NRC Research Press
REVIEW

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Towards best-practice management of mistletoes in horticulture[1]

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Abstract: Mistletoe is increasingly being reported as a horticultural pest, infecting many species grown commercially for fruit, nuts, and other food products. Unlike mistletoe impacts on forestry, the published research on mistletoe in horticulture is scant, with management guidelines reliant on anecdotes, un-replicated trials on unrelated species, and often in different countries and growing systems. We have integrated the existing work to summarize information on the most effective control strategies for mistletoe in horticulture, and call attention to the paucity of empirical research. Despite grower interest in growth regulators and herbicides, limited trials suggest chemical treatment of mistletoe is ineffective, consistent with findings from forestry and ornamental trees. Although labour-intensive, ongoing mechanical removal is the most effective strategy to minimize mistletoe impacts but, without information available on effects of mistletoe infection on yield or tree mortality, cost-effectiveness calculations are not possible. Given the range of herbivores that consume mistletoe tissues, biological control may be useful, both to prevent initial infection and also reduce impacts on infected hosts in commercial plantations. To catalyse more research on mistletoes in horticulture, we articulate six priorities for further work, emphasizing the utility of tree crops as model systems to address questions regarding mistletoe ecology and host-parasite dynamics more broadly.

Key words: integrated pest management, plantation, orchard, host quality, monoculture.

Résumé : Le gui est de plus en plus victime de ceux qui le considèrent comme un parasite en horticulture, contaminant de nombreuses espèces cultivées commercialement pour les fruits, les noix et autres produits alimentaires. Contrairement aux impacts du gui en sylviculture, les recherches scientifiques publiées sur le gui en horticulture sont peu nombreuses, sa gestion reposant sur des anecdotes, des essais non répétés sur des espèces sans rapport les unes avec les autres, souvent dans des pays et des modes de culture différents. Nous intégrons les travaux existants afin de résumer les informations sur les meilleures stratégies de lutte contre le gui en horticulture et soulignons la rareté des recherches empiriques. Malgré l'intérêt des producteurs pour les régulateurs de croissance et les herbicides, des essais limités suggèrent que le traitement chimique du gui est inefficace, en concordance avec les résultats obtenus en foresterie et chez les arbres ornementaux. Bien qu'exigeant une importante main d'œuvre, l'élimination mécanique en continu demeure la stratégie la plus efficace pour minimiser l'impact du gui, mais sans la disponibilité d'informations sur les effets de l'infection par le gui sur le rendement ou la mortalité des arbres, les calculs du rapport coût-efficacité ne sont pas possibles. Compte tenu du spectre des herbivores qui consomment les tissus du gui, la lutte biologique pourrait être utile afin de prévenir à la fois une infection initiale et pour réduire les impacts sur les hôtes déjà infectés dans des plantations commerciales. Afin de catalyser plus de recherches sur le gui en horticulture, nous formulons six priorités pour les travaux ultérieurs, soulignant l'utilité de cultures arboricoles comme systèmes modèles pour aborder les questions concernant l'écologie du gui et les dynamiques hôte-parasite en général. [Traduit par la Rédaction]

Mots-clés : gestion intégrée des parasites, plantation, verger, qualité de l'hôte, monoculture.

Received 17 December 2019. Accepted 20 February 2020.

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[1] This Review is one of a selection of papers published in the special issue from the IUFRO World Congress, Curitiba, Brazil 2019 Symposium on Mistletoes.

Botany **00**: 1–10 (0000) dx.doi.org/10.1139/cjb-2019-0205

Introduction

Horticulture is a rapidly expanding industry, accounting for 35% and 39% of the total value of crops for the USA and Europe, respectively. In addition to accounting for an increasing proportion of land-use, irrigated tree crops represent a growing component of water entitlements in many agricultural regions. While cereals and other annual row crops predominate in terms of areal extent, permanent crops — vineyards and orchards — generate far higher returns per unit area, and are disproportionately located in areas with fertile soils and temperate climates (Ramos et al. 2011).

Mistletoes infect many species of plant grown commercially for fruit and nuts. Unlike managed forests, timber plantations, and dryland agriculture, where the impacts of dwarf mistletoes (*Arceuthobium* spp.) and root-parasites have been comprehensively studied (Hawksworth and Shaw 1984; Hawksworth and Wiens 1996; Scholes and Press 2008), the role of leafy mistletoes in horticulture is still poorly understood. We have integrated previous work on mistletoe in horticulture, emphasizing fruit and nut trees, drawing on findings in reports, theses, industry conference proceedings, and workshops with growers as well as the peer-reviewed primary literature in English, Portuguese, and Spanish. Aspects of mistletoe impacts and management relating to Australia's macadamia industry were recently summarized in a report to growers (Watson 2019*a*). Here, we build on that work and expand the scope of our review to include all available work on mistletoe in horticulture. Most literature focuses primarily on control methods, evaluating the effectiveness of physical or chemical approaches. In addition to identifying the most effective control options, we summarise emergent generalities in mistletoe management and identify priorities for further work. Integrating these priorities with work in managed forests, urban landscapes, and unmanaged forests and woodlands, we emphasize the utility of tree crops as model systems to address a range of pure and applied questions regarding mistletoe ecology and host–parasite dynamics more broadly. By working cooperatively with industry partners to secure strategic investment, our recommendations can be refined into best-practice guidelines, applying the principles of integrated pest management to treat existing infections, reduce susceptibility, and minimize the effects of mistletoe infection on orchard profitability.

Horticultural systems

T1,F1 Of the many plant species grown commercially for food, a relatively small number are reported to be affected by mistletoes (Table 1; Fig. 1), and only a subset of these have been the subject of dedicated study. Divergent patterns of infection are apparent for some crop species grown in their native range versus elsewhere. Thus, avocados, cashews, pecans, and macadamias are all frequently infected by mistletoes when grown in plantations within their native range (South America, North America, and Australia; respectively), but mistletoe infection is rare when those same tree crops are grown elsewhere (Ávalos et al. 2018; Watson 2019*a*).

Two exceptions are noteworthy and warrant further scrutiny. Although native to lowland rainforests in Latin America, cacao (*Theobroma cacao* L.) is grown extensively in equatorial Africa, where plantations are frequently affected by mistletoes [Loranthaceae, especially *Tapinanthus bangwensis* (Engl. & K.Krause) Danser]. Despite being conducted almost 50 years ago, Room's research on this system (Room 1971, 1972*a*, 1972*b*, 1973) remains the most comprehensive study of any mistletoe in a horticultural setting, exploring aspects of their pollination, seed dispersal, effects on host physiology, and wider animal communities in and around cacao plantations. The other noteworthy example is European apple orchards. Originally from Central Asia, apple trees have been cultivated throughout Asia and Europe for thousands of years and, in many parts of their introduced range, they serve as ecologically important hosts for indigenous mistletoe populations (*Viscum album* L.; Varga et al. 2014). Indeed, in England and France where mistletoe is actively managed in apple orchards for decorative purposes, the decline in populations of mistletoe and their associated insect species is attributed to decreasing numbers of traditionally managed apple orchards (Briggs 2011).

Mistletoe control measures

Although we did not find published data that have quantified the impacts of mistletoe on any horticultural crop (either on host mortality, growth, or yield), there is a widespread perception that mistletoe is necessarily a destructive pest that requires control (e.g., Brown 1959; Castellón and Novara 1998; Matiello 2014). Often forming large clumps in the canopy of infected trees (Fig. 1), research on mistletoes in other systems have documented a range of direct and indirect effects including water and nutrient depletion, shading, and premature branch drop (Mathiasen et al. 2008; Watson 2019*b*). During a workshop with representatives of the Australian macadamia industry, discussions with growers revealed numerous trials of control methods to remove mistletoe and prevent reinfection, with varying success (Watson 2019*a*). Although these trials are characteristically small-scale, unreplicated comparisons conducted on single properties, the qualitative results are an instructive primer to guide larger scale trials. By integrating lessons learned from these trials with findings from other crops affected by mistletoe (both horticultural and forestry), those control measures with the greatest relevance to horticulture can be identified.

Chemical control

In most countries, there are no chemicals registered for use as mistletoe control agents, so any chemical management of mistletoe would need to establish efficacy,

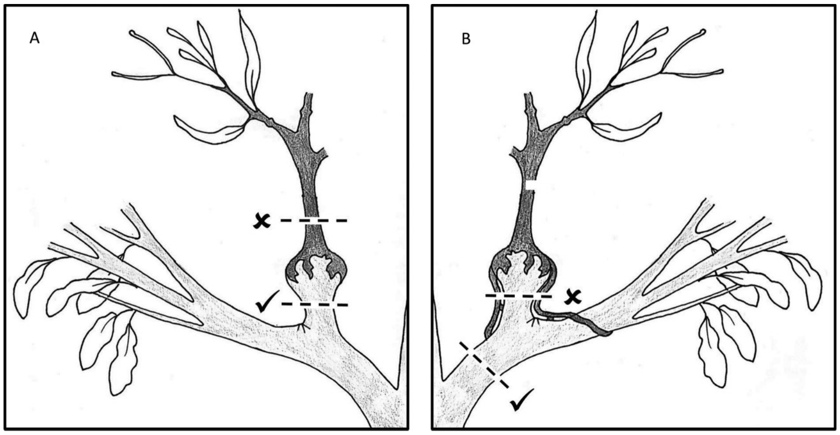
Table 1. Plants grown commercially for food that are reported to be affected by mistletoes.

Crop species	Mistletoe genera	Representative reference(s)
Cacao (*Theobroma cacao*)	*Tapinanthus*, *Phragmanthera*, *Englerina*	Room 1972, 1973
Macadamia (*Macadamia* spp.)	*Amyema*, *Benthamina*, *Dendrophthoe*	Watson 2019*a*
Mango (*Mangifera indica*)	*Dedropemon*	Sawant et al. 2008, Silva and Fadini 2017
Pecan (*Carya illinoinensis*)	*Phoradendron*	Wood and Reilly 2004
Kolanut (*Cola nitida*)	*Phragmanthera*	Asogwa et al. 2012
Citrus (*Citrus* spp.)	*Tapinanthus*, *Struthanthus*	Terna et al. 2017, Gonçalves et al. 2012
Peach (*Prunus persica*)	*Ligaria*, *Scurrula*	Amico and Vidal-Russel 2019
Almond (*Prunus dulcis*)	*Phoradendron*, *Viscum*, *Ligaria*	Paine and Harrison 1992
Apricot (*Prunus armeniaca*)	*Ligaria*, *Viscum*	Amico and Vidal-Russel 2019
Guava (*Psidium guajava*)	*Tapinanthus*	Sidahmed 1984, Zaroug et al. 2009
Cashew (*Anacardium occidentale*)	*Cladocolea*, *Psittacanthus*	Fadini and Lima 2012
Pomegranate (*Punica granatum*)	*Ligaria*, *Viscum*, *Plicosepalus*	Qasem 2009
Apple (*Malus domestica*)	*Viscum*	Briggs 2011
Pear (*Pyrus communis*)	*Viscum*	Paine 1950
Carob (*Ceratonia siliqua*)	*Ligaria*, *Plicosepalus*	Castellón and Novara 1998
Olive (*Olea europea*)	*Ligaria*, *Viscum*	Amico and Vidal-Russel 2019
Avocado (*Persea americana*)	*Phoradendron*	Zentmyer 1951, Ávalos et al. 2018
Coffee (*Coffea arabica*)	*Struthanthus*	Matiello 2014

Fig. 1. (A) Coffee plant infected with a mistletoe (*Struthanthus* spp.), the long branches of the hemiparasites shading the host canopy. (B) Detail of a mistletoe (*Dendrophthoe* spp.) infecting a Macadamia branch, note the epicortical root parallel to the host branch and multiple haustoria. (C) Macadamia plantation heavily infected with mistletoe (*Dendropthoe* spp.). Note the sparse canopy, asymmetrical growth, and tendency for the mistletoe to grow on the upper branches, shading the host tree. *Struthanthus* photograph courtesy of Jose Matiello; *Dendrophthoe* photographs courtesy of David M Watson. [Colour online.]

rates, off-target effects, safety, residues, and any trade implications. Although the use of herbicides and growth regulators has successfully controlled mistletoe in ornamental and production horticulture and forestry (Greenham and Brown 1959; Reid et al. 2008 and references therein), outcomes vary considerably between systems, with no best-practice guidelines currently available for chemical control of mistletoes in any production system. Various herbicides have been trialled using foliar spray, stem injection, or direct application to mistletoes (Brown and Greenham 1965; Minko and Fagg 1989; Vázquez et al. 2006; Reid et al. 2008; Gonçalves et al. 2012). Most of these trials have been conducted in the USA, Canada, and Mexico, focusing on dwarf mistletoes (*Arceuthobium*; Viscaceae), which can form systemic infections in coniferous hosts, fundamentally changing the growth habit of trees rendering them unsuitable for timber production (Hawksworth and Johnson 1989). Although fundamentally different to most horticultural systems (angiosperm crops and leafy mistletoes in the Viscaceae and Loranthaceae exhibit many differences in plant anatomy and physiology), the lack of success in herbicide control despite millions of dollars of research investment over many decades is instructive. Limited trials have also been

Fig. 2. Best practice procedure for pruning mistletoes from an infected host tree. (A) For mistletoes without epicortical runners, pruning on the proximal side of the haustorium is sufficient to remove the established plant. (B) For those mistletoes with epicortical runners (root-like structures emerging from the haustorium), prune the infected branch below the most proximal attachment point — any mistletoe runners left intact will likely re-sprout. Illustration by Maggie J. Watson. [Colour online.]



conducted in horticultural crops in the USA, with 2,4-dichlorophenoxyacetic acid (usually called 2,4-D) successfully used to control mistletoe in pecans if the trees were sprayed prior to bud break (Wood and Reilly 2004); this timing is critical to protect the host tree (see also Paine and Harrison 1992).

In contrast, the use of growth regulators has proven effective for mistletoe control in some settings (Berry et al. 1989; Paine and Harrison 1992; Watson and Martinez-Trinidad 2006, but see Robbins et al. 1989;Adams et al. 1993). 2-Chloroethylphosphonic acid or Ethephon (Ethrel®) is an ethylene-generating compound, which has the potential to induce ripening and improve fruit abscission. Its use for mistletoe control has been trialled in the USA to regulate *Phoradendron* species (Viscaceae) in a variety of stone fruit and nut tree species, including pecans (Joyce et al. 1987), and is the only chemical registered for mistletoe control in the USA (Shaw and Mathiasen 2013). Trials on orange trees in Brazil applied ethephon at 2.4 kg per hectare and, while some effects on mistletoe were noted, it also caused complete defoliation of host trees (Gonçalves et al. 2012). In ornamental trees, applying Ethephon at label rates effects partial abscission of *Phoradendron* sp. mistletoe shoots, but the mistletoe plants are not killed and the approach is advocated as means of slowing the intensification of existing mistletoe infections by reducing mistletoe fruiting (Lichter et al. 1991). Other chemical approaches to mistletoe control have been trialled, including soil-active herbicides, synthetic amino acids, copper sulfate, triclopyr ester, and other contact herbicides, all with either highly variable results or negative effects on host trees (Coder 2003).

Mechanical control

Although necessarily labour-intensive, mechanical removal of mistletoes by pruning the infected branches is the single most effective method for controlling mistletoes in orchards and other horticultural plantations (Brown 1959; Castellón and Novara 1998; Shamoun 1998; Shamoun and DeWald 2002). Many of the loranthaceous mistletoes infecting horticultural crops (e.g., *Dendrophthoe*, *Benthamina*, *Dendropemon*, *Struthanthus*, *Passovia*) are characterised by the presence of epicortical roots. These structures emerge laterally from the original connection with the host and form secondary attachments both distal and proximal to the original haustorium (Fig. 1). Hence, successful removal of these mistletoes requires removing all of these connections and associated tissue. While this can be achieved by cutting the infected host branch beneath (upstream) of the most proximal connection (Fig. 2), this can entail removal of large branches and, therefore, lead to considerable loss of host canopy and productivity. To be effective, mechanical removal needs to be thorough, regular, and coordinated across adjacent properties, necessitating access to tree canopies and detection of mistletoes. Mechanized pruning shapes the sides and tops of trees and removes mistletoe foliage, but follow up pruning specifically to remove mistletoes is required.

Biological control

As with chemical control, research in forestry and other plant systems has explored the use of biological control to manage mistletoes (Askew et al. 2006). A wide range of hyperparasitic fungi naturally occur on mistletoes (Wicker and Shaw 1968; Beilharz 1997), with considerable research exploring their potential for controlling mistletoe in forests managed for timber production. Rather than necessarily killing mistletoes, these pathogens reduce plant vigour and can interrupt phenology (Shamoun et al. 2003; Ramsfield et al. 2009). Although successful control of some dwarf mistletoes has been achieved via spraying host crowns with fungal inoculant, it is unclear whether these organisms are specific to mistletoes (Ramsfield et al. 2005). This lack of specificity, coupled with the widespread use of fungicides in horticultural systems to treat existing pathogens, means that fungi are unlikely to be useful in controlling mistletoe. Likewise, many of the problematic mistletoes in horticulture are known hosts for epiparasitic mistletoes (Bernhardt 1984) but, based on previous work (Wiens and Calvin 1987, see also Glatzel and Balasubramaniam 1987), it is doubtful that they have sufficient deleterious effects on their mistletoe hosts to warrant further investigation.

Mistletoes also attract a range of animal consumers, including many mammalian herbivores, which help regulate mistletoe numbers in native habitats (Watson 2001, 2019*b*). Arboreal folivores including Common Brushtail and Common Ringtail Possum favour Loranthaceous mistletoe foliage, with experimental work on captive animals and radio-tracking free ranging animals demonstrating consistently high preference for mistletoes mediated by high water content, high concentration of cations, and high digestibility (Choate et al. 1987; Canyon and Hill 1997; Petrović 2014). As well as arboreal marsupials, cattle, sheep, donkeys, goats, horses, camels, and several deer species all browse preferentially on mistletoe where available (Watson 2001). Most of the research on mistletoe consumption by herbivores relates to mistletoes on wild populations of hosts, and it is unclear whether herbivores show similar preference for mistletoes on hosts within plantations.

There have been several studies of the arthropod fauna of Loranthaceous mistletoes (Anderson and Braby 2009; Burns et al. 2011) and, unlike mammals, many insect herbivores are mistletoe specialists (Watson 2004; Burns et al. 2015). Rather than representing a subset of the insect assemblage inhabiting the host canopy, mistletoe plants support their own distinctive assemblage of insects. The best studied group is butterflies, with two diverse and cosmopolitan families (Pieridae and Lycaenidae) containing many mistletoe specialist species. Upon hatching, the larvae feed exclusively on mistletoes on a wide range of hosts, often defoliating the entire plant (Braby 2006; Uchôa et al. 2012; Moss and Kendall 2016) but leaving the host tree untouched. Integrated pest management of many pathogens, herbivores, and diseases in horticulture currently incorporates the use of beneficial insects, so trialling the addition of mistletoe-specialist butterflies to the suite of groups already used would be straightforward.

Variety selection and orchard management

In most species grown in commercial horticulture, multiple varieties have been selectively bred to maximise yield under a range of growing conditions. Although we are unaware of any plant breeders explicitly selecting for resistance to mistletoes, our (D.M.W. and M.C.) work with macadamia growers revealed consistent differences in susceptibility to mistletoes between different varieties. Thus, those macadamia varieties with more open canopies are more susceptible to mistletoe infection, compared with other varieties that have a more contiguous canopy and more upright growth habit. In addition to differences in canopy architecture and crown closure, these varieties also vary in bark roughness, bark thickness, and growth rate, which may influence the likelihood of mistletoe germination and (or) establishment (Watson 2019*a*). Ávalos et al. (2018) noted similar variation in susceptibility in avocadoes, with one variety (Hass) uninfected with mistletoe (*Psittacanthus calyculatus*, Loranthaceae).

Other aspects of orchard management that affect shading, bird visitation, and pest management may also influence mistletoe occurrence. Macadamia growers report that trees at the ends of rows and close to fences are more likely to be infected with mistletoes, as are orchards planted at lower densities (Watson 2019*a*), a pattern also noted in manioc and black pepper plantations. In addition to the crop itself, many horticultural species (including tea, coffee, and cacao) are grown beneath shade trees, including both native and exotic species, which frequently host mistletoe. Whether these mistletoes also infect the horticultural crop or have any effects (direct or indirect) on tree health or yield has not been investigated, but Matiello (2014) noted that in Atlantic forest coffee plantations, coffee plants growing beside shade trees were more likely to be infected with mistletoe. Bird deterrents (including gas guns and lasers) are used in many industries to reduce direct losses to fruit and nut eating birds, but there are no data available to evaluate any effects of mistletoe-dispersing birds. Given the extended phenology of many mistletoes and the variety of animals involved in seed dispersal, we consider it unlikely that these deterrents would have any meaningful effect on reducing mistletoe infection.

Other approaches

Many other approaches to controlling mistletoes in horticulture, forestry, and ornamental trees have been explored, including flame throwers and controlled burns, freezing, bagging, and (or) wrapping infected branches with plastic bags, and selective breeding to increase mistletoe resistance (Brown 1959; Kelly et al. 1997; Coder 2003). Most of this research has been small-scale trials conducted in the USA, in coniferous forests and plantations infected with dwarf mistletoe, and none have the demonstrated efficacy or large-scale relevance to be considered viable control measures for mistletoe in horticulture.

Recommended practice

Mistletoe has emerged as a significant issue for the horticulture industry, with growers concerned about the effects on tree growth and yield, as well as interference with routine orchard operations. Effective control of mistletoes requires increased awareness of the issue, coordinated actions across properties, exchange of information among growers regarding treatment, and the development of best-practice treatment techniques based on quantitative trials. As native organisms, eradicating mistletoes and their seed dispersers at large scales is not possible and often not permissible. Rather, the objective should be to suppress mistletoes within orchards and plantations to maximize profitability. The treatment options discussed represent short-term reactive solutions to manage existing infections. Longer-term management necessarily requires proactive approaches to document patterns, understand the mechanistic basis of observed patterns, test the effectiveness of different treatment regimes and estimate the cost effectiveness of applying them at different scales.

Detecting mistletoe is a priority, both to identify those areas requiring management but also for evaluating efficacy and optimal frequency of existing management practices. Currently, mistletoes are either only dealt with once heavily infected trees become apparent, or the entire orchard is monitored by teams on machinery, locating infected trees and removing all accessible mistletoes. Both of these are inefficient, either dealing with infections once they're already problematic or deploying teams of people to look for mistletoes, but spending most of their time on properties and blocks where mistletoe does not occur. For large-scale growers and orchard managers, locating mistletoes is best conducted by specialist teams (including drone-borne near-infrared imagery). Smaller-scale growers should involve orchard workers, where any mistletoe detected during orchard operations is flagged, either physically or digitally, to be followed up by removal teams once a pre-determined threshold is reached at either the block or whole-of-orchard scale.

Mechanical removal (pruning host branches infected with mistletoe) is presently the most effective means of controlling mistletoe in orchards and plantations. By cutting off infected branches below the lowest point of attachment, existing mistletoes are removed. If any points of attachment remain, re-sprouting is likely. For those infections on the trunk or main branches, prune off all mistletoe shoots and cut away host bark around attachment points. Rather than removing mistletoes during regular pruning of trees, mistletoe removal is best conducted independently when mistletoes are flowering, maximising detectability and reducing reinfection by decreasing mistletoe fruit abundance within orchards. Once removed from trees, mistletoe plants and infected branches are typically piled between trees rows, and then either recovered and relocated for chipping and composting or chipped in situ and distributed as mulch directly beneath the macadamia trees. Given the high concentration of cations and other nutrients in mistletoe tissues (March and Watson 2007, 2010), this latter approach is recommended. In addition to reduced handling, chipping pruned mistletoes and branches in situ will retain all nutrients within the orchard, and may also have added benefits of fostering any insects, fungi, and other natural enemies of mistletoe within the more infected parts of the orchard.

In addition to regularly removing mistletoe from established trees, reinfection can be minimized by adjusting canopy management. Current orchard operations conducted to minimize pest and disease pressure and increase seed set and yield may inadvertently increase susceptibility of trees to mistletoe infection. Thus, removing interior branches and trimming tree crowns to increase light penetration and fruit set likely increases germination success of mistletoe seeds (see Scharpf 1970), exacerbating mistletoe infection in orchards with established mistletoe plants. While some differences in canopy closure relate to variety selection, comparisons of mistletoe infection in trees of the same variety receiving different canopy management will reveal the magnitude of any association. This will also be critical to develop best practice guidelines for orchard management that incorporate the effects of different management regimes on mistletoe infection rates, enabling grower-specific cost-benefit calculations to boost long-term profitability.

Further research

This synthesis has highlighted how little we know about mistletoe in horticulture, with no published information available on the quantitative effects of mistletoe on tree health or yield. As monocultures where interactions with other plants are minimized and access to water, nutrients, light, and various natural enemies are carefully managed, orchards are ideal systems to use for addressing a range of pure and applied questions. Thus, in addition to developing more effective means to control the impacts of mistletoe on orchard operations, yield and tree health, addressing these strategic knowledge gaps will also enable a suite of questions to be rigorously answered, many of which would be prohibitively difficult in unmanaged and host-diverse systems.

Mistletoe detection

Knowing where mistletoes occur within an orchard is critical to managing their effects. Previous work in other systems has demonstrated that mistletoes are highly detectable overhead (Barbosa et al. 2016), with initial trials using drone-borne infrared cameras successfully detecting mistletoes in macadamia orchards (Johansen et al. 2018; see also Maes et al. 2018). Given the high water content of mistletoe tissues, they are measurably cooler than host crowns so will likely have a contrasting thermal signature. Further testing is needed, comparing ground-based surveys and aerial imagery, both from satellite photography and drone-borne near-infrared imaging systems. Once developed these tools will be a valuable complement to ground-based surveys for estimating mistletoe occurrence in wide range of other systems, in terms of detecting both established mistletoe plants but also dispersed seeds (see Fadini and Cintra 2015).

Chemical management and delivery options

It is important to evaluate the efficacy of different herbicide and growth regulator treatments, both with and without mechanical pruning, to determine the concentration, application technique, and timing that is most effective in controlling mistletoe. In addition to evaluating effectiveness in initial control and the likelihood of re-sprouting, estimating the cost, safety, off-target effects, residues, and any trade implications of different control options will provide the information needed to determine whether these chemicals will be appropriate for use in managing mistletoe in horticulture.

Determinants of susceptibility

Unlike natural systems, horticulture necessarily affords finely-resolved control of water, nutrient, and light availability, enabling rigorous testing of the “host quality hypothesis” (Watson 2009) to explain aggregated patterns of mistletoe occurrence. A series of trials would help clarify whether periodic water shortage affects already infected trees, either by reducing mistletoe growth or minimizing mistletoe flowering and subsequent fruiting. Manipulating fertigation regimes (especially reducing rates of phosphorous application) will clarify the role of host nutrition on mistletoe infection, establishment, growth, and phenology. Comparisons of rates of infection within growing areas will identify those varieties most susceptible to infection, with multi-species comparisons highlighting those generalized traits associated with increased resistance. Once general traits for mistletoe resistance are identified, selective experimental breeding may be able to produce new breeds that are both mistletoe resistant and highly productive.

Seed dispersal

Mistletoes are primarily dispersed by birds, with mistletoe fruit representing an important dietary component for many species (Watson 2001). Establishing which bird species are the principal seed dispersers in different growing areas will inform a better understanding of how new infections arise and how existing infections intensify. This work should be conducted in both orchards and adjacent shelterbelts and native vegetation, evaluating whether birds dispersing mistletoe seed into orchards are coming from other infected orchards, and have learned to associate orchards with ripe mistletoe fruit. In addition to informing improved orchard management, these comparisons would constitute a rigorous test of the “search image hypothesis” invoked to explain host–mistletoe resemblance (Cook 2017; Cook et al. 2020). The efficacy of bird deterrents should also be trialled during the peak fruiting season of mistletoes, especially in those orchards where they are already in use to reduce crop losses.

Potential for biological control

Surveys of orchards and adjacent areas with differing levels of mistletoe infection in different growing areas will establish which insects, fungi, and other natural enemies are likely candidates for biological control of mistletoes. While mistletoe populations in shelterbelts and native vegetation may act as seed sources, mistletoe populations in areas adjacent to orchards may boost populations of beneficial insects, especially specialist moths and butterflies that rely on mistletoes as larval food plants. Trials should be conducted in consultation with growers to evaluate the effects of existing orchard management (including the use of beneficial insects and spraying regimes of fungicide and pesticides) on insects and fungi associated with mistletoes. The role of mistletoes in supporting pollinators, parasitoids, and other beneficial insects should also be investigated, including evaluation of whether retaining mistletoe in vegetation adjacent to orchards may affect pollinator communities or boost populations of beneficial insects.

Awareness and knowledge sharing

A critical component of managing mistletoe in horticulture is raising awareness of the issue at all levels of the industry, from seasonal workers and managers all the way to investors. Developing dynamic posters summarizing key elements of mistletoe management and associated information sheets and online resources is a priority to increase awareness among orchard staff. Individual growers have tried a wide range of solutions, and there will be many innovative management techniques and novel approaches to treating infected orchards that will be relevant to some growers. Grower workshops are an effective tool to facilitate knowledge sharing (Watson 2019*a*), but targeted programmes to solicit input from growers and compile that information into a coherent and accessible summary relevant to specific growing systems/crop species would be particularly beneficial. For owners and investors, property-scale comparisons of different approaches to managing mistletoe and effects on yield and overall profitability over multiple years will be critical to demonstrating the need to incorporate mistletoe management into routine orchard operations.

Prospects

Just as forestry science has clarified our understanding of many aspects of plant ecology, we see collaborations between plant ecologists and the horticultural industry as mutually beneficial. By applying our expertise to these managed systems, not only can we help improve sustainable practice and enhance profitability, in so doing we can also enhance our understanding of the biology, ecology and physiology of mistletoes and parasitic plants more generally. Moreover, by collaborating with horticultural industries, we can explore ways to combine commercial production with biodiversity conservation in agricultural landscapes.

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