoes are transferred from the host xylem, in the form of amino acids (Marshall and Ehleringer 1990; Marshall et al. 1994). The C-parasitism hypothesis predicts that higher transpiration rates would be necessary, not only to acquire N but also to obtain heterotrophic carbon. For example, dwarf mistletoe types which belong to *Arceuthobium* and *Korthalsella* of Santalaceae (formerly Viscaceae) obtain carbohydrates from the phloem sap of the host, and, hence, they are considered as heterotrophic plants (Hawksworth and Wiens 1996).

Impacts of mistletoes on host plants
Parasitic angiosperms, especially mistletoes, affect the host plants by deforming the infected stem, reducing the growth, diminishing vigor, impairing the quality and quanti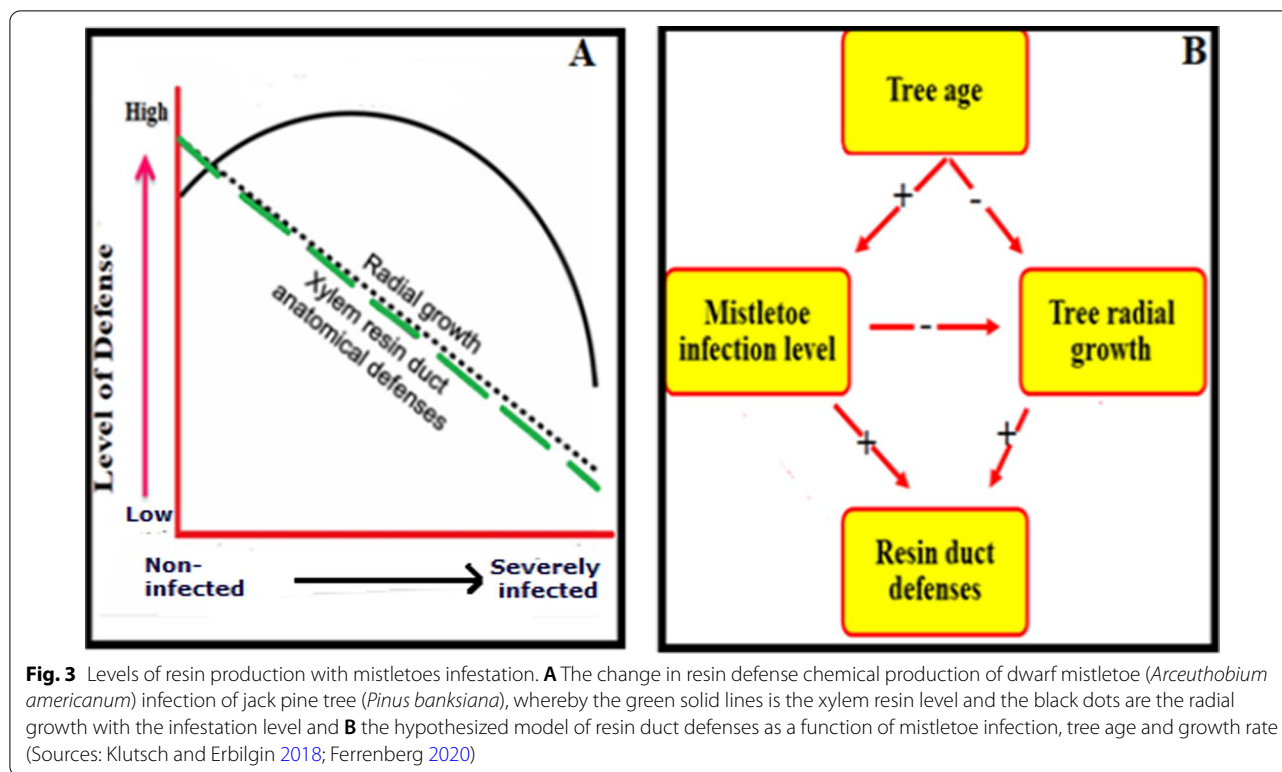ty of wood, reducing fruit set, reducing longevity, and heightening susceptibility to attack by other agents such as insects or fungi (Devkota 2005; Mathiasen et al. 2008; Nickrent 2011). Recent results showed that mistletoes can affect the reproductive success of their hosts because parasitized individuals produce less fruit and present reduced seed weight (Press and Phoenix 2005; Arruda et al. 2013). As the intensity of the attack by mistletoe increases, the photosynthetic potential of the part distal to the infestation declines leading to the death of the part (Kuijt 1969). However, the extent of damage of host mainly depends on the developmental stage, the availability of host resources, the growth rate, and the metabolic activity of the parasites (Glatzel and Geils 2009; Bell and Adams 2011).

Host defense against mistletoe infection and its mimicry of other biotic stresses
Plants are surrounded by an enormous number of biotic and abiotic stressors (Klutsch and Erbilgin 2018). Mistletoes are part of the biotic stresses that parasitize and derive their resources from the host's xylem solution (Runyon et al. 2010; Sangüesa-Barreda et al. 2012; Yan et al. 2016). The interaction between the parasitic plants and hosts is often analogous to the interaction between herbivores and plants in which both types of consumers display host preferences, reduce host biomass, alter host allocation patterns, modify plant community structure and dynamics (Pennings and Callaway 2002). Similar to other parasitic plants (e.g., *Cuscuta* spp.), mistletoes are xylem-tapping plants that have continuous uptake of sap by fluids as well as can take up and store secondary chemical compounds from the host that are used for defense and to complete their life cycles (Kuijt 1969; Yan et al. 2016; Anselmo-Moreira et al. 2019; Lázaro-González et al. 2019). This exacerbates the effects of environmental stresses such as water stress and limited resources on host trees leading to increased host mortality (Glatzel and Geils 2009; Rigling et al. 2010; Hu et al. 2016). Therefore, plants can evolve means of avoiding mistletoe infestation through a combination of chemical and anatomical defenses against a myriad of attacking organisms (Medel et al. 2004; Klutsch and Erbilgin 2018).

Host structural defenses against mistletoes
Trees interact with an array of biotic stresses such as pathogens, herbivory, and parasitic flowering plants and can offset the effects by utilizing structural features (Pennings and Callaway 2002). Structural defenses include morphological and anatomical traits and provide a fitness advantage to the plant by directly deterring the pathogen or parasitic plant from feeding as a result of lignification and suberization (War et al. 2012). It has been believed that lignification has an important role in host defense

Fig. 3 Levels of resin production with mistletoes infestation. **A** The change in resin defense chemical production of dwarf mistletoe (*Arceuthobium americanum*) infection of jack pine tree (*Pinus banksiana*), whereby the green solid lines is the xylem resin level and the black dots are the radial growth with the infestation level and **B** the hypothesized model of resin duct defenses as a function of mistletoe infection, tree age and growth rate (Sources: Klutsch and Erbilgin 2018; Ferrenberg 2020)

against pathogen invasion (Bhuiyan et al. 2009). According to Hu et al. (2017), the lignin content of the bark increased as a result of mistletoe infestation compared with the non-infected trees (Fig. 3). This lignification renders the cell wall more resistant to mechanical pressure applied during penetration as well as more water-resistant, and, thus, less accessible to cell wall-degrading enzymes (Teixeira-Costa and Ceccantini 2015) decreasing further attacks by parasitic mistletoes. In addition, the plant structural traits, e.g., spines and thorns (spinescence), trichomes (pubescence), and hardened leaves (sclerophylly) play a leading role in plant protection against herbivory and pathogens (War et al. 2012). In comparison, the spine length of many cactus acts as the first line of defense against parasitism by mistletoes, by discouraging bird perching on top of host columns, and in turn, impede seed dispersal (Medel et al. 2004). There appears, however, to be no correlation between spinescence and mistletoe infection on African plants, where common Acacia are frequently hosting a variety of mistletoes (Okubamichael et al. 2016).

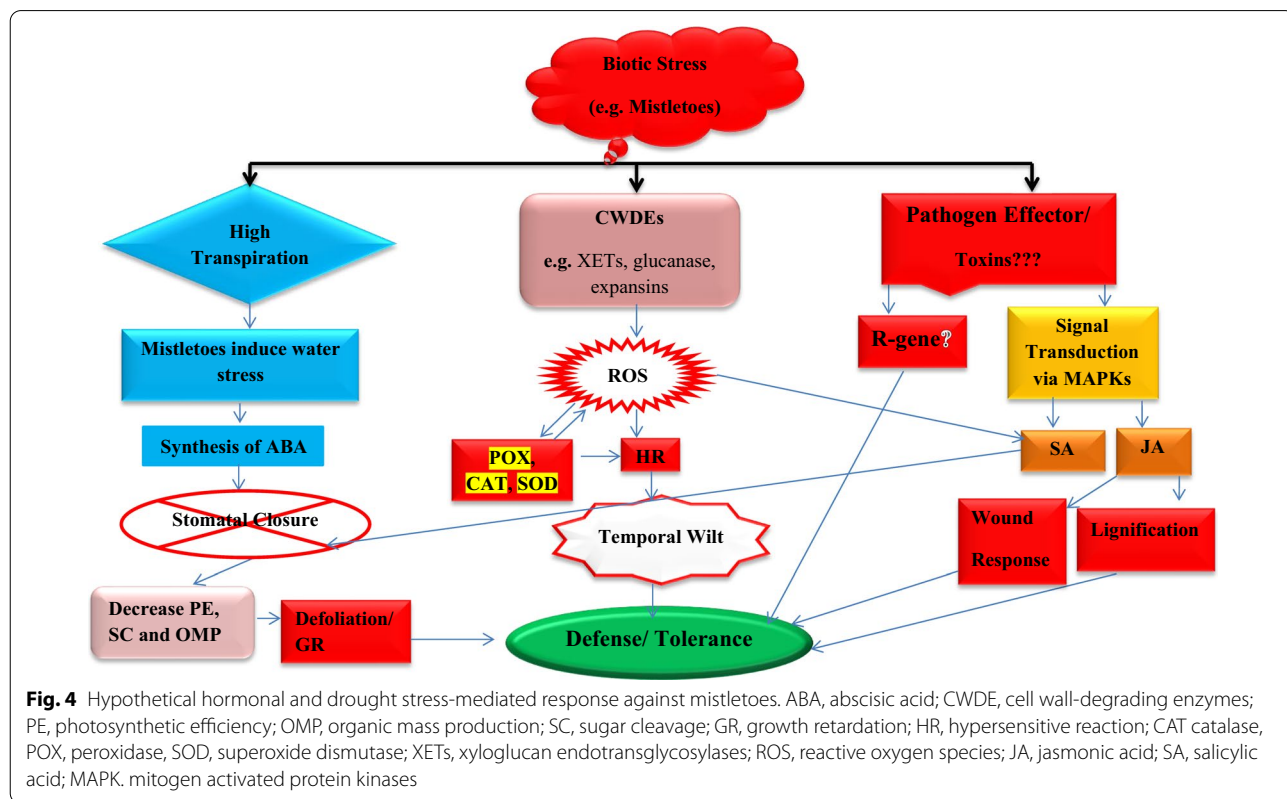### Chemical defense approach against mistletoes

There has been limited literature on the biological interactions mediated by molecules of host–mistletoes and host-hormonal defense mechanisms compared with other biotic stresses (Pennings and Callaway 2002;

Arruda et al. 2013; Cuevas-Reyes et al. 2017). Parasitic plants and host plants are frequently close relatives (Clarke et al. 2019) and thus the parasite shares the biological, physiological, and morphological characteristics of the host (Anselmo-Moreira et al. 2019). But, other studies asserted that the host chemical defense response against parasitic plants involves activating similar mechanisms to those induced-resistance against herbivores and pathogens (Pennings and Callaway 2002; Smith et al. 2009; Runyon et al. 2010; Klutsch and Erbilgin 2018). Cuevas-Reyes et al. (2017) showed that mistletoes have comparable effects with those caused by herbivores to hijack host-derived signals. However, the parasitic plants affect and are affected by host plant physiology because of similar hormonal pathways, do not alter nutrient cycling as extensively as do herbivores (Pennings and Callaway 2002).

Defense mechanisms of host plants involve the production of a variety of secondary compounds and are mediated by hormones (Table 2). Therefore, analogous with herbivore and pathogens, these plant secondary compounds may constitute important signals for the biotic stress mediated by mistletoe infestation (Press and Phoenix 2005; Escher et al. 2008; Runyon et al. 2010; Cuevas-Reyes et al. 2011; Mutlu et al. 2016; Klutsch and Erbilgin 2018; Lázaro-González et al. 2019). Lázaro-González et al. (2019) revealed that pines parasitized by mistletoe

respond against stress by changing their chemical profiles such as phenols and tannins. However, in contrast to herbivory, which in general are episodic and short-term stressors, mistletoe represents a chronic long-term biotic stressor, and hence change in chemical profile depend on the parasite load (Klutsch and Erbilgin 2018). Mistletoe-induced water stress can stimulate the accumulation of reactive oxygen species (ROS) such as H_2O_2, O_2^- and OH^- in Scots pine needles, which leads the host cell to hypersensitive reactions (HR) (Mutlu et al. 2016; Fig. 4). They further reported that increasing levels of antioxidant enzymes such as catalase (CAT) and peroxidase (POX) in Scots pine needle could result from the scavenging of H_2O_2 produced excessively in cells during mistletoe stress. Some hosts react to mistletoe haustorial invasion by producing wound periderm (Salle et al. 1984; Yan 1993), which prevents the haustorium from reaching the host xylem and eventually leading to the death of the parasite. Yan (1993) reported the production of wound periderm in *Eucalyptus oleosa* and *Heterodendrum oleifolium* infected with *Amyema preissii* and *Lysiana exocarpi* mistletoes, respectively. The formation of wound, subsequent densely stained, and lacking cellular structure indicating the cells in these areas might be dead and failure of mistletoes haustoria to penetrate host barks.

The syntheses of abscisic acid (ABA), salicylic acid (SA), and jasmonic acid (JA) in plants promote stomatal closure and play an important role in adaptive responses to both abiotic and biotic stresses (War et al. 2012). High levels of ABA and JA and the declined levels of indole-3-acetic acid (IAA) and SA in pine tree bark and wood upon mistletoe infestation have been reported by Hu et al. (2017). The observed changes in these phytohormones in pine trees upon mistletoe infestation reflect the complexity of antagonistic and synergistic interactions between IAA and SA/ JA signaling pathways and there has been cross-talk between IAA and other hormonal signaling pathways (Hu et al. 2017). Enhanced production of terpene compounds has long been associated with disease resistance mechanisms in plants (Erbilgin et al. 2017; Klutsch and Erbilgin 2018; Ferrenberg 2020). Pine tree infested with mistletoes increased in most monoterpenes (bornyl acetate, α-pinene, tricyclene, limonene, etc.), phenols, and condensed tannins to control pine trees (Lázaro-González et al. 2019) and this induced reaction of the pine tree resembling those against drought, pathogen and herbivory stress. Resins (monoterpenes) are toxic and act as mechanical deterrent effects to natural enemies, exudes from wounds to mire attackers, and seal damaged tissue (Erbilgin et al. 2017; Ferrenberg 2020).

Fig. 4 Hypothetical hormonal and drought stress-mediated response against mistletoes. ABA, abscisic acid; CWDE, cell wall-degrading enzymes; PE, photosynthetic efficiency; OMP, organic mass production; SC, sugar cleavage; GR, growth retardation; HR, hypersensitive reaction; CAT catalase, POX, peroxidase, SOD, superoxide dismutase; XETs, xyloglucan endotransglycosylases; ROS, reactive oxygen species; JA, jasmonic acid; SA, salicylic acid; MAPK. mitogen activated protein kinases

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It was further demonstrated that dwarf mistletoe (*Arceuthobium americanum*) infestation increases the resin production in jack pine trees (*Pinus banksiana*) (Klutsch and Erbilgin 2018; Ferrenberg 2020; Fig. 3B). However, as the infection level increases, the concentration of resin in the form of monoterpene drops in severely infected trees to levels below that found in healthy trees (Klutsch and Erbilgin 2018; Fig. 3A). Therefore, trees with the greatest constitutive resin duct structure have been shown to better resist attacks by mistletoes (Erbilgin et al. 2017; Lázaro-González et al. 2019). On the other hand, in a similar manner to herbivory and pathogens, host trees respond to mistletoes infestation by a reduction in growth rates (Rigling et al. 2010; Hu et al. 2017) that can be partially attributed to a drain of carbohydrates (Escher et al. 2004; Hu et al. 2017), lower N and sulfur (S) contents, minimized sesqui- and diterpene amounts (Lázaro-González et al. 2019). The loss of water to a mistletoe infestation will result in stomatal closure and turn reduction in C assimilation and/or photosynthetic rates of the host (Glatzel and Geils 2009; Fig. 4). This phenomenon is controlled by defoliation without mechanical harm to the host as the deciduous plants use it to reduce water loss during arid conditions (Meinzer et al. 2004), and in order, the defoliation promotes emissions of volatile compounds (Lázaro-González et al. 2019). Accordingly, the hydraulic system and structure of the host wood can be altered (Meinzer et al. 2004; Hu et al. 2017), which will rapidly accumulate massive amounts of ROS in the infected tissues (Mutlu et al. 2016). This, in turn, activates a cascade of reactions leading to the activation of defensive enzymes such as peroxidases, polyphenol oxidases, and ascorbate peroxidases (War et al. 2012). These mediate the induction of antioxidants and oxidative stress to achieve localized mistletoes infestation inhibition, through promoting hypersensitive reaction (HR) or programming cell death in tissues of infected plants, which is thought to limit the access of the pathogen to water and nutrients (Sharma et al. 2012; Fig. 4). Nevertheless, the defensive responses of plants to mistletoes attack still require considerable research.

Conclusions and future directions

Mistletoes have a detrimental effect on associated hosts. As a consequence of the competition of the host resources, the host diminishes growth and vigor, impairs quality and quantity of wood, and heightens the susceptibility to attack by other pathogens. In this review, host–mistletoes interaction in terms of water and nutrient uptake indicates that the mistletoes are obligate hemiparasitic plants that acquire water, solutes, hormonal compounds, and others passively, which is achieved by increased transpiration rates and lower water potential.

For these cases, they have a much higher concentration of macronutrients compared with the host. Infection of mistletoes exposes the plants to water stress and physiological disturbance. In response to mistletoe-induced drought stress, the host stimulates defense chemical signallings upon the host–pathogen interplay. Therefore, the inductions of these transcription factors trigger stomatal closure and in turn reduce the C assimilation and/or photosynthetic rates followed by defoliation and decline growth rates which make the pathogen unable to procure proper nutrients for their growth and development. Research findings also confirmed that the concentration of monoterpenes (resin), phenols, and concentrated tannins are increased in pine trees with mistletoes infestation compared with the non-infected trees, which are toxic and act as mechanical deterrents to natural enemies. Despite these defense chemicals are detected from varied types of hosts upon mistletoes attack compared with non-infected, the mechanisms of pathogenicity and hormonal-mediated host defense responses against mistletoes have rarely been studied. Therefore, future research should focus on the types of HIFs mistletoes release for pathogenicity and host–mistletoes hormonal-mediated defense responses, because the research findings revealed that mistletoes are pathogens that reduce all aspects of the host quality. In addition, global distribution, mapping, and phylogeny of the mistletoes need further studies. Moreover, managing the mistletoes population through monitory approaches is vital to change their spread and intensification and to boost the quality and productivity of forests.

Declarations

Ethics approval and consent to participate
Not applicable.

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