Oral Presentations

Phylogenetic relationships in *Phoradendron* (Viscaceae)

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Keywords: *Phoradendron*, Systematics, Phylogenetics

Phoradendron Nutt. is a genus of New World mistletoes comprising ca. 240 species distributed from the USA to Argentina and including the Antillean islands. Taxonomic treatments based on morphology have been hampered by phenotypic plasticity, size reduction of floral parts, and a shortage of taxonomically useful traits. Morphological characters used to differentiate species include the arrangement of flowers on an inflorescence segment (seriation) and the presence/absence and pattern of insertion of cataphylls on the stem. The only trait distinguishing *Phoradendron* from *Dendrophthora* Eichler, another New World mistletoe genus with a tropical distribution contained entirely within that of *Phoradendron*, is the number of anther locules. However, several lines of evidence suggest that neither *Phoradendron* nor *Dendrophthora* is monophyletic, although together they form the strongly supported monophyletic tribe Phoradendreae of nearly 360 species. To date, efforts to delineate supraspecific assemblages have been largely unsuccessful, and the only attempt to apply molecular sequence data dates back 16 years. Insights gleaned from that study, which used the ITS region and two partitions of the 26S nuclear rDNA, will be discussed, and new information pertinent to the systematics and biology of *Phoradendron* will be reviewed.

The *Viscaceae*, why so successful?

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Keywords: Endophytic system, Epicortical roots, Epiparasite

Mistletoe is the term used to describe aerial-branch parasites belonging to the order Santalales. For this study we are recognizing the monophyletic Viscaceae as one of five mistletoe families within the order as opposed to some researchers who include the family within Santalaceae. Three genera, *Ginalloa, Korthalsella,* and *Notothixos,* contain only a few species each, are relatively poorly known, and are not included in the present report. The remaining genera, *Arceuthobium*, *Dendrophthora*, *Phoradendron*, and *Viscum* are speciose, with New World *Phoradendron* considered the largest mistletoe genus in the World, and the work of Ashworth suggests that *Dendrophthora* belongs within *Phoradendron*. The Old World genus *Viscum* is also large and when all of its far-flung species are described may equal or surpass *Phoradendron* in size. *Arceuthobium* is best known as a severe forest pathogen in Western North America and Europe. Botanists and foresters have long been interested in the physiological and structural interactions between parasite and host, particularly within an ecological framework. As it turns out, mistletoe is exceptionally creative in its adaptations to changing conditions. Examples include 1) sinker dimorphism, 2) infected rays, 3) transfer cells, 4) systemic growth, 5) endophyte immortality, 6) cuticular epithelium, 7) direct vessel-to-vessel connections, 8) epicortical roots, and 9) epiparasitism. These innovations are listed in no particular order, but herein we will illustrate how they fit into the whole of viscoid structure, function, and evolution.

Mistletoe with giant woody gall: Interpretation of the anatomic-hydraulic connection between *Psittacanthus robustus* and *Vochysia thyrsoidea* and the discovery of new complex structures in the haustorium

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Keywords: Wood anatomy, Hydraulic architecture, Haustorium

The connection between mistletoes and host demands the formation of anatomically hybrid hydraulic systems. These systems must be highly functional because mistletoes have high stomatal conductance and more extreme negative water potentials than their hosts. These connections represent important morphogenetical and functional challenges for both plants. Specifically, for the hosts, these connections are a source of stress and overload because their canopies are competing with plants that have a largely different water balance. This work tested the hypothesis that these connections are functionally possible because of the presence of an assembly of morphoanatomical adaptations of the hybrid system. We performed hydraulic architecture measurements to study the connections between the large mistletoe *Psittacanthus robustus* and the short savanna tree *Vochysia thyrsoidea*. The combination innovative techniques allowed us to reinterpret the organization and differentiation of the haustorium and the formed gall. We observed several anatomical changes that appear to be functionally beneficial for the water flux through the connection between the parasite and the host. We also discovered a new structure, which we call a vascular bulb that is present at the interface on the side of the parasite. The vascular bulbs found at the connection consist of a pear-shape neoformation compounded of dozens of short and wide tracheids. Each of these structures connect to a single host vessel with a probable high vascular capacitance. Also, the parasitized branches of the host showed relatively high contact between vessels, thin vessel-vessel walls and thin pit membranes. All of the observed features in the host suggest its adaptation to a high flux water regime, which explains how small trees can host large mistletoes for several years without signs of harm. These ontogenetic observations also allow us to hypothesize about a possible role of auxins in the vascular differentiation and connection.

A single mistletoe can cause a system hydraulic effect in the host tree

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Keywords: Wood anatomy, Hydraulic, Systemic effect

In Loranthaceae and Santalaceae, the most widespread and diverse mistletoe groups, the level of infestation of hosts can vary from one single mistletoe per tree (e.g. *Psittacanthus robustus* parasitizing several possible hosts) to dozens growing on the same host tree (e.g. *Phoradendron crassifolium, Struthanthus martianus* both generalist mistletoes). Within these large mistletoes, it is clear that they have the capacity to harm, and even kill, host branches. However, it is not clear if this localized impact affects other parts of the host tree. To explore the impact of the mistletoes on the parasitized trees, we performed various anatomical and hydraulic measurements: dye (safranin 0.1%) injection into the xylem in the field in order to evaluate the frequency of embolisms; water potential measurements using a pressure chamber; and wood anatomy measurements, such as vessel frequency and diameter. We compared the impact of the presence of one single parasite in the following situations: 1) parasitized branches; 2) non-parasitized branches in a position of the canopy opposite to the parasite fixation site (is this on the same tree as a parasitized branch? maybe make that a little more clear); and 3) branches in non-parasitized trees (not sure which of these are plural or not - just make sure you check which ones should be). Generally, we found a 20-50% increase in the frequency of embolized vessels in parasitized trees when compared to non-parasitized trees. Specifically, we found that this increment was greater when strictly looking at the parasitized branches; significant increases in embolism frequency were also seen in non-parasitized branches of the parasitized trees in relation to non-parasitized trees, but on a smaller scale. Additionally, we observed consistently lower water potentials in the non-parasitized branches of parasitized trees in comparison to branches of the non-parasitized trees. These different approaches together show that the presence of a single mistletoe can impact the hydraulic architecture of the parasitized tree. In other words, systemic effects can be detected in a tree bearing a single mistletoe. Further evaluation is needed to understand the possible cumulative effects of the presence of several large mistletoes infesting a single tree.

The role of generalist avian frugivores in determining the distribution of the mistletoe *Phoradendron leucarpum*

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Keywords: Oak mistletoe (*Phoradendron leucarpum*), Seed dispersal, Avian frugivore

The oak mistletoe (*Phoradendron leucarpum*) is a stem parasite found across the southern United States (US) that is dependent on avian frugivores for seed dispersal and serves as the sole larval host plant for the great purple hairstreak (*Atlides halesus*) in the eastern US. Mechanisms driving observed oak mistletoe habitat relationships are unclear. Because most mistletoes are restricted to a narrow range of suitable recruitment sites and avian frugivores are more visible than other guilds of seed dispersers, mistletoe-frugivore systems offer good opportunities for the study of seed dispersal and the effect of frugivores on plant distributions. We collected presence-absence data on oak mistletoe shrubs and avian seed dispersers from forested habitats in eastern Virginia and North Carolina during winter (Jan-Mar) 2016. This data was analyzed using occupancy models, and the resulting detection probability estimate of 0.216 (SE = 0.177) for the cedar waxwing (*Bombycilla cedrorum*), a focal avian frugivore, emphasizes the need to account for imperfect detection when estimating distributions of avian seed dispersers. We also discuss methodology and preliminary results from oak mistletoe planting experiments in the field and greenhouse.

Phylogenetic relationships in *Phoradendron* (*Viscaceae*)

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Keywords: Mistletoe, Deciduousness

Deciduousness in mistletoes is confined to Misodendraceae and a few *Loranthus* species and *Desmaria mutabilis* in the Loranthaceae. All Viscaceae are evergreen. The range of deciduous *Loranthus* species frequently overlaps with evergreen Viscaceae. In all forest biomes evergreen and deciduous tree species coexist, albeit in different proportions. This does not apply for mistletoes as deciduous mistletoes are absent in tropical forests even on deciduous hosts. Conceptually deciduousness in mistletoes is disadvantageous because mistletoes have limited stem- and root-storage capacity for nutrients, a handicap when new foliage is flushed. The genus *Loranthus* comprises evergreen species in warmer climate, and deciduous ones in climates with winter frosts. This suggests that frost was a driving factor in the evolution of deciduousness in *Loranthus* but not in co-occurring *Viscum* species. We studied anatomical properties of the haustoria and the wood of deciduous and evergreen mistletoes and wood anatomy of their hosts in Eurasia and South America. All *Loranthus* species have a simple, cone shaped haustorium which connects large diameter vessels of their hosts to large vessels of the mistletoe. Large vessels are highly conductive but susceptible to frost embolism which interrupts water flow and thus promotes deciduousness. Co-occurring *Viscum* species have drought tolerant leaves and complex haustoria with extensive cortical stands and sinkers. In winter they are able to compensate water loss from very narrow host vessels which freeze only at low temperatures. For mistletoes of the southern hemisphere a consistent pattern linking deciduousness to vessel diameter or vessel arrangement of mistletoes and host trees was not found. Deciduousness could have evolved in the biogeographic origin of deciduous mistletoes in Deep South Antarctica, where climate was relatively mild but highly seasonal before the Drake Passage opened. Insufficient photosynthetic gain and high respiration in the long dark, but mild winters could have promoted deciduousness.

Bird abundance and diversity are associated with oak mistletoe in Willamette Valley oak woodlands

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Keywords: Wildlife, *Quercus garryana*, *Phoradendron villosum*

Restoration of oak ecosystems in the Pacific Northwest often involves selectively thinning stands of oaks in order to reduce competition for sunlight. Trees with obvious signs of disease or infection, such as the native parasitic mistletoe (*Phoradendron villosum*), are typically selected for removal. However, the potential effects of removal of mistletoe-laden trees on wildlife that may be associated with mistletoe are unknown. Mistletoes provide important habitat for wildlife in many ecosystems around the world, but the relationship between Oak Mistletoe and wildlife is almost completely undocumented. In order to investigate relationships between Oak Mistletoe and wildlife diversity, we quantified microhabitat features, such as dead wood and cavities, related to mistletoe infection in Oregon White Oaks (*Quercus garryana*) at 5 sites in the Willamette Valley, Oregon. We quantified breeding bird use of those trees during the 2014 breeding season. Our results suggest that 1) structural heterogeneity within the crown of the tree and 2) avian species richness and abundance are positively associated with mistletoe load. We conclude that trees with mistletoe in the crown provide valuable habitat for some oak associated wildlife species.

Dwarf Mistletoe-induced defense chemical accumulation in jack pine alters tree resistance to a non-native bark beetle-associated fungi

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Keywords: Tree-mediated interactions, Chemical defenses, Systemic induced resistance

The distribution of dwarf mistletoe (*Arceuthobium americanum*) in jack pine (*Pinus banksiana*) and the current range expansion of mountain pine beetle (MPB, *Dendroctonus ponderosae*) overlap in Alberta, Canada. However, it is not known whether dwarf mistletoe-induced changes in physical and chemical characteristics of jack pine may impact MPB, therefore affecting establishment of a non-native insect in the boreal forest. We identified the systemic induction of defense chemicals and changes in physical characteristics of phloem in the main stem of jack pine from dwarf mistletoe infection. Further, we examined whether these changes could induce pine resistance to a fungal symbiont of MPB, *Grosmannia clavigera*, and alter interactions between MPB and competitor beetles. While the accumulation of phenolics was positively associated with dwarf mistletoe infection severity, phenolic accumulation was not related to resistance to *G. clavigera*. In contrast, dwarf mistletoe infection had a non-linear effect on the induction of monoterpene concentration, with the highest induction in trees with moderate dwarf mistletoe severity compared to trees without infection or with high severity infections. This change in monoterpene concentration was associated with induced resistance to *G. clavigera* in trees with moderate dwarf mistletoe severity and induced susceptibility in trees with severe dwarf mistletoe infection. We also found that while dwarf mistletoe-induced changes to pine physical characteristics (i.e. phloem thickness) negatively impacted MPB success, the induced chemical changes decreased the adverse effects of competing subcortical insects on MPB performance. Tree-mediated interactions among multiple, often simultaneous, biotic disturbances may impact MPB establishment through systemic induced resistance mediated by the coordination of different defense chemical pathways.

A Dispatch from the East: Divergent responses of White Spruce and Red Spruce to Eastern Dwarf Mistletoe infection along the coast of Maine

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Keywords: Ecophysiology, Hormones, Gas exchange

Nineteenth century deforestation followed by pastureland abandonment and subsequent recolonization has resulted in the replacement of red spruce/balsam fir-dominated forest stands with white spruce-dominated stands over large areas of the Maine coast. White spruce commonly die as a consequence of eastern dwarf mistletoe (EDM) infection, after displaying profound alterations in development, physiology, and growth. In curious contrast, red spruce, which is also classified as a primary host of EDM, do not generally suffer whole-tree mortality in response to infection. Instead, we observe senesced red spruce branches bearing the signatures of EDM infection on healthy trees. These congeneric host species growing in close proximity provide us with a compelling natural system in which to examine parasite-host interactions and the mechanisms of host decline versus those of host tolerance of infection. In this presentation, I will describe our observations of infected white spruce and red spruce, hypothesized mechanisms of white spruce decline/mortality and red spruce tolerance, and our plans for future study. Our findings suggest that, in white spruce, infection results in perturbations to hormone metabolism (cytokinins and abscisic acid) and reductions in host needle size, which, combined, result in densely self-shaded, long-lived infected branches with lower ratios of photosynthetic to non-photosynthetic tissue. These infected branches receive a disproportionate share of whole-tree resources, but may be less able to contribute to the whole-tree carbon balance. With time and the accumulation or more and larger infections, whole-tree carbon balance in white spruce is compromised to the point of mortality. In contrast, we hypothesize that the greater intrinsic drought sensitivity of red spruce may predispose this species to stomatal closure induced by EDM infection, upsetting the carbon balance of infected branches in a manner that induces their shedding. Branch shedding, in turn, may protect red spruce from infection-induced whole-tree mortality.

Morphologic analyses of dwarf mistletoes (*Arceuthobium*, Viscaceae) in series Campylopoda using multivariate statistical and phylogenetic approaches: interspecific comparisons and contrasts with western dwarf mistletoe (*Arceuthobium campylopodum*)

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Keywords: Classification, Western North America, Multi-variate analysis

The classification of dwarf mistletoes (*Arceuthobium*, Viscaceae) in the Section Campylopoda, Series Campylopoda continues to be one of the most contested and controversial taxonomic questions in *Arceuthobium*. Recent treatments have either reduced or recombined ser. Campylopoda taxa to synonymy with or as subspecies of western dwarf mistletoe (*A. campylopodum*). Morphological and molecular evidence supporting the reclassification of dwarf mistletoes under western dwarf mistletoe, however, remains scant and disregards nearly one century of taxonomic studies. The work presented herein, therefore, assessed the morphological discontinuities among several dwarf mistletoes in ser. Campylopoda endemic to western North America to that of western dwarf mistletoe using univariate statistical procedures, multivariate analysis of variance, and discriminant function analyses. Phylogenetic relationships among the ser. Campylopoda taxa parasitizing white pines (Pinus, subgenus Strobus) were also explored using parsimony tree estimation and a mixed dataset consisting of continuous morphologic and host specificity data. Statistical analyses clearly demonstrated that all of the dwarf mistletoes we compared to *A. campylopodum* can be readily delimited to species according to interspecific differences in male and female plant morphology. Multivariate means for male and female plants did not intersect in multivariate space among taxa and, collectively, the predicted species membership for each of the dwarf mistletoes was rarely incorrect when assessing only male or female plant parts via discriminant function analysis. Phylogenetic reconstruction utilizing morphologic and host affinity data supported statistical inferences. Results of the latter analysis were compared to the most recent molecular phylogenetic study of *Arceuthobium* and comparative differences are discussed. The analysis of morphological characters and host affinities supports the taxonomic classification of the dwarf mistletoes studied as separate species from *A. campylopodum*.

The Relationship Between Dwarf Mistletoe Infestation Intensity and Stand Structure, Canopy Fuels, and Surface Woody Debris in Lodgepole Pine Forests

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Keywords: Lodgepole pine, Dwarf mistletoe, Fuel loads

Lodgepole pine dwarf mistletoe (DM; *Arceuthobium* americanum Nutt. ex Engelm.) and wildfire are fundamental disturbance agents driving ecosystem structure and function throughout the lodgepole pine (*Pinus contorta* Dougl. ex Loud.) dominated forests of the Rocky Mountains. Previous studies have suggested that DM influences ecosystem processes and stand dynamics by altering mortality patterns, stand demographics, and individual tree biomass distributions, and that these changes may interact with future disturbances such as wildland fire. Despite considerable work on the effects of DM on tree growth and mortality there remains limited quantitative data on the effect of DM on stand structure and surface and canopy fuel loads in lodgepole pine systems. The overall objective of this study was to characterize the relationship between DM infestation level and stand structure, canopy fuel loading, and surface fuel loading in high elevation lodgepole pine dominated forests. Overall, our findings suggest that DM infested stands 1) exhibit unique stand structure and dynamics from unaffected stands and 2) have increasing surface fuel loads and decreasing canopy fuel loads as DM infestation becomes more severe. Alterations to forest structure in infested stands may positively affect wildlife habitat quality, and may result in stands that are more resilient to a variety of disturbances due increased spatial heterogeneity and diversity of tree ages. Alterations to the fuels complex suggest conflicting impacts of DM on potential fire behavior as increased surface fuel enhances potential surface fire intensity, while decreased canopy fuel reduces the potential for active crown fire. In addition to influencing potential fire behavior, surface fuel (woody debris) provides wildlife habitat, creates microsites that enhance germling success, and serves as an important global carbon pool. Our findings reflect the significant impacts of DM on forest communities and provide some insight into the mechanisms driving complex disturbance interactions in this system.

The Little Bang Theory: Explosive seed discharge in Dwarf Mistletoe

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Keywords: Reproduction, Development, Dispersal

Dwarf mistletoes, genus *Arceuthobium*, are parasitic flowering plants, forest denizens, and noteworthy pathogens of coniferous species. In western North America, *A. americanum* (lodgepole pine dwarf mistletoe) primarily infects *Pinus contorta* var. *latifolia* (lodgepole pine): severe infestations lead to reduced tree growth, premature tree mortality, and compromised timber quality. A detailed understanding of dwarf mistletoe reproduction – including seed dispersal – is required to better appreciate how these organisms behave as parasites. Dwarf mistletoes spread their seeds by a remarkable explosive process that involves the buildup of hydrostatic pressure within a gelatinous fruit tissue called 'viscin'. This presentation will describe work my group has done to determine: (1) the anatomy and biochemistry of the dwarf mistletoe fruit, showing how structure drives function; (2) the physical parameters of discharge measured with a high-speed camera; and (3)

how thermogenesis (endogenous heat production) via alternative oxidase activity might trigger the final discharge event. The results to be presented range from our published data to correlative speculation, and have engaged techniques borrowed from the disciplines of plant anatomy, plant physiology, chemistry, molecular biology, and physics. We are beginning to form a cohesive narrative of dwarf mistletoe seed dispersal and reproductive development.

Macrofossil evidence of Eocene dwarf mistletoes (*Arceuthobium*) and their implications for the Baltic amber forest

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Keywords: Paleobotany, Baltic amber, Paleoecology

Eocene Baltic amber forms the largest deposit of any fossil resin worldwide. The vast majority of the material derives from the Samland Peninsula of the Kaliningrad area and is well-known for its plenitude of well-preserved inclusions of organisms from many taxa, comprising cryptogams, vascular plants, fungi and particularly many arthropods. However, plant inclusions only represent a small proportion of Baltic amber inclusions and they have been rarely investigated since the most comprehensive works dating back to the 19th and early 20th century. Up to now, the botanical origin of Baltic amber remains controversial, as does the floral composition of its source forest. However, reliable knowledge about the â€˜Baltic amber forestâ€™ is needed to identify possible amber source plants, to understand evolutionary histories of certain plant taxa, but also to facilitate the interpretation of the Eocene habitats of the entrapped animals. In our recent study of the Baltic amber flora, we discovered six new mistletoe species of the *Arceuthobium* lineage, representing the oldest macrofossil evidence of dwarf mistletoes. The fossils share morphological features with extant *Arceuthobium*, comprising the presence of decussate squamate leaves, the shoot structure, the shape of the internode cross section, petiolate divided fruits and their arrangement and the stomata morphology. Differences to extant dwarf mistletoes, such as the number of perianth segments, the non-fusion of the squamate leaves and the presence of oblanceolate leaves suggest an affiliation to the stem lineage of the genus. The occurrence of six species of dwarf mistletoes in a single amber deposit suggests *Arceuthobium* being keystone species of the Baltic amber source area. As in extant conifer forests, Eocene *Arceuthobium* species probably influenced the structural complexity of the forests, leading to more open woodlands but also affecting the local species diversity.

The role of host specificity in speciation: Insights from American *Orobanche* (Orobanchaceae)

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Keywords: Orobanchaceae, Phylogenetics, Cryptic speciation

Parasitism has evolved at least 12 times among angiosperms. Each of these lineages provides an independent opportunity to understand evolutionary causes and consequences of plant-plant parasitism. A recent fine-scale molecular phylogenetic study of holoparasites in the western-hemisphere clade of *Orobanche* (Orobanchaceae) not only supports the uniqueness of seeral recently described species, but it has revealed abundant undescribed diversity. Although these cryptic species have overlapping ranges and are nearly indistinguishable morphologically, they are easily recognized by their distinct, distantly-related hosts. In other words, previous studies of *Orobanche* have underestimated diversity and overestimated host range. Given the taxonomic richness of mistletoes and the abundance of many host-specific taxa, similar evolutionary processes may be shaping mistletoe diversity.

Fire and Dwarf Mistletoe in Western North America

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Keywords: Fire, Dwarf mistletoe, Ecology

Dwarf mistletoes (*Arceuthobium* species) and fire interact in many important ways in the fire-prone coniferous forests of Western North American. Fire directly effects (kills) dwarf mistletoe by killing the host, host branch, or heating the aerial shoots. Fire is a primary determinant of natural dwarf mistletoe distribution on the landscape, and time-since-fire controls many aspects of dwarf mistletoe epidemiology. Prescribed fire is important for management of dwarf mistletoes, while fire suppression and selective logging are thought to have increased the abundance of dwarf mistletoe in western forests. Conversely, dwarf mistletoes can influence fire by causing changes in forest composition, structure, and fuels. This can influence fire in two ways. 1. Increased potential for torching and crown fires by providing vertical fuels continuity, especially fuels ladders in the form of witches brooms and litter that accumulates in the brooms. Canopy base height is likely reduced in most infection centers. 2. The mortality center that can develop in very old and persistent infection centers, that have escaped fire, can significantly reduce tree density, canopy connectivity, and canopy bulk density. Dead tops and dead branches reduce canopy bulk density, and young trees can be quickly infected and some may remain dwarfed by infections of the tree leader. It is possible that a fire might not burn as severely in such a center, as fuels connectivity and canopy bulk density is reduced. This may be one contributor to fire complexity in the west. Two dwarf mistletoes can be compared to illustrate fire interactions in Oregon and Washington State USA. *Arceuthobium americanum* (lodgepole pine dwarf mistletoe) and *A. tsugense* (western hemlock dwarf mistletoe) occur in two very distinct fire regimes characteristic of their hosts. Lodgepole pine (*Pinus contorta*) is typically an early seral species, sometimes both early and late seral, of mixed or high severity fire regimes with fire return intervals of 20 to 80+ years, while western hemlock (*Tsuga heterophylla*) is a late seral species co-occurring with early seral, and long-lived, Douglas-fir (*Pseudotsuga menziesii*) in regions with a high severity fire regime, although not always, and a fire return interval of 150 to 400+ years. *Arceuthobium americanum* persists on the landscape in unburned patches and spreads from these refugia directly into the regenerating lodgepole pine. *Arceuthobium tsugense* persists in refugia associated with riparian areas, wetlands, and patches of low severity fire. However, because Douglas-fir dominates the landscape for 200 years or more, *A. tsugense* must persist for several hundred years in refugia before moving into the surrounding forests. Western hemlock begins to co-dominate with Douglas-fir after 200 years or so, and becomes

especially abundant in canopy openings, which forms the basis for spread of *A. tsugense* given a seed source. Fire and dwarf mistletoe interactions are an important key to understanding the epidemiology of dwarf mistletoes in the western USA, yet dwarf mistletoes interactions with fire should also form a foundation for understanding fire ecology in fire prone western coniferous forests.

Multiple vs. Single Connections: what does it mean for the parasite?

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Keywords: Haustorium, Multiple unions, Single unions

Hemiparasitic mistletoes that infest the stem of hosts form two main types of connections: multiple unions and solitary unions. We carried out an extensive literature review considering a wide variety of mistletoe species in order to review the different connection types. Additionally, for few of each of the two types, we took measurements of water potential from the parasitic plants and hosts to understand the ability of the various species to divert resources from their respective host. The results show that epicortical roots were the only type of multiple union observed in the various mistletoe species. Species that form epicortical roots can attach to the stem of the same host multiple times and can extend meters from the initial connection site. The haustorial morphology and anatomy observed for the species with multiple unions are very similar among the different species. On the other hand, the haustoria of parasites forming solitary unions present a wider diversity of morphologies, including woody galls, wood roses, and clasping unions. This morphological variety is accompanied by several anatomical variations observed at the host-parasite interface. In the case of parasites forming solitary unions, few species are reported to survive the loss and/or rupture of their haustorial system. Regarding water potential, the values obtained for parasitic species were lower than those obtained for the host species during the period of analysis as expected. However, within the parasitic group, parasites forming multiple unions had lower water potentials than the ones with solitary unions. Considering these results, we propose that during the evolution of the parasitic life form, selective pressure may have been stronger on parasitic species forming solitary unions. Specifically, we suggest that this stronger selective pressure on parasitic species forming solitary unions may have resulted in a wider variety of morphological and anatomical structures.

Of mistletoes and mechanisms: advances in understanding their ecological role and ecosystem function

Dave Watson, Charles Sturt University

Keywords: Ecology, Facilitation, Productivity

I review recent advances in understanding the role mistletoes (Loranthaceae) play in woodlands and forests, as well as the factors underlying their inherently patchy distribution. I draw together findings from several studies into mistletoe seed dispersal, dispelling the "just so" story that mistletoe specialist frugivores are coevolved dispersers and suggesting they are better considered exploitative opportunists. Building on results of the large-scale removal experiment, I delve deeper into the community-level findings to uncover the underlying mechanisms. Rather than those groups depending on mistletoe nectar or fruit, insectivores were found to exhibit the greatest declines following mistletoe removal. Indeed, once the response of ground-feeding insectivores is removed, no significant treatment effects persist. This counter-intuitive finding is consistent with the emerging view of mistletoes and other parasitic plants as facilitators, boosting diversity from the bottom-up via highly enriched litter-fall.

On tropical mistletoes: Noteworthy advances, recent insights, emerging opportunities

Dave Watson, Charles Sturt University

Keywords: Tropical, Review, Synthesis

Mistletoes are an enigmatic group of plants, their parasitic habit, co-evolved partnerships and cultural prominence inspiring researchers for centuries. Pliny the Elder, Linnaeus and Darwin were fascinated by European mistletoe *Viscum* album, noting its dependence on trees for nutrition and birds for seed dispersal. As explorers and naturalists returned from far-flung lands with specimens and observations, it became clear that mistletoe was not an aberrant European plant but a diverse group of hemiparasites with a global distribution. For tropical biologists, mistletoes have emerged from obscurity, with recent evolutionary and ecological research shining a light on their diversification and ecological partnerships. Here, I highlight some recent findings and suggest that mistletoes offer valuable opportunities for further tropical research, representing tractable models to address many meaningful questions. In 2001, I noted "Tropical regions, in particular, are underrepresented in the mistletoe literature" but, between now and then, research involving tropical mistletoes has flourished. By continuing to build on this foundation and occasionally pausing to check whether conceptual frameworks need adjusting or overhauling, tropical mistletoes will continue to inform many aspects of ecological thought and evolutionary theory.

Epiparasitiam in mistletoe (Santalales): An overlooked topic in forest biology

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Keywords: Epiparasite, Misteltoes, Biogeography

The term mistletoe refers to aerial-branch parasites belonging to one of five families in Order Santalales. Epiparasites, also termed hyperparasites, are mistletoe found on other mistletoe. The host to an epiparasite is termed the "parasitic host" or simply "host", and its host the "terrestrial host". Three broad categories of epiparasites are recognized, chance, obligate, and autoparasites. Two families, Loranthaceae (L) and Viscaceae (V), contain the vast majority of mistletoe

species (approx. 97 %) and also the largest number of epiparasites. We surveyed the literature for all possible combinations of epiparasite/parasitic host (V/V, L/V, L/L, V/L) and determined frequencies of all combinations and distributions of occurrence. Most epiparasites occur on Loranthaceae parasitic hosts, whereas Viscaceae provide the larger number of epiparasites. About 30 species, mostly Viscaceae, are considered likely obligate epiparasites, with New World *Phoradendron* and Old World *Viscum* having 9 species each. Nearly all *Phoradendron* obligate epiparasites grow on *Phoradendron* parasitic hosts, whereas those of *Viscum* grow mainly on Loranthaceae hosts. Data suggests that species abundance is a major factor influencing whether mistletoe serve as host to other mistletoe. We found no reports of epiparasitism in Misodendraceae and only scattered reports for Santalaceae. In *Phacellaria* (Amphorogynaceae) all species are obligate epiparasites, mainly on Loranthaceae. Epiparasitism is worldwide in occurrence but is most common in tropics and subtropics. The largest number of reports came from Oceania, the smallest from Africa.

Poster Presentations

Interactions of Dwarf Mistletoe, Mountain Pine Beetle, and Fire in the Lodgepole Pine Forests of Central Oregon

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Keywords: Disturbance interactions, Lodgepole pine, Forest structure

Lodgepole pine (*Pinus contorta*) forests are widely distributed throughout western North America and are subject to two disturbance agents that cause mortality on a large scale, mountain pine beetle (*Dendroctonus ponderosae*) epidemics and fire. The relationship between mountain pine beetle and subsequent stand development, fuels succession, and potential fire behavior has been extensively investigated in recent years. However, lodgepole pine dwarf mistletoe (*Arceuthobium americanum*), a third disturbance agent extremely common in these forests, has been largely left out of conceptual models of interactions between forest structure, mountain pine beetle, and fire. Dwarf mistletoe occurs in over 70% of post-mountain pine beetle lodgepole pine stands in central Oregon. It is well-known that dwarf mistletoe influences individual tree structure, but we found that stand-level dwarf mistletoe infection severity also has a significant influence on stand structure. There is evidence of decreased representation and diameter of the dominant and codominant crown classes with increased stand-level dwarf mistletoe severity, while representation of suppressed trees increases. Surface fuel loadings are generally unaffected by dwarf mistletoe, while canopy base height and canopy bulk density decrease as stand-level dwarf mistletoe severity increases. Following a fire, the proportion of post-mountain pine beetle lodgepole pine stands with dwarf mistletoe dropped substantially. However, when restricted to stands with live trees remaining, dwarf mistletoe remained in over 70% of stands. We hypothesize that the influence of dwarf mistletoe on stand structure and fuels loadings has implications for future fires and mountain pine beetle epidemics which must be incorporated into conceptual models to understand the disturbance dynamics of lodgepole pine forests.

Spread and Impact of Douglas-fir Dwarf Mistletoe in Southwest Oregon, 1992-2013

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Keywords: Douglas-fir, Dwarf mistletoe, Oregon

Douglas-fir dwarf mistletoe (*Arceuthobium douglasii*) Engelm, is a parasitic, flowering plant found almost exclusively on Douglas-fir (*Pseudotsuga menziesii*). It is widespread on Douglas-firs in the Cascade and Siskiyou Mountain ranges of southwest Oregon. Studies have shown that heavy infection of Douglas-fir dwarf mistletoe reduces growth of host trees and contributes to an increase in mortality. Ten permanent plots to measure the spread and impact of Douglas-fir dwarf mistletoe were installed in the southern Oregon Cascade Mountains on the Rogue River-Siskiyou and Umpqua National Forests in 1992. The level of dwarf mistletoe was measured using the Broom Volume Rating system (a modification of the Hawksworth six-class dwarf mistletoe rating system rating) every five years and most recently in 2013. After 21 years, Douglas-firs that were heavily infected (greater than half of the live crown was affected) had significantly less growth and higher mortality than uninfected or lightly infected Douglas-firs. The percentage of infected Douglas-firs increased from 47 to 60 percent in the 21-year period. The effects of Douglas-fir dwarf mistletoe infection were particularly great in small Douglas-firs (less than 29 cm diameter at breast height (dbh)). Over 30 percent of uninfected small trees became infected in the 21-year period, whereas only 10 percent of large (greater than 53 cm dbh) Douglas-firs became infected. The level of mortality of infected small Douglas-firs was over seven times the level experienced by infected large trees. The results suggest that large Douglas-firs that are currently heavily infected most likely became large before becoming heavily infected. Severe dwarf mistletoe infection of young Douglas-firs in southwest Oregon will almost certainly adversely affect their potential survival and growth. Land managers hoping to maintain and recruit large Douglas-fir on these sites should consider management objectives that minimize the risk of dwarf-mistletoe infection to regeneration and small trees.

Is western hemlock dwarf mistletoe a keystone resource for insects in Pacific Northwest old-growth forests?

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Dwarf mistletoes, parasitic angiosperms that infect coniferous trees throughout the Western United States, may have keystone functions because they facilitate old-growth forest structural diversity and provide essential wildlife habitat. At the Wind River Canopy Crane Research Facility, we investigated whether western hemlock dwarf mistletoe (*Arceuthobium tsugense*) has keystone functions for insects within old-growth forests by providing essential pollen and nectar resources. Over the course of the dwarf mistletoe flowering season, we observed visitors to dwarf mistletoe flowers and sampled the insect community within the upper canopy where aerial dwarf mistletoe shoots and flowers occur. The number of floral visitors peaked at prime dwarf mistletoe flowering, suggesting that the insects are tracking the floral resource availability. Based upon the observed patterns and frequency of floral visitations, as well as life history traits, we suggest that *Apis mellifera*, syrphid flies, tachinid flies, and *Vespa pensylvanica* likely provide pollination services. These data, along with phenology data of other flowering species, indicates that western hemlock dwarf mistletoe is the sole source of nectar and pollen within old-growth forests during the late summer. We argue for treating dwarf mistletoe as a key resource for the northern forest biological community rather than as a forest pest.

The Geographic Distribution of Red Fir and Noble Fir Based on Infection by Pacific Silver Fir Dwarf Mistletoe

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Keywords: Noble fir, Red fir, Distribution

The distribution of red fir (*Abies magnifica*) and noble fir (*Abies procera*) in Oregon has long been debated. The objective of this study was to determine if selective parasitism of red fir and noble fir by Pacific silver fir dwarf mistletoe (*Arceuthobium tsugense* subsp. amabilae) could be used to provide additional data supporting one of the geographic distributions proposed for these true firs. The research was conducted in the central Cascade Mountains of Oregon. A total of 11 stands infested with Pacific silver fir dwarf mistletoe were sampled to compare host susceptibility. At each study area, 10 temporary circular plots with a 6-m radius were placed around large, severely infected Pacific silver firs. Each live tree greater than 1.4 m in height in the plots was examined and the following data were collected: species, diameter, and dwarf mistletoe rating (6-class system). Incidence of infection for each tree species was summarized for each study area. Pacific silver fir and noble fir were principal hosts of Pacific silver fir dwarf mistletoe in Oregon, but red fir was immune to this dwarf mistletoe. Populations of true firs morphologically resembling noble fir south of latitude 44o N were immune to infection by Pacific silver fir dwarf mistletoe. Populations of noble fir north of latitude 44 degrees N were severely infected. The complete immunity of red fir and trees morphologically resembling noble fir to Pacific silver fir dwarf mistletoe south of approximately latitude 44 degrees N in Oregon supports the classification of these true fir populations as red fir, and not noble fir. The severe parasitism of trees resembling noble fir by Pacific silver fir dwarf mistletoe north of latitude 44 degrees N in central Oregon supports the classification of these populations as noble fir.

Dwarf mistletoe (*Arceuthobium cyanocarpum*) threatens natural regeneration of whitebark pine (*Pinus albicaulis*) following mortality of mature whitebark pine at Newberry National Volcanic Monument in central Oregon

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Keywords: *Pinus albicaulis, Arceuthobium cyanocarpum*, Regeneration

Whitebark pine (*Pinus albicaulis*, WBP) is a keystone species that plays important ecological roles in subalpine forests of western North America, but is currently threatened by multiple stressors. *Arceuthobium cyanocarpum* has been reported in localized settings on WBP in central Oregon, northern California, northern Nevada and central Wyoming. To determine severity of this dwarf mistletoe (DM) on WBP after mortality of mature WBP due to DM and mountain pine beetle, DM surveys were conducted in central Oregon. Systematic sampling was used with 20 fixed-radius plots (and nested fixed-radius plots for seedlings) measured thus far at Newberry National Volcanic Monument (the Dome area). Severity was rated using Hawksworth 0-6 Class System (DMR). Topkill in live WBPs and current mortality (standing dead) due to DM were also recorded. Means were calculated but Wilcoxon tests were used to test for differences in these attributes among WBP trees > 2.54 cm diameter at breast height (DBH, 1.37 m) vs. seedlings. Few larger WBPs were alive and mean DBH of WBP trees was only 6.45 cm. DM appears more damaging to remaining WBP trees than seedlings. Incidence of DM was much higher ($p = 0.0005$) on WBP trees (mean 69%) than seedlings (mean 18%). Of the infected WBP, mean percentage of trees with bole infections was 65% and 89% for seedlings. DMR was much greater ($p = 0.0014$) for trees (mean 3.0) than seedlings (mean 0.76). Percentage of trees with topkill due to DM was higher ($p = 0.011$, mean 17%) than for seedlings (mean 4%). Current mean percent-mortality due to DM in trees was 8% and none in seedlings. Due to high incidence of DM and overall DMR on remaining WBP trees, recruitment of large-diameter WBP is threatened. Heavily-infected WBP may never reach cone-bearing age or maturity and could be outcompeted by other conifers.