Tree Infection Process In American Mistletoe

(Phoradendron serotinum)

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The life cycle of the American mistletoe (***Phoradendron serotinum***) occurs in the plain sight of everyone in the Southeastern United States. This mistletoe is a common parasite found in trees growing in open areas, around buildings, along forest edges, and in disturbed areas. This publication was prepared to help people understand how mistletoe infects trees. Only by understanding the infection process can we understand tree symptoms and potential treatment regimes. As in many plant lives, mistletoe begins life as a seed. The seed is delivered / deposited on a tree twig.

Seed Germination

A mature mistletoe seed lives for only a short time, being prone to drying out and to fungal attack. In addition, mice and ants remove seeds from tree surfaces. A germinating mistletoe seed is extremely vulnerable on the open surface of the twig. Most seeds die within the first day outside their fruit covering. Light is needed to stimulate seed germination. The top portion of the embryo (the cotyledons) begin to develop chlorophyll but stay stuck down to the twig attached with dried viscin. As the top is held firm, the radicle (embryonic root) expands and curves away from light (negative phototropism) which pushes it into the twig. The radicle is well developed except it has no root cap. Gravity or gravitropism does not appear to have any impact on growth of the radicle.

Mistletoe seeds do not have strong dormancy. Germination is constrained by the surrounding fruit material slowing oxygen movement inward. As long as the fruit coat is intact, the oxygen content at the seed surface is relatively low. Once the fruit coat is pierced, broken, or removed, oxygen content at the seed surface nears atmospheric levels and can initiate the germination process. Passage through the digestive tract of an animal is not required. The species of tree and surface upon which a seed is deposited matters little for germination. As mistletoe begins to grow, it must successfully establish growth regulator communication with the tree or the seedling mistletoe will quickly succumb to the harsh environment of the bark surface. Rapid tree xylem and bark growth rates can prevent successful infection.

Twig Size & Vigor

Mistletoe establishment on a tree twig is dependent upon many climatic and biological circumstances. One critical feature is the size of the resources base from which it must draw essential elements. Once estab-

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lished, mistletoe uses growth regulatory signals to mimic tree twigs in order to draw resources. Until firmly established, mistletoe is involved in a careful growth regulation give-and-take with the infected twig and the branch to which the twig is attached. A twig needs to be of a certain size (diameter) to sustain an infection. The mistletoe must gain access to the twig, not disrupt resource flow out of the twig to the branch, and not enlist a strong defensive reaction. Small twigs may be quickly compartmentalized if infections are not effective and accepted.

Twigs must be large enough to support the development of the parasite and not reduce its regulatory contribution to the branch tissues below. Twigs smaller than 1/4 of an inch in diameter are usually sealed-off and die before mistletoe can dominate resource delivery pathways. Twigs in the 1/2 to 3/4 inch diameter range are large enough to be generating significant resources for both establishing mistletoe and for maintaining effective connections with the branch. Larger twigs must have thin bark and accessible lenticels available for infection. Twigs larger than one inch in diameter begin to develop more corky and thicker bark, which demands more energy from the germinating mistletoe seed to affect entrance into the tree. Mistletoe must become established on a vigorous and growing twig. Marginal twigs being prepared for cladoptosis by the tree, mistletoe infection will push the branch to seal-off these twigs.

Penetration & Establishment

As the radicle pushes into the twig, the tip spreads out and forms a small disk called a holdfast or an infection disk. This fattened and flattened end of the radicle produces secretions which dry and harden, tightly attaching the holdfast to the twig. On the underside of the holdfast, small strings of cells (papillae) push into lenticels and bark fissures reaching the living cortical and phloem cells of the twig. These papillae use mechanical force pushing against the holdfast and enzymes which break-down and separate the materials which hold living twig cells together. The thinness of the bark is critical to infection success.

There remains a minimal defensive response to penetration and infection by the tree. Tree defensive reactions are slowed and moderated by mistletoe producing tree-active growth regulators and by minimizing cellular oxidation. Mistletoe, during establishment, is completely dependent upon the tree for water and nutrition. The cotyledons (embryonic leaves) expand and leaves develop quickly once the vascular connections are functional. The vascular connection phase of mistletoe establishment may take one month up to a year. Rapid tree growth rates, or any kind of strong tree defensive reaction, will prevent further contact and the infection will fail.

Strands & Sinkers

Two types of mistletoe cell orientations now develop beneath the infection disk: A) longitudinal strings or strands of tissue running along the twig just under the bark in the cortex and phloem, and, B) a set of cells called sinkers which push just through the cambium to where new xylem cells are forming.

Sinkers develop vascular tissue immediately next to twig vascular tissue. The mistletoe xylem is positioned opposite pits and openings in the twig xylem cell walls. Once the vascular twig xylem cells die and become active in transporting water, nitrogen compounds, and other essential elements from the roots, the mistletoe vascular xylem dies, leaving open connections to the twig vascular xylem. The bulk flow of materials from the vascular xylem connections amount to approximately 10% of the resources entering the mistletoe. Resources entering across the apoplast from living twig cells to living mistletoe cells account for about 90% of all resources used by mistletoe.

The remainder of living sinker cells, not associated directly with twig vascular xylem, pair-up with the living cells which encase and surround the active vascular xylem cells of the twig. The sinker cells are not forced deep into the xylem, but push past the cambium and into the Springwood as it is forming for the season. Sinkers are positioned to mimic ray cells and depend on the cambium of an active twig to grow around mistletoe tissue. Once many of these cell contacts are developed, the cortical strands and sinkers as a unit are called a haustorium.

Tapping Into The Tree

The cells of the haustorium (resource exchange interface) that are adjacent to living twig cells, develop special cells walls and membrane structures. These specialized cells are called transfer cells, flange cells, or labyrinth cells. These cells have large surface areas abutting the living twig cells and the apoplast. They absorb water, organic nitrogen compounds, growth regulators, and carbohydrates. These unique cells transport back to the tree growth regulators which keep open and magnify resource transport pathways, and prevent defensive compartmentalization.

Haustoria are involved in active, energy dependent uptake of resources from living xylem and phloem twig cells. Haustoria must continue to expand over time to gather more resources in support of an expanding mistletoe crown of foliage. Old portions of the haustorium are shed and die as they are grown over by more annual increments of twig growth. As the twig cambium radially expands, growing around and interfacing with the mistletoe tissue, mistletoe develops its own radially expanding meristem to maintain its relative position around the twig cambium. If the mistletoe cannot maintain its haustorium growth rate to match the twig, it will be covered and the infection fail. Fast growing trees and twigs may be attacked as much as slow growing trees in a similar seed dispersal environment, but the mistletoe infection success rate will be much less trying to maintain fast growth rates..

Shoot Expansion

Once haustoria are established, mistletoe shoots begin to expand and develop leaves. The new shoot tips will grow, and after a short period, the tip will be aborted, leading to opposite shoots continuing to grow. This branching pattern and brittleness of the stems keep mistletoe in a small diameter, spherical shape. Wind and ice storms will break off mistletoe before the branch fails, providing tree owners with a rare up-close view of the plant.

Mistletoe stems and leaves have an abundance of chlorophyll which allows for strong photosynthesis. Mistletoe generates more than 75% of its own food, jumping to 95% at some parts of the season. Mistletoe photosynthesizes anytime the air temperature is above 55^{o}F and the tree roots are active, which means mistletoe is photosynthesizing most of the year. It does not have an effective dormancy process. In order to effectively photosynthesize, mistletoe needs a constant supply of water and organic nitrogen compounds (amino acids). These resources are exclusively supplied by the tree.

Running Wide Open

To assure adequate water resources, and collection of organic nitrogen compounds carried in the water stream, mistletoe keeps its stomates open. The high transpiration flow rate out of mistletoe leaves is orchestrated by large potassium concentrations and large cytokinin concentrations, both of which act to lock the stomates open in light. The high transpiration rates deliver organic nitrogen compounds processed by the tree roots and carbon fixed by tree leaves to the mistletoe tissues. The cytokinins leaking into surrounding tree tissue can also initiate multiple tree bud formation and release, causing a growth reaction called ìbrooming.î

Because mistletoe does generate most of its own food through photosynthesis, the amount of light available in a tree crown and at the infection site is important. Successful mistletoe infections are found high-up and around the outside edge of tree crowns. Here light can power mistletoe photosynthesis. Fast tree growth and large areas of tree foliage production can shade mistletoe, making it more parasitic and less successful.

Infection Changes Everything

Mistletoe draws water and other resources to its tissues by use of growth regulators. The tree resource delivery path which brings mistletoe more resources is consolidated and strengthened over time. Drought conditions may slow tree foliage growth and food production as tree stomates partially or fully close in the day. Mistletoe leaves under the same conditions, are transpiring a large portion of the branchesí water with stomates wide-open. When tree food production is constrained by stress, mistletoe increases its proportion of resources used and expands its foliage to the detriment of the branch.

Internal resource allocation changes in a tree brought about by mistletoe infection include much less food (sugars and associated stored starch availability) transported to tree roots and much more organic nitrogen (amino acids from tree root absorption and processing) provided to the mistletoe. Growth regulators produced by mistletoe disrupt the resource transport and allocation systems of the tree. Mistletoe acts to attract water, nitrogen, soil elements, and limited carbohydrates using growth regulators pushed across the resource exchange interface.

Water Loss

The greatest resource problem for the tree is the loss of water to mistletoe. Mistletoe develops close contacts with living tree cells immediately surrounding water conducting xylem. Mistletoe, with a rapid stomatal opening and poor closing response, has a much lower water potential (more negative) than the tree. In daylight, mistletoe stomates are usually wide open regardless of water tension in tree and soil. Mistletoe is able to preferentially pull large amounts of water from the tree amounting at times to more than two times the water volume pulled to tree foliage with the same surface area.

Under water stress conditions in a tree, mistletoe respiration and transpiration increase while tree transpiration and food production declines. Tree transpiration slows during drought and when roots are flooded for extended periods, while mistletoe transpiration increases. Over time (if the tree does not die) mistletoe continues to gain foliage area at the expense of the tree. Mistletoe continues to pull water from the tree well out of proportion to its foliage area. The functional result of large mistletoe tissue potassium, solute, and cytokinin concentrations is very poor water use efficiency. When mistletoe is flowering and fruiting -- even at night -- water pulled into the mistletoe is great relative to the tree. Liquid water droplets can also develop around the edges of mistletoe leaves over night and then evaporate with the dew (guttation).

Conclusions

Mistletoe is effective as a parasite because of its growth regulation battery of signals. It chemically ìwiresî itself into the tree resource allocation system and skirts tree defences. Trees are stressed, decline, and are pushed to structural failure and biological dysfunction by mistletoe. Elimination of mistletoe, especially in socially significant and old trees is critical.

A publication on general mistletoe features, tree hosts, tree damage and its poisonous nature is: **Mistletoe (*Phoradendron serotinum)* Infection In Trees**, (University of Georgia School of Forest Resources publication FOR03-7. 2003. Pp.4). A publication on treating mistletoe infections is: **Treating Mistletoe (*Phoradendron serotinum*) In Trees** (University of Georgia School of Forest Resources publication FOR03-9. 2003. Pp.4). A publication which provides a list of important research papers and literature on American mistletoe is: **Selected Literature on Mistletoe Infection in Trees**, (University of Georgia School of Forest Resources publication FOR03-10. 2003. Pp.2).