PROCEEDINGS OF THE 6th ANNUAL WESTERN INTERNATIONAL FOREST DISEASE WORK CONFERENCE

Vancouver, British Columbia
December 1958

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FOREWORD

The Sixth Western International Forest Disease Work Conference was held at Vancouver, British Columbia, December 2-5, 1958. Thirty-five members registered. About 45 members and guests, including several from the Hungarian Sopron Forestry School, participated in all or most of the regular discussions. On the evening of December 2 Dr. Nordin, Ottawa, Canada, and Dr. Hansbrough, Washington, D. C., reported on national developments in disease research, including plans of the pathology sections for the International Botanical Congress, August 1959, at Montreal. At the Wednesday evening banquet the group was privileged to hear from Mr. A. F. MacBean, Chief Forester, MacMillan & Bloedel Ltd., Vancouver, B. C., who showed color slides and described his recent trip to Russia.

December 4 was spent on the campus of the University of B. C. In the morning the group visited the University laboratories and greenhouse of Forest Pathology (Dr. J. E. Bier) and Forest Ecology (Dr. V. J. Krajina). Dr. Krajina with the help of color slides described his work on nutrient responses of conifers. After the talk the group visited the greenhouse where Dr. Krajina and graduate student Mr. Morrison showed effects of nutrient deficiencies on B. C. conifers and discussed their culture tests in more detail. In the afternoon the conference was the guest of the Forest Products Laboratory in their new campus-located building. Director Ken G. Fensom in charge of the Forest Products Laboratory welcomed the group to the building and described the general research program. Professor H. W. Eades later showed the visitors through the Wood Pathology section of the Forest Products Laboratory. After the laboratory tour the group met in lecture session to hear talks by Jack Roff on redheart and decay of lodgepole pine, Miss Robinson on black stain in red cedar, and Bob Kennedy on weight and strength loss associated with brown and white rots. A pre-dinner social hour, hosted by Mr. and Mrs. Jack Bier at their Point Grey home, provided a pleasant and memorable climax to the day's work.

Executive Committee

J. W. Kimmey, Chairman
H. R. Offord, Secretary-Treasurer

Program Committee

J. E. Bier
Keith R. Shea
A. K. Parker, Chairman

CHAIRMAN'S WELCOME

Fellow members of the Western International Forest Disease Work Conference, and guests, welcome to our sixth annual meeting.

Here we are back in British Columbia. We held our first conference at Victoria in 1953 and since then have completed the circuit of meeting places in the United States and Texas; so now we are starting the second cycle. Those of you who attended the Victoria conference remember the grand start our conference series was given as a result of the efforts of our Canadian members and their gracious hospitality. I am sure that you all have looked forward, as I have, to this second conference in Canada with our genial British Columbia hosts.

I am sorry that the expected delegates from our Mexican membership will not be with us. We hope that their participation in our conferences will in future meetings become a regular thing.

I extend a special welcome to you members and guests who are attending your first conference, and I urge each of you to participate freely in our discussions so that we may all benefit from this added professional knowledge in our conference. Although prepared papers will be read, much of the benefit from these conferences results from our informal discussions, with everybody participating. Please do not wait for the panel leaders to ask for your opinions.

The general theme of our conference this year is titled "Parasitism" and deals with parasite-host relationships, such as host susceptibility, resistance, and klendusity to various pathogens. Parasitism is basic to disease research, for parasites cause all pathogenic tree diseases. We will have two panel discussions of "facultative parasitism" and two panel discussions of "obligate parasitism." After the panel speakers present their papers the panel moderators will lead general discussions of the material presented and any related subjects that bear on the topics. The purpose of these panel discussions is to point out our forest disease problems and through the participation of everybody here to solve them or to determine how to go about solving them through research.

Dr. Parker, Chairman of our Program Committee, and Dr. Bier and Dr. Shea, the other committee members, have expended much time and effort in organizing our program for this conference. These men I heartily thank in the name of the entire membership for their willingness and unflagging efforts in arranging an excellent 4-day program for us.

Art's committee has arranged an all-day trip for us on Thursday to the University of British Columbia campus, where we will see research in progress on forest products, forest ecology, and forest diseases.

The extent of the benefits that result from this conference will depend largely upon the thoroughness of our discussions. All pertinent knowledge possessed by this group should be brought to light in each discussion. The measure of our attainment then will depend on you. I hope that each of you will enjoy every minute of the next 4 days, and I feel certain that you will.

James W. Kimmey
Conference Chairman

PARASITISM AND HOST-PARASITISM RELATIONSHIPS

Randal E. Fitzpatrick

My talk can only be considered an introduction to my topic--parasitism and host parasite relationships. In discussing the subject I shall confine my remarks to parasitism as it relates to the phytopathogenic microorganisms--the fungi, the bacteria, and the viruses.

The attacks of the fungi and the bacteria have many things in common and we can treat them together. The viruses on the other hand have little in common with the other two, so we must treat with them separately.

To begin with, let us set the stage by reminding ourselves of the relative sizes of the protagonists in this battle between the green plants and their microparasites. Consider exactly what we are doing when we look at diseased tissue under the microscope. Let us draw some simple comparisons. Let us take a leaf, say one 10 centimetres long, that is about 4 inches. This leaf under a relatively low magnification--say 100 diameters--becomes 10 metres long; that is over 30 feet. Where there are no veins, it will be but a few centimetres thick, or about as thick as a stout plank. Viewed from the surface, the epidermal cells will appear to fit together like pieces of a fine jigsaw puzzle, each piece averaging 3-4 millimetres across. The stomatal openings will appear as tiny lens-shaped slits, about 2 millimetres long and half a millimetre wide.

As we look down on the surface we may see some fungus spores, perhaps a condium of the apple scab organism. It will be somewhat smaller than a grain of wheat; Alternaria spores will be larger and more like oats. Should the leaf be wet, we might even find a zoospore of the potato blight organism, <u>Phytophthora</u> <u>infestans</u>, swimming about. This will be a tiny sphere about the size of the head of a pin. Bacteria will be mere flecks of dust, and virtually invisible; viruses will be completely so.

As we shall not be able to tell much about host parasite relationships at ~~this magnification, let us turn to higher power. Let us use an immersion~~ lens, and for convenience a magnification of 1000 X. Now we can see the bacteria; for example <u>Erwinia</u> <u>amyllovora</u>, the pear fireblight organism, looks like a small grain of rice 1½ mm. long and ½ mm. wide. The zoospore is about the size of a small cherry, and the apple scab spore the size of a respectable radish. Rust uredospores are slightly larger and they show their markings plainly. The viruses are still invisible, of course; let us leave them out of the discussion for the time being and concentrate on the fungi and the bacteria.

Let us go back to our leaf. Our 10 cm. leaf is now 100 metres long--about 110 yards, the length of a football field. The stomatal openings show plainly--they are almost an inch long and a quarter of an inch wide. The jigsaw pattern of the epidermal cells is now coarser than the average puzzle.

A section through the leaf shows it to be about 8 to 18 inches thick. The epidermal cells are protected by a layer of cuticle comparable in many ways to a sheet of cork. This will be a millimetre thick. Like cork, this material is practically impervious to fluids; it can neither be corroded by enzymes nor enfeebled by toxins.

Beneath the cuticle lie the cell walls proper. In foliage leaves these consist principally of cellulose. They form, in effect, cotton bags with walls averaging a millimetre thick. Fluids pass through them readily and cellulose digesting enzymes dissolve them. They vary in size and shape, but at this magnification they have dimensions of 1 to 5 inches; in other words, sizes corresponding to the common fruits--plums, oranges, apples and bananas.

These cellulose sacks are lined on the inside with the thin gels of cytoplasm in which are embedded the specialized cell structures, the nucleus and the plastids. Let us watch now what happens when a fungus parasite attacks our leaf. Let us take for our model infection by <u>Botrytis cinerea</u>. This is a rather unspecialized parasite. In unventilated greenhouses it causes a putrid dying of the leaves and young shoots of a variety of plants.

The spores of Botrytis are some 10 to 15 microns in diameter. At a magnification of a thousand they are, therefore, about as big as a cherry; remember the leaf itself is over a 100 yards long.

Let us assume that, because of high humidity, the leaf has on its surface a drop of water, which at this magnification will be a respectable pool. Into this pool a spore has fallen. Now if the water has been lying on the leaf for some hours, it will have dissolved in it salts which have diffused through the cuticle in infinitesimal amounts, and the longer it has lain on the leaf, the more its salt content will have increased. These salts furnish a nutrient medium for the spore; they stimulate it to germinate.

The germ-tube of Botrytis is an elongated sausagelike affair. It will appear to be about the thickness of the tip of my little finger. This germ tube pushes out from the spore and grows towards the surface of the leaf in the direction of the diffusion gradient. When the tip of the germ-tube meets the cuticle, it swells, and in a few hours forms a disceform organ of attachment, the appressorium. This process is initiated by the stimulus of contact. It is independent of the nature of the surface on which the tube is growing, and it will occur equally well on a glass slide.

The fungus now excretes a mucilagenous cap over the tip of the germ-tube and the appressorium. This serves to glue the appressorium to the leaf surface, so that even heavy downpours of rain cannot wash it off.

With the formation of the appressorium spore germination is concluded, and real infection begins. This involves the penetration of the parasite into the host. This too is initiated mainly by the stimulus of contact; for the same processes are enacted when Botrytis spores germinate on paraffin wax membranes.

The process by which the fungus penetrates the cuticle is purely mechanical. Only a very few fungi possess enzyme systems capable of decomposing substances of the nature of cutin and suberin. The cuticle of the leaf, therefore, presents a special problem to the fungus. Chemically it consists principally of cutin in which plates of wax are embedded. In our model at a magnification of a thousand it is represented by a sheet of cork a millimetre thick.

The fungus penetrates the cuticle by forcing through it a fine pointed wedge-shaped outgrowth from the underside of the appressorium. The pressure needed to do this may be as much as seven atmospheres, which is roughly the same as the pressure in the cylinder of a high-powered airplane engine.

After the infection wedge of the young hypha has pierced the cuticle, it meets its second obstacle, the outerwall of the epidermal cell. In order to obtain nourishment from its host, the Botrytis fungus must pass through this wall and reach the inside of the cell. The wedge pushes on into the cell wall and at the same time secretes an enzyme which softens or dissolves it. Once inside the cell, the hyphal strand grows to its natural diameter, and the fungus begins to take nourishment from the cell itself. Infection has been established.

Now you will at once recognize that there are many variants of the process by which infection takes place. Some fungi, instead of penetrating directly into the cell, may insinuate their hyphae between epidermal cells and extrude only specialized hyphal branches, haustoria, into the living cell itself. The blister rust fungus does this. Other fungi gain entrance through the stomata; and still others, of course, can infect only where there has been a wound of some sort. The point to observe is that with the fungi there is an active attack, dependent only on the spore germinating under suitable conditions.

The methods and materials by and from which the fungi draw sustenance from their hosts are determined by their inherent physiological capabilities. Some parasites exude toxins that kill the host tissue well in advance of their mycelial growth, while they themslves feed as saprophytes on these dead tissues. For example, with Rhizoctonia on potato, which behaves in this way, the hyphal strands press themselves against the epidermal cells of the stem like an appressorium. The underlying cells are poisoned by the metabolic by-products of the fungus. As these cells die, the fungus invades them, and as it does so, those beneath are killed. Parasites that first kill the tissues and then colonize them are called "perthophytes." They are really saprophytes strictly speaking; the infection locus is an island of dead tissue in the host organism from which staling products diffuse out to kill more tissue, and enlarge the substrate on which the parasite can feed. Many wound parasites act in this way.

On the other hand, there are innumerable examples of parasites that are able to attack the uninjured host directly, and without damaging it with toxins. These feed on the living substance of their hosts and are generally described as "biotrophs."

Some biotrophs need to feed saprophytically before they can make their attack. For example, the hail fungus Coniothyrium diplodiella, which causes a white rot of grape, invades only after its mycellium has developed on the areas of the fruit that have been injured by the hail stones. Hysterographium on ash behaves in a similar way.

Other fungi, such as the late blight of potato organism, attack directly. In the case of fungus, Phytophthora infestans, the zoospores swim in the infection drop for a while, then come to rest and form a membrane about themselves. A germ tube is produced, and this either penetrates the cuticle and outer cell wall of the epidermal cell or enters the leaf through a stoma and penetrates a substomatal cell. In either event, the contents of the invaded cell soon coagulate and the fungus grows on, spreading between the cells and producing fine houstoria, which enter adjacent cells killing them almost immediately.

In contrast to this situation, there are other fungi--rusts, powdery mildews and the like--who's attacks do not immediately bring about the death of the invaded tissue. Indeed, these fungi seem only able to thrive so long as the cells they are attacking are living. Such fungi are almost invariably obligate parasites and cannot be cultured on any sort of artificial medium.

Now, what does all this mean in terms of fungus physiology? It presumably means that whereas the perthophytes and the facultative parasites possess a complement of enzymes that are capable of breaking down and resynthesizing complex organic materials, notably proteins, the obligate parasites lack some of these enzymes, and consequently cannot synthesize all of the materials that must go into their living substance. With the obligate parasites the synthesis of most of the key materials for life seem to be entirely dependent on the enzyme systems of their hosts. To say this, is not, of course, to say that these fungi possess no enzyme systems of their own; they most obviously do. What makes them obligate parasites is the specialization of their enzyme systems, and the more highly specialized the parasites are, the more highly specialized are those enzyme systems. The parasitism of the fungi is determined by the types of enzymes they are capable of synthesizing, and the effects these enzymes have on the hosts they attack.

The same thing is true of the bacteria, but in contrast to the fungi, the phytopathogenic bacteria are incapable of mechanical penetration of the plant body where it is protected by a cutinized layer. So the phytopathogenic bacteria must either attack by way of non-cutinized areas, such as root hairs or stigmas, or circumvent the cutinized areas by passing through natural apertures, such as stomata or hydathodes, or by entering through wounds.

Remembering our model again, the stomatal openings are about 10 times larger than the bacterial cell. Now in a disease like black rot of cabbage where the bacteria enter through the stomata and hydathodes, what happens in this. The bacteria are washed or spattered, quite by accident, onto the surface of the leaf. Here they get into the gutation drops on the hydathodes and, with the return movement of transpiration, are sucked into the cavity beneath. There they multiply, and in doing so secrete enzymes that rapidly disintegrate the cell walls, and ultimately kill the tissue.

On the other hand, the pear fireblight bacteria, Erwinia amylovora, when transmitted by pollinating insects to the stigmas and nectaries of the flowers, at first multiply saprophytically in the nectar drops, and there form mucilagenous bacterial colonies, or zoogloea. These make their way actively through the intercellular spaces of the style. In the case of the nectaries, which are covered by an epidermis, the bacteria swarm in the nectar drop, the pass by their own locomotion through the stoma down into the air chamber beneath. From both these locations in the flowers they are able to work their way into the twigs, and finally into the branches where they kill large areas of bark and seriously damage the tree.

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Now let us turn to the viruses.

In order to visualize the size relationships of the viruses and the plant body, we shall have to turn to the electron microscope in order to obtain a sufficient increase in magnification. Let us select one that will give us a picture magnification of a 100,000 diameters.

At this magnification the virus particles, of say tobacco mosaic virus, are about the length of a paper match (3 cm.). The leaf, originally 10 centimetres long, is now six and a quarter miles long. The individual cells of the leaf are as large as good size rooms and the cuticle and cell walls are each 4 inches thick.

The cuticle is a solid structure built up in layers, but the cell walls where they touch adjacent cells are pierced by narrow channels through which strands of cytoplasm pass from one cell to another. These are so-called plasmpdesma. Were it possible to observe living cells with the electron microscope we should undoubtedly see a certain amount of movement of cytoplasm through the channels, and with it, in virus infected material, virus particles.

The virus particle is a simple structure. Unlike the bacterium, it has no means of locomotion, and unlike either the fungi or the bacteria, it apparently has no enzyme systems of its own. Consequently it can neither swim into the plant body, nor dissolve its way through the cell walls. The viruses are, therefore, wholly wound parasites. The cell wall must in some way be ruptured in order for them to reach the site of their infection, which is the living cytoplasm. Moreover, the wound must be of a sort that ruptures the cell wall without drastically damaging its contents.

Now it happens that the extremely fine stylets of the homopterous insects, the aphids and the leafhoppers fulfill these requirements rather well, and it is probably for this reason that these insects are by far the most common vectors of the plant viruses.

I shall not attempt to go into virus-vector relationships in detail, but I should like to make the following points:

First, there seems always to be a specific relation between the virus and its vector, for while it is true that many viruses are spread by more than one aphid or leafhopper species, those viruses that are spread by aphids are not spread by leafhoppers, and vice versa.

The second point is that the length of time that the insects retain their infectivity varies from virus to virus, and is a characteristic of the virus and not of the vector.

The last point is that although there is evidence that certain viruses can multiply in the bodies of their vectors, and, some evidence that infectivity can in certain cases be passed on to the offspring, neither of these phenomena are at all common. It is safe to say that the majority of viruses do not multiply in the bodies of their vectors, and that transmission from parent to offspring is indeed rare.

Having said this much about virus-vector relationships, let us return to the virus in the plant cell.

We have said that the virus particle is a simple structure--it is--relatively speaking. According to our best present knowledge it consists of two types of material--protein and nucleic acid.

Now on the molecular scale, both these are large and complex structures. Proteins are built up from some twenty-odd amino acids. These are linked together through nitrogen atoms into chains; the so-called polypeptide chains. These chains are twisted together and crosslinked to form the protein structure. When proteins are degraded or digested by enzymes, which are themselves proteins, the polypeptide chains are the first units to come apart. These are then broken further into shorter chains, and finally into the individual amino acids. Now, since the individual amino acids are configurations of some 10 to 100 atoms, and are by no means simple structures themselves, it can readily be appreciated that the protein molecule is indeed a gigantic structure.

The nucleic acid is also a complicated structure. It consists of four basic units, two of which are purines and two are pyrimidines, again organic molecules of some complexity. These units are each attached to a pentose sugar molecule, that is, one having five carbon atoms, and these pentose groups are joined together through phosphorous atoms, and again, the structure is that of a long chain.

Nucleic acid is thought to be the basis of the genetic material of all living organisms. The chromosomes and the genes are largely composed of a combination of nucleic acid with some protein. Moreover, there is a theory of heredity which holds that the information that the genes transmit from generation to generation, is coded by the arrangement of the purine and pyrimidine groups on the nucleic acid chains.

Now not even the electron microscope can show us the details of the construction of these materials, but indirect evidence and analogy with what is known about some of the bacterial viruses, has led us to believe that the nucleic acid forms a core in the virus particle, and that the protein material, wrapped around this, serves to protect it, very much as the wood in a pencil serves to protect the lead.

Indirect evidence also suggests that what happens when the virus enters the plant cytoplasm is this: First the protein sheaf is removed, either in part or in whole. The free nucleic acid then in some way alters the metabolic processes of the host so that virus nucleic acid and virus protein are produced in sufficient quantity for new virus particles to be constituted, and so a new generation of virus is produced. Thus viruses are thought to reproduce in an entirely different way to other organisms, and consequently their parasitism is of a different order.

May I now recapitulate what I have said about parasitism by drawing some analogies? In these days of automation it is fashionable for mathematicians, engineers and cyberneticists to construct theoretical machines that will reduplicate themselves indefinitely. In other words, machines that will behave like living organisms. Some have gone even further and constructed fanciful factories of machines that will do this.

Let us consider the green plant as such a factory. The enzymes will be the machine tools. Their component parts, the amino acids, will be the cutting tools, the gears, the shafts, the wheels, and so on. These, bolted together by the nitrogen atoms, will give machines of different characters and functions. The genes will be the controllers, the computors, the pattern makers, the electronic brains of the factory, so to speak.

Now in the green plant this factory is run by fuel manufactured by special machines that drive this energy from sunlight. This fuel--sugar--is converted into other forms by other machines, and is used or stockpiled as required.

Now, the fungi and bacteria are similar factories, but their information centres lack one thing; they do not know how to build machines for converting sunlight into fuel.

The saprophytic micro-organisms overcome this difficiulty by raiding fuel stores of green plant factories that have ceased to operate, and are being demolished. Now, in doing so, they may pick up some odd parts of the wrecked machines--indeed they usually have machines of their own to assist in this wrecking--but in general they feed these parts back into their own furnaces, melt them down, and build their own parts out of the raw materials they contain, rather than incorporate the whole part into their new machines. The perthophytes do the same thing, only in their case the waste products in their sewage and the smoke from their chimneys, so to speak, are the principal factors that cause the adjacent factories to shut down.

The true parasites go a little further; they have machines that wreck the factory walls, and, to a greater or lesser extent, machines that wreck the machines within them.

The obligate parasites do not immediately wreck the factories of their hosts. What they do is to use some of the fuel supply, and at the same time pick off some of the machine tool parts from the production lines--parts that they themselves have no machines for making. Now, as long as they do not take too much fuel, or cause too much disruption of the production lines, both factories will operate reasonably well. The success of the obligate parasite depends on its not disrupting the organization of its hosts until it has accumulated all the materials it needs to complete its life cycle.

Now, how shall we construct a model for the viruses? The viruses are hardly factories in themselves since they seem to have no machine tools; all they seem to possess are information centres. What they seem to be doing when they get into the host factory is to order certain machines of the host to build virus computor parts and, as a sufficient number of these are built, to assemble them into more virus information centres, and so to procreate themselves.

Observe that, although the viruses may produce considerable disruption in the factories of their hosts, they seldom completely wreck them. In other words, the successful viruses never kill their hosts.

Now, I have been a parasite on your time long enough. Let me hope a successful one. May I wish you well in your deliberations, and thank you.

CRYPTODIAPORTHE CANKER ON WILLOW

J. E. Bier

Summary. A close correlation was found to exist between the development of the willow bark canker, caused by *Cryptodiaporthe salicina* (Curr.) Weh., and the moisture content of the bark. When this was expressed as a percentage of the amount of water required to saturate the sample under experimental conditions, relative turgidities of 80 percent or more inhibited canker development which, however, occurred normally at lower percentages. Studies of the epidemiology of this disease in the Vancouver area afforded evidence in support of the limiting effect of bark moisture on canker development. Thus during the dormant season of 1957-1958 the monthly average temperature was significantly higher than the minimum temperature for the growth of *C. salicina* on potato dextrose agar and the relative turgidity did not reach the inhibiting value of 80 percent. Cankers continued to develop throughout this period. During the growing season while temperatures were still more favourable for fungus development no extension of cankers occurred, apparently because, during the growing period, the relative turgidity was in excess of 80 percent. Canker development was prevented during the winter by placing dormant twigs in water, which likewise increased the moisture content of the bark above the 80 percent level.

SOME PHYSIOLOGICAL AND ANATOMICAL CHARACTERISTICS OF POPULUS SPP. AS RELATED TO INFECTION BY CYTOSPORA CHRYSOSPERMA FR.

W. J. Bloomberg

Summary. Differential resistance to Cytospora chrysosperma Fr. canker was observed in three species of poplar growing at a nursery on Lulu Island, B. C. The species concerned were Populus trichocarpa T & G, a native: P. regenerata and P. robusta var. bachelieri. The latter two are hybrids. The resistance to Cytospora increased in the order named.

Laboratory experiments with cuttings of the above species demonstrated a negative correlation of the bark moisture content and canker growth. Experiments using three fixed levels of cutting moisture content and three temperature levels showed significant differences in canker growth between levels of both factors and for all species.

Experiments with fixed levels of both atmospheric moisture and cutting moisture content showed significant differences of growth rate between levels for both factors and for all species. The differences were correlated with bark and wood moisture changes measured during the experiment.

Greenhouse experiments with four-month-old plants of Populus regenerata and P. robusta showed infection could be obtained only when plants were subjected to a drought regime and were exposed to low atmospheric humidity.

Anatomical differences observed in the bark tissues of the three species suggest a basis for differences in water economy and hence differences in physiological resistance to Cytospora infection.

THE ATROPELLIS CANKER DISEASE OF LODGEPOLE PINE

J. C. Hopkins

The canker of lodgepole pine referred to here is the one caused by an inoperculate discomycete termed Atropellis piniphila (Weir) Lohman and Cash. It has been reported on several species of pines, but only on lodgepole have high incidence rates been recorded. In Alberta it occurs sporadically throughout the range of the host, and several areas of high incidence rates, one within the area allocated to the Hinton mill, have been discovered. Molnar (3) has reported severe damage in association with attack by Cronartium stalactiforme in the Grizzly Hills Forest Reserve, near Kelowna.

Except for reports of its distribution, and some taxonomic work, very little has been reported since the original contribution by Weir (5) in 1921. Seaver (4) proposed incorporation of the genus Atropellis into the genus Godronia but was unfortunately unaware of a paper by Lohman and Cash (2) in which they had revised the characters of the genus Atropellis. I have therefore decided to retain the terminology used by Lohman and Cash for the present.

The canker develops on stems and branches, and is characterised by a copious resin flow over the surface and by a bluish-black discoloration of the underlying tissues. Growth of the pathogen is exceedingly slow, but girdling may eventually occur and result in the death of the host. Prior to girdling, the deleterious effect on growth of the host is unknown, but observation of stems or branches, infected with a single canker, suggests that it is slight until the later stages of the disease. However, in areas of high incidence rates, the situation is complicated by the occurrence of multiple stem and branch cankers which might be expected to have an adverse influence on growth.

Development of the pathogen in culture, as in the host, is exceedingly slow. The media supporting the most rapid growth were soya and oat digest dextrose agars, with slightly slower growth on Sabauraud's dextrose and potato dextrose agars. On malt and yeast extract agars, growth was exceedingly slow. Temperature studies indicated an optimum value of around 18°C. Growth was only slightly less at 14° and further reduced only slightly at 10°, but at 24° growth was much slower than at 10°, and none occurred at 29°C.

Studies on pH relations indicated that, in media containing McIlvaines buffer, the optimum value occurred at 4.0. Above 4.0 the growth rate fell off rapidly, and at 5.5 growth was barely detectable. Below 4.0, the reduction was slight down to 3.0, but was much less at 2.5 although the weight of mycelium produced at 2.5 was similar to that formed at 4.5.

An investigation of vitamin requirements revealed a total deficiency for thiamin.

Proof of pathogenicity has hitherto been lacking although the ubiquity of apothecia of Atropellis on older cankers, and the isolation from cankers of cultures which appeared morphologically identical to cultures derived from ascospores of Atropellis, provided strong evidence. In the isolations from the blue-black zone of the canker, 312 slants were prepared and of these 230 yielded isolates of Atropellis, 62 remained sterile, and 20 developed other organisms, mainly common airborne contaminants. Successful isolations were also made from cankers on two dead trees which had probably been dead for at least two years since no adherent needles remained. Isolations were also obtained from a canker retained for a year in the field station laboratory and a few were even obtained from the same canker retained in the same place for a further year.

Last summer, re-isolation of cultures was carried out from five of the inoculations made two years ago using culture mycelium. These five inoculations induced blackening of the wood typical of the naturally occurring infections. But 145 inoculations had been made. Thirty two of these had been prepared by drilling a hole deep into the wood and inserting the mycelium close to the base of the bore hole, and four of the five successful inoculations came from this group. The remaining inoculations had been made either by drilling a hole to just beyond the cambium or by making a shallow slit into the wood. In all cases the inoculations were protected by cotton wool and polythene. Numerous inoculations showed minute signs of blackening which suggested that initial invasion had occurred but that further advance had been checked.

The normal entry zone of the pathogen is not known, but analysis of the position of canker centres indicated that of 80 trunk cankers 78 per cent originated at stem nodes and 22 per cent at internodes. The reason for this greater susceptibility of nodes is unknown but it might be related to moisture accumulation.

After invasion of the xylem, the most rapid penetration occurs longitudinally within the sapwood. The rate referred to is, however, relative since growth is actually very slow. Except for the very young specimens, the apices of the cankers lie at some depth in the sapwood, leaving tissue between them and the cambium for subsequent colonization. Thus the fungus may be present for several years at any one level before the adjacent cambium is killed. This removed the possibility of investigating canker age --size relations by tracing the stages in development of single cankers.

Penetration radially inwards, although slower than in other directions, is more rapid through ray tissue than through xylem and the hyphae spread from the ray cells into the adjacent tracheides by way of the pits, simple or bordered. Tangential penetration within a ring may then occur with little invasion of adjacent rings, resulting in the formation of a length of blackened ring, one or two tracheides in width. This directional spread is probably the result of the restriction of the bordered pits largely to the radial facets of their walls, and through which further invasion could readily proceed.

Dispersal is apparently carried out primarily by wind borne ascospores. Vaseline smeared slide traps were set up early in the past summer and heavy counts were obtained right through until early October. Analyses have not yet been completed but spores were released during or just following rain throughout the sampling period although the numbers decreased towards the end of this period as the temperatures dropped. One of the most interesting results has been the collection of spores from the canker on a dead tree. The absence of needles on it suggests that the tree had been dead for at least two years. This, together with the isolations from cankers on dead trees, referred to earlier, constitutes strong evidence that the pathogen is able to continue to live and function actively for a considerable period after the death of the host, and thus may be said to have converted from a parasitic to a saphrophytic mode of life.

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INDIRECT CONTROL OF FACULTATIVE SAPROPHYTES IN THE SOIL

Ernest Wright

Introduction

It has long been established that damping-off fungi are facultative saprophytes that are able to survive in the soil for long periods of time because of their ability to live on dead organic matter and other debris. For this reason they can be controlled by changing the equilibrium within the soil to favor microorganisms other than damping-off fungi. This may be done in many ways: by altering soil pH, by the use of certain fertilizers, by changing the nitrate-nitrogen content of the soil, by revising watering schedules, by using cultural practices that are disadvantageous to facultative saprophytes and also by planting proper rotation crops. Soil fumigation is considered a direct means of control.

Literature

Much of the early work on damping-off control in the United States was done by Hartley and his co-workers. In one of his early papers, Hartley and Bruner (3) reported that ragweed was severely infected with Rhizoctonia; whereas Russian thistle showed marked resistance. It was suggested that ragweeds in unweeded beds probably serve as ideal hosts for over-wintering of this damping-off fungus. While ragweed is certainly not a rotation crop to be recommended, it is not uncommon for nurserymen to disc it under in the spring when preparing the seed beds without too much thought of the consequences.

Eliason (2) found that buckwheat when used as a rotation crop greatly increased damping-off of red pine. In deciduous forest nurseries it was found that damping-off was most severe when legumes were used as rotation crops and was considerably less when corn or wheat was the preceding crop (8). Later it was found that a similar relationship applied to ponderosa pine seedlings (9). In general it can be stated that damping-off is frequently most severe in newly established nurseries (5).

Rotation Crop Tests

There are a number of ways that rotation crops may decrease or increase damping-off. As already indicated rotation crops may become hosts for the over-wintering of damping-off fungi. Wheat and corn both have root-rots caused by Gibberella and probably carry-over the Fusarium imperfect stage which sometimes causes damping-off or root-rot losses of tree seedlings. Clover and other legumes quite frequently are infected with Rhizoctonia and Pythium root-rots that may carry-over to succeeding crops. It would be difficult indeed to find a rotation crop that did not have this disadvantage to a greater or less extent. It appears, therefore, that factors other than the carrying-over of a disease from the rotation crop are involved in the increase or decrease of damping-off.

Quite extensive tests have been made on the influence of rotation crops on the damping-off of broadleaf seedlings. The results from replicated greenhouse tests on the damping-off of American elm are shown in the following graph. These tests were based on nine crock replications kept at regulated temperature and moisture conditions. The fall collected soils were held in refrigeration until spring at which time the entire series was run. An interesting feature of this test is that damping-off losses were uniformly heavier in the fall collected soils than for the same rotation soils collected in the spring. The damping-off fungi isolated from infected seedlings were primarily Rhizoctonia and Phthium and an occasional Fusarium. There were other tests completed which also included species such as Chinese elm, black locust, and desert willow. The trend was similar in that wheat and corn were the best rotation crops; whereas legumes, particularly clover soil, showed the heaviest damping-off. A similar trend was shown for ponderosa pine (9).

Soil Amendment Tests

Since legumes are nitrogen supplying crops, soil nitrate-nitrogen was also found to be relatively high. This was by no means surprising (6) and suggested that other treatments might also be used to reduce nitrate-nitrogen in the soil such as the addition of carbohydrate material in the form of wheat straw, sawdust, or even glucose before sowing seed beds (6). A number of these amendments have been tested in both greenhouse and field trials (figure 2). For large scale operations, sawdust has proven the most practical. The application of glucose is a fast means of reducing the nitrate-nitrogen in the soil, but it has the disadvantage of tending to crust the soil (7). This, of course, is highly undesirable when the seedlings are emerging. Application of sawdust and acidification have proven desirable for ponderosa pine as shown in the following table (9). Similar treatments have also proven fairly satisfactory in Douglas-fir seed beds.

Effect on Microflora and Microfauna

The reduction of nitrate-nitrogen reduces damping-off losses, but it is evident that other factors are also involved. Another way that rotation crops as well as various soil amendments can influence facultative saprophytes in the soil is by changing the balance of the microflora and fauna of the soil. There are several ways to study such changes, none of which are entirely satisfactory. Dilution plate tests have been made of the various rotation soils before and after treatment. It must be admitted that very few satisfactory clues have been obtained in dilution plate studies. The only definite trend has been that the more numerous the microorganisms in the soil the less the damping-off. This appears to agree with the reduction of nitrate-nitrogen in the soil by the addition of carbohydrates and rotation crops. The fierce competition for nitrate-nitrogen by other soil microorganisms reduces the available nitrate-nitrogen and carbohydrates in the soil which subsequently reduces the virulence of the facultative damping-off saprophytes and thus holds them in check. Studies using the Cholodny slide technique and modifications thereof have proven desirable as supplements to dilution plates but cannot be used quantitatively and therefore fail to furnish the pertinent information desired (8). Direct control by use of some soil fumigants is effective in controlling facultative saprophytes in the soil (4) but may lead to increased damping-off losses (1) or may eliminate most or all other soil microorganisms, including mycorrhizal fungi. This could be undesirable, particularly for 2-0 stock used in field plantations (10).

Tentative Conclusions

The control of facultative saprophytes in the soil, such as those that cause damping-off, may be accomplished in some instances by encouraging the multiplication of all the micropopulation of the soil which reduces the nitrate-nitrogen supply. This happens when the soil is acidified, or various amendments are added, particularly carbohydrates. There may also be a growth stimulating effect on the host itself when the soil is acidified.

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NEEDLE BLIGHT OF DOUGLAS-FIR

A. K. Parker

Needle blight of Douglas-fir is the last disease to be considered at this session on facultative saprophytes. It is considered last because there is some doubt as to whether the causal agent, Rhabdocline pseudotsugae Sydow, is facultative or obligate in behavior. Thus, the fungus helps to bridge the gap between typical examples of the facultative saprophytes which we have considered and typical examples of the obligate parasites which we will be considering.

Rhabdocline pseudotsugae is obligate in that it has not been shown to grow on artificial media, it has a narrow host range and hyphae are intercellular with intracellular haustoria. The fungus is facultative in that it kills host cells long before the end of a one-year life cycle. When spores of Rhabdocline are disseminated during June, germination and penetration take place within approximately two weeks, and haustoria are formed in host cells from adjacent intercellular hyphae.[1/] Two to three months later small yellow areas appear on the needles where successful penetration has taken place. Microscopical examination reveals that the fungus is spreading and killing the host cells it has invaded. One to three months later the fungus has stopped spreading and the yellow areas have become reddish-brown. Mycelium builds up in the necrotic areas and the fungus produces mature apothecia the following June. Unlike typical obligate fungi, which do not kill host tissues until a very late stage in development, Rhabdocline appears to behave in an obligate manner for only 15 to 20 percent of a one-year life cycle. There may be exceptions to the one-year life cycle, however, because mature apothecia occur on the two- to six-year-old needles as well as on the one-year-old needles. It is not yet known whether the fungus is able to penetrate the one to five-year-old needles or whether it is able to penetrate only the current year's needles and then live in an obligate manner for two to six years before producing mature apothecia. Perhaps the differences we accept between obligate and facultative fungi are useful on occasion but actually quite artificial. If there are fundamental differences between the two types of parasitism, it is doubtful whether we have yet been able to define them.

During the last several growing seasons we have been studying two aspects of the Rhabdocline problem. We have been studying what appear to be variants or races of the fungus, and have been trying to clarify the life cycle of the fungus.

During June, when apothecia are mature, typical Rhabdocline may be found on the one-year-old and older needles. Needles have small reddish-brown

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[1/] Van Vloten, H. Rhabdocline pseudotsugae Sydow, Oorzaack eener ziekte van Douglasspar. Proefschrift, Landbouwhoogeschool te Waganingen. 168 pp. 1932.

spots which are irregular in outline. Spores are discharged from the lower surface of the needles for the most part, but occasionally from both the upper and lower surfaces.

An apparent variant of typical Rhabdocline is one we have been referring to as Type A. It may be found on the two-year-old and older needles. Needles have comparatively large reddish-brown areas occurring as definite bands. Spores are discharged from only the lower surface of needles.

A second apparent variant of typical Rhabdocline is what we have been calling Type B. Type B causes what Dr. Childs refers to as the Hebo disease and may be found on the one-year-old and older needles. Needles have reddish-brown spots which are generally smaller than those of typical Rhabdocline. The spots are irregular in outline and spores are discharged from the upper surface of the needles. Occasionally, near the latter part of the spore dissemination period, spores are also discharged from the lower surface of affected needles.

In order to determine if we were dealing with races of Rhabdocline or with differences in the reaction of fir to Rhabdocline, a series of inoculation experiments was carried out. Seedlings from an area near Victoria and from the nursery at Duncan on Vancouver Island were transplanted to pots. Another set of seedlings from an area near Cranbrook in the East Kootenay region of Interior British Columbia, and from the forest nursery at Cranbrook, were transplanted to pots. Seedlings in the Duncan nursery were grown from seed gathered in the coastal region, and seedlings in the Cranbrook nursery were from seed gathered in the Interior. Seedlings were divided into five groups and each group contained seedlings from the four sources. One group was inoculated with typical Rhabdocline in the Interior; the second group was inoculated with typical Rhabdocline on the coast; the third group was inoculated with Type B on the coast; the fourth group was inoculated with Type A on the coast; and the fifth group contained the controls for all the inoculation experiments. Controls accompanied all groups except at the time of inoculation. Inoculation was carried out in June 1957 by placing the seedlings under trees severely infected with the different types of Rhabdocline. Glass slides were placed on the pots to act as spore traps, and in this manner it was determined that all seedlings received adequate inoculum.

Of the 213 seedlings used for the experiment 135 survived the first year. Fifty of the 213 seedlings were used as controls. Twenty percent of the seedlings inoculated with typical Rhabdocline from the Interior were moved to the coast after inoculation, and 25 percent of the seedlings inoculated with typical Rhabdocline, Type B and Type A from the coast region, were moved to the Interior after inoculation.

With the exception of seedlings obtained from near Cranbrook and inoculated with Rhabdocline in the coast region, 20 to 89 percent of the seedlings inoculated with spores of typical Rhabdocline and Type B developed mature apothecia. Symptoms developed on only the 1957 needles. Seedlings inoculated with Type A spores and all surviving control seedlings did not develop symptoms at the end of one year.

Seedlings with symptoms developed the same type of apothecia and lesions that were associated with the source of inoculum, and therefore variations in morphological manifestations of the disease have been attributed to differences inherent in the fungus rather than to differences in the host or environment. Support for this conclusion was obtained from the recent observation of Type A apothecia on the same needles having apothecia of typical Rhabdocline, and of Type A apothecia on the same tree having Type B apothecia.

Further studies are now underway to determine other differences between the apparent races and typical Rhabdocline. At the present time we know that the spores of Type A are smaller and slightly different in shape to those of typical Rhabdocline, and that the germ tube of Type A is generally vertical and smaller than that of typical Rhabdocline when spores are placed on identical media and under the same conditions of environment. Furthermore, typical Rhabdocline has a one-year or more life cycle, while Type A has a two-year or more life cycle. The two-year life cycle for Type A was determined by making fall cuttings from the current year's growth of trees inoculated with Type A spores, and removing the cuttings away from a source of inoculum. Only 10 percent of the cuttings survived the next 15 months, but 67 percent of these developed Type A lesions. In addition, the 2-year life cycle was demonstrated by the inoculation of 6 small saplings in the field for two successive years. Before the first inoculation the current year's growth from one half of the branches was removed. Type A lesions developed in the second and third years on the 2-year-old needles of the branches untouched but not on the branches from which the current year's growth had been removed. The differences between typical Rhabdocline and Type A are quite great, perhaps great enough to warrant a new species. At the moment, however, there are still a number of morphological features needing comparison. The morphological features of Type B have not yet been examined critically.

Inoculation and disease development in the field has been rather unsatisfactory because of the relatively low survival of seedlings and the low number of needles successfully inoculated on any one seedling. Some of the seedlings inoculated in the field developed lesions on less than a dozen needles. Field inoculations are also unsatisfactory for studying the life cycle of Rhabdocline. Several attempts in the past to infect seedlings in the greenhouse were complete failures. As a result of these difficulties studies have been initiated on spore dissemination and germination, and on the early infection phases. Studies involve only typical Rhabdocline at the present.

By using spore traps and weather instruments in the field, and by observations in the laboratory, it was found that 100 percent relative humidity was necessary in order to initiate swelling of the mature apothecia. Swelling, which forces open the envelope covering the apothecia, is a prerequisite for spore discharge. Temperatures ranging from 1 to 28° C. did not inhibit swelling at a relative humidity of 100 percent. Spores were discharged at relative humidities of 100 down to 85 percent. At 100 percent relative humidity spores were discharged at temperatures ranging from 1 to 28° C., with the greatest number being discharged at temperatures ranging from 10 to 20° C.

For a number of years we had been trying to obtain spore germination without success. Temperatures and humidities were varied and a great many solid media and solutions were tried. Occasionally one or two spores would germinate, but generally the spores would remain unchanged or swell and burst. Last year it was found that by placing spores on solid media which had a firm surface film in plates free of water droplets, germination would be initiated within 24 hours at 10° C. The same results were obtained on freshly prepared media by increasing the agar content of media. Potatoe dextrose agar was found to be superior to malt, glucose-asparagine and water agar. When leaving the ascus spores are generally one-celled but become two-celled prior to germination. Germination occurred at temperatures ranging from 1 to 20°, but not at 25° C. The best temperature for germination was found to be 10° C. Germ tubes would attain a length equal to that of the spore at this temperature, before ceasing growth altogether. At 15 and 20° C. most germ tubes would swell and break soon after forming. At 1 and 5° C. germination took longer than at 10° C. and there was approximately 50 percent mortality due to swelling and breaking. Perhaps our previous failure to obtain infection in the greenhouse may have been due to keeping the newly inoculated seedlings too wet for too long, and at temperatures unfavorable to spore germination.

One of the most puzzling aspects of the <u>Rhabdocline</u> problem is the variation in infection of needles of different ages. In any one year the 1 to 6-year-old needles on any one tree may have mature apothecia. But the needles of any one year may be more severely affected than needles of any other year. For example, the needle blight epidemic of 1950 near Cranbrook was due almost entirely to apothecia on the 1947 and 1948 needles. The outbreaks last year and this year at Invermere were almost entirely due to apothecia on the 1-year-old needles, although a few needles of other ages were affected. It would appear that <u>Rhabdocline</u> is able to infect needles other than those of the current year or that the fungus is able to vegetate (that is, live in an obligate manner) for several years. If the fungus is able to infect needles older than those of the current year, however, one would expect all ages of needles on artificially inoculated trees to be infected to some degree at least, rather than having infection appear on only the one-year-old needles. Because we have quite good evidence that both Type A and typical <u>Rhabdocline</u> may exist in an obligate manner for one and one-half years and then produce mature apothecia on the 2-year-old needles, it may be possible that the obligate existence is extended for even longer periods under certain conditions.

It is not uncommon in any one year to find trees unaffected by <u>Rhabdocline</u> situated among severely infected trees. However, trees unaffected one year may very well be affected the following year. This year, in an area severely affected the past two years, trees which did not have their 1-year-old needles affected were found scattered throughout an area where most trees had them infected. During June and July yellow areas began showing on the one-year-old needles of these resistant trees. By September they were reddish-brown lesions and by next June they will have mature apothecia. In the belief that these trees would continue to show at least a greater degree of resistance than their neighbors, an attempt was made to discover differences between the readily susceptible trees and those partially resistant. It was hoped that an answer to this type of resistance would also provide an answer to the whole problem of variation in needle infection with age of needles.

In 1930, Brown[2] stated that the water content of Rhabdocline affected needles was lower than in healthy needles. In order to determine if there was a similar relationship between highly susceptible trees and partially resistant trees, 28 pairs of trees in 3 different areas near Invermere were selected for determining the moisture content of needles. The 1957 needles of one tree of each pair were severely hit by Rhabdocline while the 1957 needles of the second tree of each pair were essentially free of Rhabdocline during the year previous to June 1958. Trees were Christmas tree stock of sapling size and care was taken to select pairs whose members were adjacent to one another and of approximately the same size. The current year's growth was removed from the terminal portion of each of 3 branches on every tree for determination of moisture content. Determinations were made during the first week of July, September and October. Moisture was calculated as percent of the ovendry weight after drying the needles for 24 hours at 70° C.

There was an average of 7 percent less moisture in needles of resistant trees during July than in needles of infected trees (Table 1). In September there was 10 percent less and during October, 8 percent less. This trend was evident in 19 of the 28 pairs of trees throughout the summer. Two pairs in July and 6 pairs at the September and October determinations did not follow the trend. It is doubtful that the 10 percent maximum difference in moisture content between resistant and infected trees indicated a significant influence on the host-parasite relationship, particularly since the trend was not consistent and since individual values obtained for a single tree were at times greater than 10 percent. It is more probable that the values reflect a more general condition of the trees.

Table 1.--Moisture content of needles on Douglas-fir trees resistant and susceptible to Rhabdocline pseudotsugae

Time of year	Average moisture content (% o.d.w.)		
	All trees	Resistant trees	Susceptible trees
July	153	149	156
September	184	179	189
October	150	146	154

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[2] Brown, A. B. Observations of leaf fall in the Douglas-fir when infected with Rhabdocline pseudotsugae Sydow. Ann. Appl. Biol. 17: 745-754. 1930.

Quite apart from the Rhabdocline study the results are interesting in several ways. The period of highest foliage moisture content, during the first week of September, occurred after the driest part of the year and at a time when soil moisture was at its lowest level. The soil moisture level at the time of the July determinations was 22.6 percent; at the time of the September determinations 9.7 percent, and at the time of the October determinations 13.3 percent. Another point of interest is that September was the period of greatest fluctuation in needle moisture levels of individual trees. It appeared that the greater the moisture stress on a tree, the greater the difference in moisture content between needles of different branches on the same tree. Moisture content of foliage on individual trees tended to level off in periods of plentiful or perhaps adequate moisture. The irregular pattern of dying branches and twigs frequently encountered during drought periods may be accounted for by these differences in foliage moisture levels, and perhaps account for the attack of certain fungi causing cankers.

Another aspect of the resistance phenomenon encountered in this study is under investigation and appears to hold more promise of explaining variable host susceptibility than moisture relationships. Preliminary work has shown a relationship between phenol content of Douglas-fir needles and resistance to Rhabdocline. The current year's needles of 30 trees, half of them showing some resistance to the fungus and the other half appearing highly susceptible, were analyzed for phenol content. Resistant trees were found to have, on the average, 80 percent more phenol than the susceptible trees, although there was considerable variation in both groups. Infection by Rhabdocline appears to lower the phenol content of the attacked needles even lower in the susceptible trees, but there appears to be a limit to what the fungus can overcome. The working hypothesis formulated is that there is considerable variation in the phenol content of needles on different trees, and that environmental conditions influence either the phenol content of the needles or the ability of Rhabdocline to reduce the phenol content to the level necessary for complete development. Just what member or members of the phenol group are present and might be responsible for inhibiting the fungus is not known.

HOST-PARASITE INTERACTIONS IN WOODY-PLANT VASCULAR DISEASES[1/]

Harold S. McNabb, Jr.

Woody-plant vascular diseases can be divided into two main groups; those diseases of the "active" functional tissues, outer sapwood, and those that deteriorate the "passive" functional tissues, heartwood and inner sapwood. One type of the former group, the woody-plant wilts as they are most commonly called, is the subject of this presentation.

Host-parasite interactions present in woody-plant, wilt diseases are best illustrated by oak wilt [caused by *Ceratocystis fagacearum* (Bretz) Hunt] and Dutch elm disease [caused by *Ceratocystis ulmi* (Buisman) C. Moreau], and to a lesser extent by Cephalosporium wilt of elm (caused by *Dothiorella ulmi* Verrall & May) and Verticillium wilt of elm and maple (caused by *Verticillium ablo-atrum* R. & B.). Therefore, this discussion, by means of a critical review of the literature and present theories, will present these interactions as they occur during the cycles of these diseases.

The main source of inoculum in woody-plant wilt diseases is diseased material. The causal organism may fruit on diseased trees as in mat and pad formation between bark and wood tissues in oak wilt (13), coremia formation in insect galleries in Dutch elm disease (41) and pycnidia formation on the bark of killed twigs in Cephalosporium wilt (12). In Dutch elm disease, the parasite may become established initially in down elm wood, i.e. wood piles, as well as living trees (41). In the case of the oak wilt fungus though, this initial occurrence in down oak wood appears next to impossible because of the effect of dryness, heat and competing organisms on this parasite (16, 35). The Verticillium organism is able to live as a saprophyte in soil (33).

Indirect transmission of these disease organisms is usually by means of insect carriers. The life habits of these carriers clearly fit the overall disease cycle. In the case of Dutch elm disease, the smaller European elm bark beetle breeds in diseased elm wood with the resulting adults carrying fungus spores to their natural feeding place, twig crotches on healthy elms (41). In oak wilt, the mat and pad becomes exposed to the external environment when pressure from the expanding pad cracks the bark (28). These fruiting structures attract insects of the sap and fungus feeding type as do fresh wounds on healthy trees (30). Spores of

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Dothiorella ulmi are carried on the bodies of leaf-feeding insects (12). Present theories also propose that both the oak wilt organism and Verticillium fungus are obtained from diseased xylem tissue by small bark beetles during their feeding or breeding habits (7, 33). Normally, the Verticillium organism enters through root wounds from adjacent soil (33).

Direct transmission of the fungi causing oak wilt and Dutch elm disease occurs through root grafts between healthy and diseased trees (27, 41). This phenomenon of root grafting between adjacent trees of the same species in a stand is quite common and may be of more biological importance than has been thought previously.

The infection court in indirect transmission is a wound into the susceptible tissue, outer sapwood. This wound may or may not be made by the agent of transmission. In oak wilt and Verticillium wilt, existing wounds usually serve as the infection court (30,33). In Dutch elm disease and Cephalosporium wilt, the insect carriers produce the infection-court wound during their feeding habits (12, 41). This latter method indicates a more efficient relationship between the carrier and the disease cycle.

The condition of the wound is an important factor in successful infection. Exposed susceptible tissue, outer sapwood, is necessary for establishment of the disease organism. The freshness of the wound becomes important where the carrier may not produce the wound, i.e. oak wilt (30). When the carrier does make the wound, as the feeding nitch by the elm bark beetle, the microecology of such an infection court may be very important in the resulting infection phenomenon.

Time of year and condition of the host are important factors in successful infection. If the optimum period for production of inoculum coincides with the transmission habits of the carrier, the condition of the host is then the most important factor determining successful infection and colonization of the host by the parasite. When the optimum host condition for infection is present during the period of optimum transmission conditions, the disease cycle continues at a very efficient rate. This is the situation present in the wilt diseases under discussion.

A note of caution is in order at this point. Many artificial inoculation studies in the past have not approached the natural inoculation conditions. For example, the small beetle that flies from the fruiting structure of the disease organism does not carry a million spores in a 10 ml. water suspension with him when he presents himself at the infection court on the healthy tree. In fact, only a relatively small number of spores can be assumed to be adhering to the body of the beetle and unless atmospheric moisture is present, i.e. rain, the moisture conditions within the infection court regulate the amount of water present. This is an extreme example, but it illustrates the need for critical analysis of artificial inoculation experiments in determining the relationship between host condition and successful infection and colonization by the parasite.

Studies on the indirect transmission of oak wilt indicate the optimum period for natural infection to be spring and early summer (15, 29).

This period coincides with the active growth period of the oak tree. In one study, infection by indirect transmission ended during the same week that wound callus growth on oak ceased (30). The application of growth inhibitors to elms that were later artificially inoculated with the Dutch elm disease organism indicated a suppression of disease symptoms (4). The inhibition of growth expressed itself in inhibiting early-wood productions. When the disease organism was reinoculated upon cessation of chemical treatment and resumption of early-wood formation, symptom development was normal. These observations indicate some correlation between early-wood formation (possibly production of large vessels) and optimum infection and colonization of the host by these two wilt organisms.

The optimum colonization of the host by wilt disease organisms is thought to be accomplished by the translocation of spores in the sap stream. Gross observations that indicate discontinuous patterns of fungal induced sapwood discoloration and the discontinuously distributed fungal mycelium in diseased vessels suggest this conclusion (1, 2, 11). Studies on elm indicate a rapid distribution of spores of the different elm wilt disease organisms takes place during the period of active host growth (1). During other seasons, movement was restricted and slower. This translocation of spores in the sap stream is also indicated in oak wilt (45) although doubt has been raised because of the difficulty experienced in finding spores in xylem sections (19). Recent circumstantial evidence substantiates sap stream distribution (6, 21).

The lack of systemic distribution of the Dutch elm disease organism in resistant oriental elms and the apparent tolerance many members of the white oak group have to oak wilt suggest possible physical and chemical barriers to this distribution. In oak wilt, lateral distribution of the organism is slow and limited in members of the white oak group (31). The possible physicochemical and morphological similarities in early-wood xylem tissues of oriental elms and late-wood tissues of susceptible elms has been theorized and is being investigated (21). Purely morphological resistance to elm wilt diseases has been suggested (1). Physicochemical resistance will be discussed later.

The sapwood discoloration symptom present in these wilt diseases has also been used as an indicator of the location of the disease organism (1). This same browning reaction is commonly associated with many types of wounds on woody plants. Many species of bacteria and fungi can be isolated from such localized discolorations (1). Infection is localized and not complete.

The previous paragraphs have established the wilt organism within its host. The host reaction to the disease organism is manifested by two distinct symptoms; the external one of wilting foliage and the internal one of vessel blockage by tyloses and gums.

The leaf symptoms found in these diseases have suggested the presence of a toxin in the disease reaction. This toxin theory has been indicated by *in vitro* studies with these disease organisms (18, 25, 33, 43, 46). Other *in vivo* studies with oak wilt have suggested the opposite to be the case (5, 6). The death of the oak leaves is associated with the plugging of conducting vessels. The basic leaf symptoms in oak wilt seem to arise as a result of both water and nutrient deficiencies (6).

A brief critical analysis of the present use of the word toxin is in order at this point. The classical definition of this term usually includes a chemical, allied to proteins, formed as a specific secretion product in the metabolism of an organism that may produce an injurious effect upon living tissues. At the present, the use of the word toxin has been extended to include any material arising from the parasite or its action upon the host that causes an abnormal reaction in the host (14). This latter definition is too broad for this speaker to accept and therefore, is not used in this discussion.

The internal symptom of vessel blockage by tyloses and gums is characteristic of these woody-plant wilts. Both tyloses and gums are found in elm Verticillium, oak wilt, Dutch elm and Cephalosporium wilt diseased trees (1, 12, 36, 38, 47) but only gums in maples with Verticillium wilt (38).

The phenomenon of tylosis and gum formation is not limited to these disease reactions. A number of hardwoods form such structures normally during the aging of woody tissue (22). The inner sapwood and heartwood of many oak species contain tyloses (44). In pine, some roots and the first year's growth of the cone axis may normally contain tracheids with tyloses (10). Certain abnormal conditions also promote tylosis formation. These include wounding and drought (6, 8). Other indications suggest that tyloses are not readily formed during the period of plant dormancy (6).

A description of the type of tylosis under discussion is in order at this point. This structure is an outgrowth of a living ray or wood parenchyma cell into the lumen of an adjacent vessel. Where pits between these two cells have small apertures, only gums are formed (9).

Two basic theories have been proposed for tylosis formation. The presence of air within the vessels as a cause of tylosis production has been suggested (26). This would result if the continuous sap stream were broken. The other theory implicates decomposition products of wounded cells as playing a decisive role in tylosis formation (24).

An examination of these theories when considering wilt disease reactions is interesting. A number of conditions are indicated which could cause the sap stream to be broken. Fungus mycelium and spores could possibly cause initial stoppage of the flow (6, 29). The oak wilt organism produces a polysaccharide material in vitro which is capable of vessel blockage (6, 43). Studies on wilts of herbaceous plants have suggested initial vessel plugging to be associated with decomposition products from cell walls (23, 34, 40). This could be accomplished by hydrolysis of pectin substances in the middle lamella and primary cell walls by fungal enzymes. This has been theorized for the diseases under discussion when one considers the sapwood discoloration present and the production in vitro of pectin depolymerase by both the oak wilt and Dutch elm disease organisms (3, 20).

The possibility that growth regulators initiate tylosis growth is also present. The fungi responsible for oak wilt and Dutch elm diseases produce growth promoting substances in vitro (3, 20). In the case of oak wilt, methionine may be one of these substances (6). Other studies indicate tylosis formation is stimulated upon application of auxin to roots of oak (42). Tyloses were not produced in maple, but instead "amber plugs" (42). The latter are suggestive of the reaction present in Verticillium wilt of maple (38) and gross "pathological heartwood" appearance in wounded maple tissues (17). A possibility also exists where the basic stimulus for tylosis growth is coupled with hormonal balance in the vessels.

In concluding this discussion on host response, a recent paper by Beckman (4), presents an extremely interesting theory for this tylosis production. He suggests that the physiochemical state of the parenchyma cells is at an active growth state during optimum host-parasite reactions. The primary cell wall is a metabolically active portion of the cell that integrates with the cell protoplasts (32). Mechanical coherence in the cell wall is decreased, but permeability is increased, during growth (37). It is suggested that the constituents of the entire cell, including the primary wall, are in a highly distended, permeable, and reactive state when under the influence of optimum auxin concentrations. It is possible then, that exoenzymes from the parasite could better permeate and have greater effect in cells that are in this highly permeable and reactive condition, than in strongly differentiated cells. This speaker would also like to suggest that the breakage of the sap stream could cause an inbalance in auxin and/or nutrients near the parenchyma cells which are in this highly reactive state. This could initiate reactions within these cells which result in growth and/or production of materials such as gums.

The above paragraphs have been an attempt to briefly discuss the host-parasite interactions in woody-plant wilt diseases. As one can see, there is much to be accomplished in the future in studies on these diseases. Much of the material presented still lies in the realm of theory.

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LIFE HISTORIES OF WESTERN TREE RUSTS IN RELATION TO SURVIVAL AND SPREAD OF THE PARASITE

Wolf G. Ziller

This brief review is based entirely on the species of tree rusts known to occur in British Columbia. The perhaps bold assumption is made that nearly all species of tree rusts indigenous to western North America can be studied and collected in British Columbia. The tree rusts of the west (approximately 60 species) have been lumped into 10 groups, the species of each group representing one distinct type of life history. The data for the life histories were, whenever possible, taken from collections and personal observations rather than from reports in the literature. A diagram will be shown for each group (Figs. 1-10), illustrating the life cycles of members of that group.

Group 1: *Melampsora epitea* Thuem., *Melampsora* spp., *Pucciniastrum* spp., *Uredinopsis* spp., *U. phegopteridis* Arth., *Melampsoridium betulinum* (Fr.) Kleb., *Puccinia coronata* Corda.

Figure 1 represents the life cycle of a newly discovered (5) race of *Melampsora epitea* the aecial state of which causes the hemlock needle rust *Caeoma dubium* C. A. Ludwig. With slight variations the diagram may be considered to represent all western tree rusts which overwinter in the dead leaves of the telial host in the form of teliospores. In the case of many species of *Melampsora*, *Pucciniastrum*, *Melampsoridium*, even *Puccinia coronata*, the rust frequently overwinters in the living buds of the telial host as well, in the form of a diploid mycelium. This mycelium produces uredinia in spring and thus ensures the rust's survival in the absence of an aecial host (e.g. *Melampsora paradoxa* Diet. & Holw. on *Salix* on Vancouver Island.)

In the case of *Uredinopsis*, short-cycling and thus independence of the aecial host is usually accomplished with the thick-walled overwintering amphispores, which can infect the young fern fronds in the spring. Those species of *Uredinopsis* lacking amphispores, like *U. phegopteridis*, depend for their survival entirely on the firs, their aecial hosts.

U. phegopteridis has been collected on both fir and oak fern, but only in localities where the two host plants grow together.

Collections of *U. longimucronata* on the Queen Charlotte Islands, a region noted for its absence of fir, support the theory that amphispores ensure survival to the rust without the need of host-alternation.

Little is known of the life histories of species of *Pucciniastrum*, but, like those of *Melampsoridium betulinum* and *Puccinia coronata*, they probably resemble the *Melampsora* type of life history.

Group 2: Uredinopsis hashiokai Hirats. f. (U. aspera Faull) and U. pteridis Diet. & Holw.

Recent studies (4) have demonstrated that U. hashiokai and U. pteridis represent a new type of life cycle in the tree rusts (Fig. 2). The phase on the telial host, bracken fern, is hardly unusual for species of Uredinopsis, except perhaps for the lack of amphispores. On the aecial hosts, species of Abies, infection by basidiospores takes place at the usual time, in May, and at the usual court of infection, immature needles of fir. The period between infection and appearance of pycnia and aecia is, however, exceptionally long; it also seems to vary significantly according to the species of fir infected: it is much shorter in alpine than in grand fir. Once aecia have fully developed, which takes 4 months in alpine fir and 12 months in grand fir, they continue spore production year after year, interrupted each year only by a period of dormancy from fall until the following spring. The infection does not spread within the needle or into the twig. No new aecia develop once the first crop of aecia begins to sporulate. The infections thus remain localized but become perennial. Most remarkable of all, the normal life span of the host needle is not noticeably shortened by the rust parasitizing it. The parasite causes no hypertrophy or abnormal growth and little or no discoloration of the needle. There is perhaps no better example than this of host tolerance to an obligate parasite.

Since these two rusts do not produce an overwintering diploid mycelium and lack amphispores, they depend on their aecial hosts for survival: the rusts are found only in localities where both alternate hosts, fir and bracken fern, grow together.

The need for artificial spermatization to produce aecia on infected needles in the greenhouse indicates that the two rusts are heterothallic.

Group 3: Milesia spp.

Figure 3 applies only to the life cycle of M. laeviuscula (Diet. & Holw.) Faull, the needle rust of fir and Polypodium (3). Although it is the only species of Milesia known to cause needle rust in the West, it can be assumed that other western species of Milesia have a similar life cycle.

The cycle is not complicated nor very unusual: the diploid mycelium in the overwintering fern fronds assures survival to the parasite and makes it independent of its aecial hosts. This was confirmed by an interesting collection in the field: M. laeviuscula was found to occur on the Queen Charlotte Islands, a region noted for the complete absence of fir.

The life history of M. laeviuscula is noteworthy for the exceptionally long period required for maturation of the aecia. Thus, aeciospore dispersal and infection of Polypodium by aeciospores is delayed until late fall and winter, as shown in the diagram. This is a good example of the parasite's adaptation to our warm coastal climate where the most vigorous growth of Polypodium occurs in late fall.

Field observations and inoculation tests have shown that fall infections of Polypodium do not develop uredinia (nor telia) until the following spring, about four months after inoculation, whereas spring and summer infections develop uredinia three weeks after inoculation (3). It has been shown experimentally that, whereas the fir needles are susceptible to infection only as long as they are immature, basidiospore inoculum is available in the field during the entire summer.

Group 4: Hyalopsora aspidiotus (P. Magn.) P. Magn.

The outstanding criteria of the life cycle of H. aspidiotus (Fig. 4) are the tri-ennial habit in the fir host and the entirely systemic and perennial habit in the fern host. Pycnia develop one, and aecia two years after infection; the infected needles die after their third growing season. On the oak fern the rust becomes systemic and perennial. It overwinters in the rhizomes and produces uredinia and telia on the young fronds in spring. To doubly ensure survival, spread, and independence from the aecial hosts, amphispores are produced in fall, which overwinter on the dead fronds and may infect the young, living fronds in spring. No rust is better equipped for survival on its telial host. Perhaps the haploid phase on fir is becoming obsolete and therefore rare.

It has been possible to confirm experimentally that the rust overwinters in the shizomes of oak fern. Many collections of the rust on fern made at the Queen Charlotte Islands confirm that Hyalopsora aspidiotus can thrive without completing its life cycle on its aecial hosts.

Group 5: Pucciniastrum goeppertianum (Kuehn) Kleb, Chrysomyxa monesis Ziller, C. pirolata Wint.; C. woronini Tranz.; and Gymnosporangium spp.

Figure 5 serves to illustrate the life cycle of the rusts which are annual in the aecial, and perennial and systemic in the telial hosts. It is a relatively heterogeneous group, the members of which would best be considered separately.

The diagram as we see it represents Pucciniastrum goeppertianum, which causes needle rust of fir and broom rust of huckleberries. The telia require more than a year to develop and after they are formed, they overwinter and germinate in spring like other species of Pucciniastrum.

In Chrysomyxa monesis, C. Pirolata, and C. woronini the time of spore dispersal and the period required for spore maturation are the same as in other species of Chrysomyxa. However, their life cycle differs from the normal Chrysomyxa cycle in that the rusts have become systemic: partially systemic and annual in their aecial and totally systemic and perennial in their telial hosts.

In *Pucciniastrum goeppertianum*, as well as in *Chrysomyxa woronini*, the lack of uredinia makes host-alternation obligatory.

The two spruce cone rusts have been causing considerable damage to spruce seed in British Columbia. The systemic and perennial habit of *C. monesis* in plants of *Moneses uniflora* (L.) Gray has been demonstrated.

The life cycle of most species of *Gymnosporangium* is essentially like that of *Chrysomyxa woronini* and will not be further discussed.

Group 6: *Melampsorella caryophyllacearum* Schroet.

This rust (Fig. 6) has become systemic and perennial in both its aecial and telial hosts. It is thus excellently equipped for survival and spread, and would be difficult to control. Fortunately, the aeciospores are of apparently very low virulence, which may explain the scarcity of infections on checkweed in stands heavily infected with the broom rust. The broom rust of spruce, *Peridermium coloradense* (Diet.) A. & K., is closely related to this rust and has once been considered synonymous with it.

In an unpublished experiment sparse infections on *Stellaria media* (L.) Cyr. were obtained with aeciospores of the broom rust of fir, but negative results with the broom rust of spruce as inoculum.

Group 7: *Cronartium* spp.

The life histories of this well known group of rusts (Fig. 7) hardly need be restated, and little, if anything, new can be contributed at the present time.

A number of inoculation experiments with the *C. coleosporioides* Arth. complex have been carried out by the writer, although their taxonomic significance has not been analyzed yet. Consistent and ample infections on native species of *Castilleja* were obtained with *Peridermium stalactiforme* Arth. & Kern and *P. filamentosum* Peck, the latter originating from the Santa Catalina Mountains near Tucson, Arizona. Infections of *Castilleja* with *P. harknessii* Meinecke were either sparse or negative.

Group 8: *Chrysomyxa* spp.

The life history of the non-systemic *Chrysomyxas* (Fig. 8) very much resembles that of the *Milesias* (Fig. 3) discussed previously. It differs from the typical *Milesia* cycle only in the shorter period required for maturation of the aecia and the longer period required for maturation of the uredinia. In both genera, the uredinia and telia form simultaneously in spring from an overwintered diploid mycelium, and members of both genera are known to survive without their aecial hosts.

Two species of *Chrysomyxa* are known to occur on cultivated rhododendrons on Vancouver Island, *C. piperiana* Sacc. & Trott. ex Cummins on the broadleaved *R. macrophyllum* type and *C. ledi rhododendri* (de Bary) Savile on many of the small-leaved exotic species. Neither of the two species have been shown to occur on spruce in British Columbia.

Group 9: *Chrysomyxa weirii* Jacks.

C. weirii is the only microcyclic tree rust occurring in British Columbia. Only teliospores and basidiospores are produced in its life cycle (Fig. 9). The absence of pycnia indicates that the fungus is homothallic. Since spread of the rust can occur by basidiospores only, we may expect that it spreads slowly. Morphologically and biologically the rust resembles the European microcyclic spruce needle rust *C. abietis* Unger, which has larger teliospores and seems to be more destructive than *C. weirii*. The simple life history needs no further comment.

Group 10: *Coleosporium* spp.

The best known representative of this last group of life histories (Fig. 10) is *C. asterum* (Diet.) Syd. The life history of our western form, *Peridermium montanum* Arth. & Kern, has not been demonstrated and might differ slightly from the eastern form.

Again, like *Pucciniastrum epilobii* Otth and many other rusts, species of *Coleosporium* have assumed the semi-perennial and partly systemic habit of overwintering in their telial hosts, which accounts for survival independent of their aecial hosts, the pines. Like in *Cronartium*, infection of the needles occurs in late summer and fall. The aecia sporulate in spring, the telia in late summer and fall.

Aecia in our Victoria collections, as far as it could be determined, were all on needles two years old and older. It seems that the older needles are more susceptible than the young ones, as in the case of *Cronartium ribicola* J. C. Fisch.

Grindelia stricta DC. has been infected with *Peridermium montanum* (unpublished); further experiments are planned.

Discussion

We are now in a better position to discuss and analyze the life histories of our western tree rusts in toto. It is noteworthy that all western tree rusts have perennial plants as their telial as well as aecial hosts. It is therefore not surprising that a large number of the tree rusts, also, have adopted the perennial habit: it certainly increases the parasite's chance for survival and spread.

Usually the perennial rust is at least partially systemic, with the exception of the two perennial but localized needle rusts of fir, *Uredinopsis pteridis* and *U. hashiokai*. Very often the aeciospores of systemic rusts have lost much of their virulence, which reduces the rusts' spread and prevents them from becoming epiphytotic, as for example the systemic spruce cone rusts, and the broom rusts of spruce and fir. Certainly, those which have not lost their aeciospore virulence, like most species of *Cronartium*, belong to the most devastating tree rust parasites.

It is no mere coincidence that nearly all tree rusts have retained the primitive hetero-eu form of life cycle, and that most of them occur on conifers. The phylogenetic basis for this phenomenon has been investigated by H. S. Jackson (1). Although we have a few heter-opsis forms in *Gymnosporangium*, *Chrysomyxa*, and *Pucciniastrum*, and one or two micro- and endo-forms, aut-eu and brachy-forms are lacking entirely among the western tree rusts.

Short-cycling, of course, is not to be confused with autoecism. Short-cycling occurs on the telial hosts of 60 percent of our tree rusts. Short-cycling is by necessity restricted to those species which have either overwintering urediniospores (amphispores), or repeating spores developed from an overwintering mycelium. Short-cycling eliminates the need for an alternate host, although the capacity to infect an alternate host is retained. Short-cycling is of definite advantage for the survival of the parasite.

It is practically impossible to detect the presence of a rust in its dormant, overwintering state prior to fruiting. Therefore, the import and export of plants which are hosts of potentially destructive rusts should be prohibited if the rust is known to overwinter in the host and if the rust does not already occur in the new area.

Susceptibility of conifer needles to infection depends largely on the barrier the cuticle can offer to penetration by the germ tube. It has been shown experimentally (2, p. 186; 3, p. 888) that mature needles of Douglas-fir, western hemlock, and grand fir resist infection to rust. It seems difficult to explain, therefore, why young pine needles should be less susceptible to infection (by *Cronartium ribicola* and *Coleosporium asterum*) than old needles.

I would like to conclude this review with the encouraging observation that nearly all our native tree species can be protected from rust by excluding the alternate hosts from the area surrounding them.

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The Tree Rusts of British Columbia

* = species of unknown life cycles
( ) = species suspected but not known to
attack trees in British Columbia

Chrysomyxa
chiogenis
empetri
ledi var. glandulosi
ledi var. groenlandici
ledi var. ledi
(ledi var. rhododendri)
*(ledi var. vaccinii)
ledicola
monesis
piperiana
pirolata
weirii
*woronini

Coleosporium
asterum
(madiae)
(tussilaginis)

Cronartium
*coleosporioides
comandrae
comptoniae
ribicola

Gymnosporangium
betheli
clavariiforme
clavipes
cornutum
inconspicuum
nelsoni
nidus-avis
nootkatense
tremelloides
tubutatum

Hyalopsora
aspidiotus
*(polypodii)

Melampsora
albertensis
epitea f. spp.
medusae
occidentalis
paradoxa

Melampsorella
caryophyllacearum

Melampsoridium
betulinum

Milesia
*(darkeri)
*(dilatata)
laeviuscula
*(polystichi)
(vogesiaca)

Peridermium
*coloradense
*harknessii
*holwayi
pseudo-balsameum
*stalactiforme

Puccinia
coronata

Pucciniastrum
epilobii
goeppertianum
*(guttulatum)
*(pyrolae)
sparsum
*(vaccinii)

Tranzschelia
(discolor)

Uraecium
*holwayi

Uredinopsis
hashiokai
longimucronata
phegopteridis
pteridis
struthiopteridis

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45 species known to attack conifers
11 species known to attack broadleaf trees
8 species known to attack both conifers
and broadleaf trees
48 species known to attack trees
15 species of unknown life histories
Total species: 59

Forest Biology Laboratory,
Victoria, B. C., Canada.

December 1958.
W. G. Ziller.

Characteristics of the Life Cycles of Western North American Tree Rusts

Diagram No.	Names of rusts	Spore states	Extent of infect.			Duration of infect.				Overwinters as:			Alternate host required
			local	partially systemic	systemic throughout	annual	bi-ennial	tri-ennial	perennial	teliospores	amphispores	mycelium	
1	Uredinopsis spp.	0,I	x			x							+
		II,III	x			x				x	(x)		-
1	U. phegopteridis	0,I	x			x							+
		II,III	x			x				x			+
2	U. hashiokai, U. pteridis	0,I	x						x			x	+
		II,III	x			x				x			+
3	Milesia spp.	0,I	x			x							+
		II,III	x			x						x	-
4	Hyalopsora aspidiotus	0,I	x					x				x	+
		II,III			x				x		x	x	-
1	Pucciniastrum spp.	0,I	x			x							+
		II,III	x	(x)		x			(x)	x		(x)	-
5	P. goeppertiamm	0,I	x			x							+
		III		x					x	x		x	+
6	Melampsorella caryophyllacearum	0,I		x					x			x	+
		II,III			x				x	x		x	-
1	Melampsoridium betulimum	0,I	x			x							+
		II,III	x	(x)		x			(x)	x		(x)	-
7	Cronartium spp.	0,I		x					x			x	+
		II,III	x			x							+
8	Chrysomyxa spp.	0,I	x			x							+
		II,III	x			x						x	-
5	C. monesis, C. pirolata	0,I		x		x							+
		II,III			x				x			x	-
5	C. woronini	0,I		x		x							+
		III			x				x			x	+
9	C. weirii	III	x			x						x	-
10	Coleosporium spp.	0,I	x						x?			x	+
		II,III	x	(x)		x			(x)			(x)	-
1	Melampsora spp.	0,I	x			x							+
		II,III	x	(x)		x			(x)	x		(x)	-
1	Puccinia coronata	0,I	x			x							+
		II,III	x	(x)		x			(x)	x		(x)	-
5	Gymnosporangium spp.	0,I	x			x							+
		III		x					x			x	+

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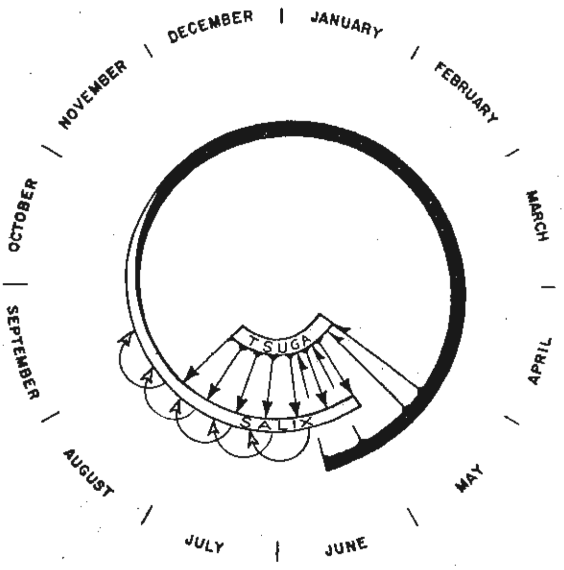
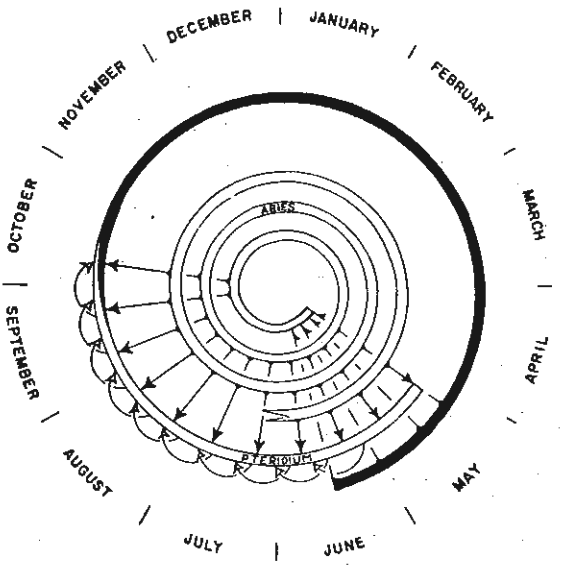
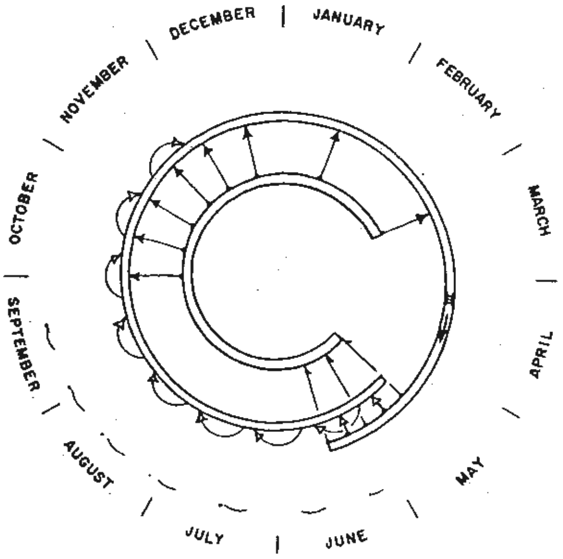
W. G. Ziller



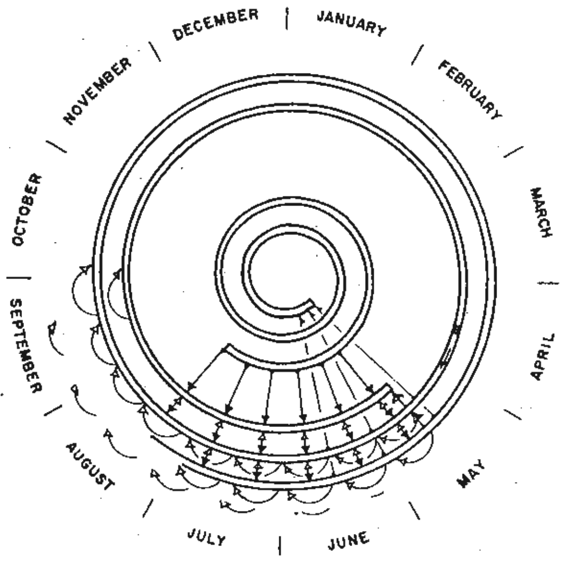
1. *Melampsora epitea* f. sp. *tsugae*



2. *Uredinopsis hashiokai* and *U. pteridis*



3. *Milesia* spp.

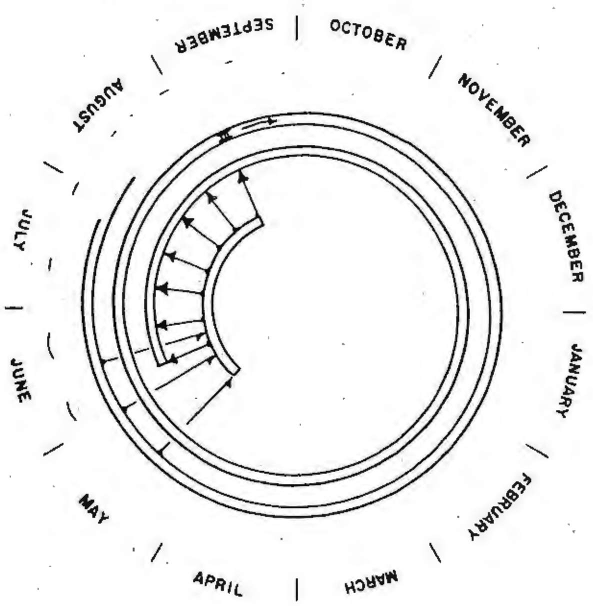


4. *Hyalopsora aspidiotus*

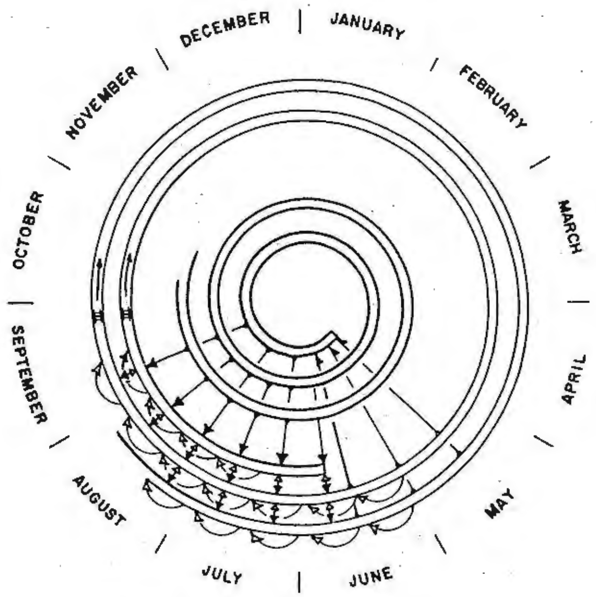
Diagrams of the principal types of life cycle found in Western North American tree rusts.

Legend:

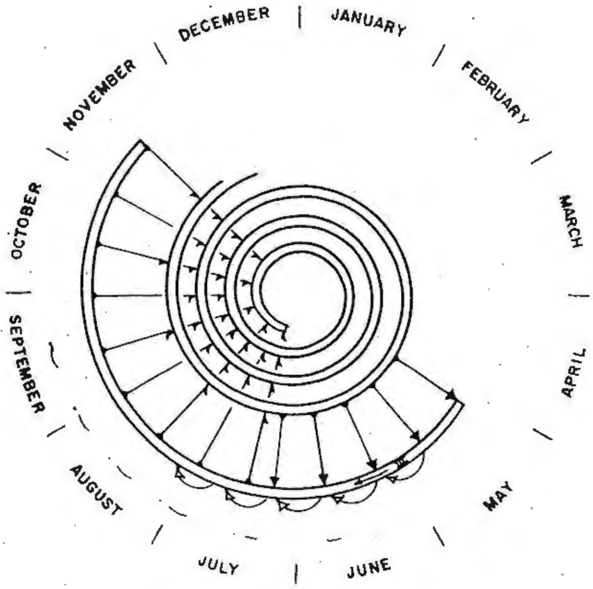
- ⟶ Infection by aeciospores
- ⟶ Infection by urediniospores
- ⟶ Infection by basidiospores
- ▭ Living rust in living host
- ■ Living rust in dead host



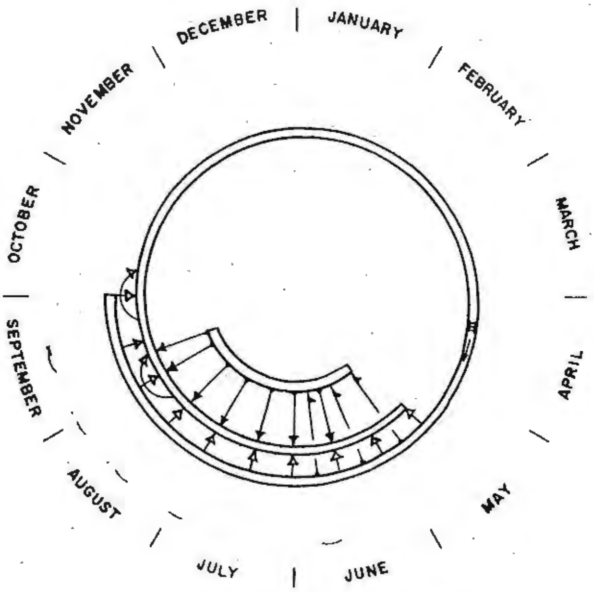
5. *Pucciniastrum goeppertianum*



6. *Melampsorella caryophyllacearum*

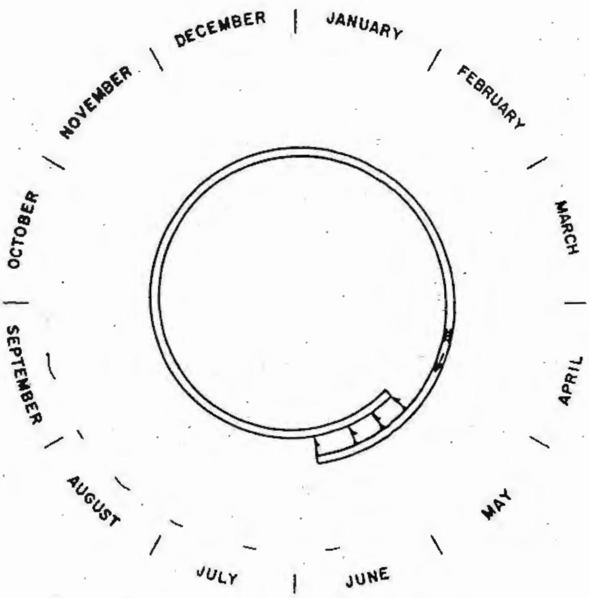


7. *Cronartium* spp.

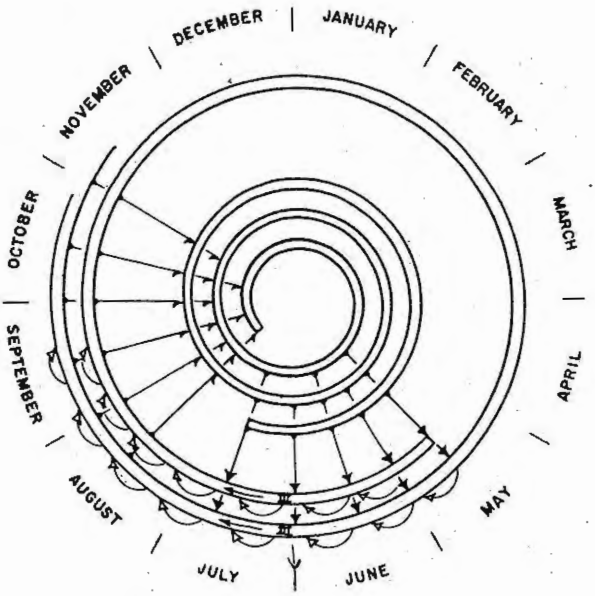


8. *Chrysomyxa* spp.

Diagram of Western tree rusts (cont'd.)



9. *Chrysomyxa weirii*



10. *Coleosporium* spp.

Diagram of Western tree rusts (cont'd.)

THE QUESTION OF HETEROECISM IN SOME WESTERN TREE RUSTS

Willis W. Wagener

In the development of our knowledge of the western tree rusts there was a period, not too many years ago, when some of the most active field specialists in this group considered that heteroecism, or the alternation of generations between hosts, was an unvarying and obligate attribute of all rusts with a Peridermium stage on conifers. In their view, all that was needed to complete our knowledge of the life cycle in these forms was to determine the unknown alternate host connections. This viewpoint was so thoroughly ingrained that strong field indications of direct aecial transfer by rusts, such as in our western gall rusts, were sometimes ignored in favor of relatively improbable clues that the infection might have had its source in some alternate host.

The existence of such a viewpoint is easy to understand. In case after case the presence of an alternate host had been demonstrated and the link established between rust stages that previously had been known only as individual entities. The efficacy of control of obligately heteroecious rusts, such as Cronartium ribicola, by the destruction of hosts for one side of the alternation had been convincingly demonstrated, attesting to the unvaryingly obligate nature of the alternation of generations in such cases.

During the World War I period the concept was shaken by the report by Haack (4), later confirmed under controlled tests by Klebahn (7), both from Germany, of the direct aecial infection of Pinus sylvestris by Peridermium pini. A similar direct aecial transfer from pine to pine of a western gall rust, designated by him at the time as Peridermium harknessii but later regarded as distinct from that species, was reported independently by Meinecke (9) from the United States during the same period. Prior to that time it had been assumed that this rust alternated between pines and oaks in a manner similar to Cronartium cerebrum of the eastern United States. Meinecke did not reject this possibility completely, but, on the basis of the failure of numerous attempts to infect coast live oak with aeciospores from our native western gall rusts and the negative character of much of the field evidence for a connection between the Peridermium and a Cronartium occasionally found on oaks in California, he concluded that at least any heteroecious connection was not an obligate one. This led him to conclude, for the Peridermium, that (quote) "although it is highly probable that the fungus is heteroecious, this heteroecism must be facultative," (end quote). No evidence in support of the opinion was offered.

The validity of this supposition was at once questioned by Fromme (2), who pointed out that heteroecism implied an alternation of generations and held that to be considered facultatively heteroecious a species must be capable of producing both generations on the host of one generation. The demonstrated ability of aeciospores to reinfect the host species on which they were borne he regarded as conclusive proof of autoecism but not of facultative heteroecism. He raised the question as to whether the spores of the Peridermium for which direct aecial infection had been experimentally demonstrated might be morphologically aeciospores but functionally teliospores or urediniospores.

In a second paper four years later (10), Meinecke differentiated between typical *Peridermium harknessii*, forming galls on *Pinus ponderosa*, *P. contorta*, and other pine species at interior locations in California, and a coastal form which he called *Peridermium cerebrum*, attacking Monterey and other coastal pines. It was this second form that had been used in his initial experiment on direct aecial transfer from pine to pine reported in his 1916 paper and not typical *Peridermium harknessii* as the name used in his first paper had implied. In the second paper he reported 32 positive cases of direct aecial infection with the coastal Peridermium, principally from *Pinus radiata* to *P. radiata*, but also from *P. attenuata* to *P. radiata* and from *P. radiata* to *P. muricata*. In addition, there were 45 positive infections with typical *P. harknessii* from *P. ponderosa*, *P. contorta*, and *P. jeffreyi* to *P. radiata*, *P. contorta*, and *P. jeffreyi*. In the paper he states that the aeciospores of *Peridermium harknessii* very readily produce uredinia and telia on *Castilleja miniata*, but with no experimental proof in support of the statement. Apparently he considered that no experimental support was needed for a result coinciding so completely with accepted relationships. He reported that inoculations on *Castilleja foliolosa* failed, perhaps due to the poor condition of the plants used.

On the question of the existence of facultative heteroecism raised by Fromme, Meinecke pointed out that both he and Klebahn had found only typical aecidioid germination of aeciospores of the rusts for which direct aecial infection had been shown, without the slightest suggestion of promycelia or sporidia. He rejected as unsubstantiated Fromme's statement that "a species must be capable of producing both generations on the host of one generation to be considered facultatively heteroecious," pointing out that autoecism cannot be facultative.

In a third paper, "Experiments with repeating pine rusts," published in 1929 (11) Meinecke reported a considerable extension of his basis of successful aecial transfers of the coast gall rust for which, without a validating description, he proposed the name *Peridermium cerebroides*(?), and of *Peridermium harknessii*. Infections were obtained both through wounds and without wounding. Attempts at direct aecial infection with aeciospores of *Peridermium occidentale*, *P. pyriforme*, and what he designated as *P. filamentosum* on Jeffrey pine but which in all probability should more correctly have been called *P. stalactiforme*, all proved unsuccessful. For the aecial material of *P. harknessii* employed in the tests Meinecke stated that its identity was proved by the successful inoculation of plants of *Castilleja* (*miniata?*) with aeciospores from typical galls. He also stated that inoculations of *Castilleja* plants with the same aeciospore material from *Pinus contorta* and *P. sabiniana* that had been used for four groups of successful aecial transfers to pines likewise were successful without exception, whereas the check plants remained uninfected. However, no details of these infection tests on *Castilleja* were included in the paper and no record of them has been found in the files of the former San Francisco Branch. Thus we have no information on how many plants were used, where and when they were obtained, or what precautions were taken to avoid contamination. These may be important considerations in judging the validity of his results.

Now let us turn to the work of another investigator and his conclusions. For a period of 20 years in Washington, D. C., George G. Hedgcock, with the help of several co-workers and of field collectors in the Division of Forest Pathology, carried on infection tests with tree rusts of the United States, among them the two Peridermiums for which Meinecke had demonstrated direct aecial infection from pine to pine. The results of this really tremendous effort for the western rust species included in the tests have never been published. They have not been completely summarized, but for what Hedgcock termed the short-cycle form of *Peridermium harknessii* alone 3,069 pines of 34 species were inoculated, of which 611 developed positive infections. About 10 percent lived to develop aecia, but none of these produced any pycnia. Infection tests with aeciospores of this form were carried out on 154 plants of 7 species of *Castilleja*, *Orthocarpus*, and *Pedicularis* in the Scrophulariaceae and on 114 plants of 24 species of *Quercus* and *Castanea*, all with negative results. Hedgcock did not make clear what experimental evidence of his own he had for the existence of what he termed the long-cycle form of this rust, but his conclusion was that there were two forms, one autoecious and existing only in the aecial stage and the other heteroecious, with the alternate stage on *Castilleja* or other members of the Scrophulariaceae. In an unpublished manuscript left by him he makes no mention of the concept of facultative heteroecism advanced by Meinecke, but it seems apparent that on the basis of his own tests he did not subscribe to it.

Judging from Hedgcock's results, the great bulk of the gall rust population in the West represents the autoecious form. Some unpublished tests support this conclusion. In a Master's thesis submitted at the University of Washington in 1955, James W. Lorbeer (8) reported attempts to infect, under controlled conditions, plants of *Castilleja miniata* from along the Stevens Pass highway in Chelan County, Washington with aeciospores of *Peridermium harknessii* from *Pinus ponderosa* in California. The tests were uniformly negative. The following year plants of *Castilleja hispida* and *Pedicularis bracteosa* from near Lake Wenatchee, Washington were exposed in humidity chambers to *harknessii* aeciospores from *Pinus contorta* with negative results. A similar series of plants of the two species, exposed similarly to aeciospores from *Pinus contorta* of what he designated as *Cronartium filamentosum* but which should more properly be regarded as *Peridermium stalactiforme*, or *Cronartium coleosporioides* f. *stalactiforme* produced uredinia and telia on both exposed species. A second trial with *harknessii* aeciospores from *P. contorta* applied to *Castilleja hispida* remained negative. Infection tests on 8 groups of *C. hispida* plants in the field, using *harknessii* aeciospores from *P. contorta* and covering part of the plants with cellophane after spraying with water, failed to develop infection. Moreover, Lorbeer noted that the numerous wild plants of *C. hispida* and *Pedicularis bracteosa* in the Lake Wenatchee area remained free of the rust through two seasons, although *Peridermium harknessii* galls were very numerous on lodgepole pine there and in lesser numbers on ponderosa pine.

In 1956 I undertook infection tests in California on *Castilleja applegatei* and *C. miniata* with aeciospores from *harknessii* galls on *Pinus ponderosa*, *P. sabiniana*, and *P. contorta*. Part of the test plants were defoliated by a crop of worms before their presence was detected, but results were negative on all 12 remaining plants, whereas tests with *Peridermium stalactiforme* aeciospores in the same enclosure were positive.

In addition to the predominance of the autoecious form of *Peridermium harknessii* in the West, it should be pointed out that this rust in the East, formerly known as the Woodgate rust (Boyce; (1)), is entirely autoecious.

If we accept Hedgcock's conclusion that there are both autoecious and heteroecious forms of *Peridermium harknessii*, how are we to reconcile this viewpoint with Meinecke's reported success (10,11) in infecting both pines and *Castilleja* with the same aeciospore material of this fungus? Without more knowledge of his tests on *Castilleja* and of the number, origin, and time of lifting of the plants that he used, it seems quite possible that what he took for positive infections from aeciospores of *Peridermium harknessii* may actually have been the result of contaminations from an heteroecious rust, most probably from aeciospores from the Peridermium stage of what we must call, in the present state of nomenclature, *Cronartium coleosporioides* f. *stalactiforme* on lodgepole pine. In the Sierra Nevada I have found, as recently noted in a communication in the Plant Disease Reporter (13), that plants of *Castilleja miniata* are likely to develop natural infections in the field if left there beyond early June, even if no rust is known to be present for some distance around. Not all plants become infected, and it is possible that by chance the plants that he exposed to the *harknessii* aeciospores had become contaminated whereas the checks had not. This becomes more plausible when coupled with indications that the number of *Castilleja* plants employed in the tests may have been very small and the checks may have consisted only of one or two plants.

From the nuclear standpoint, also, the existence of both heteroecious and autoecious forms of the rust seems more probable than a condition that would permit facultative heteroecism. The latter would be very difficult to explain cytologically. The late H. S. Jackson, in his very valuable paper "Present evolutionary tendencies and the origin of life cycles in the Uredinales" (6), advanced the hypothesis, from an analysis of steps in the apparent shortening of cycles in the genus Endophyllum, that "these repeating Peridermiums are endo-forms, derived from the haploid generation of species of *Cronartium*, in which the reduction division no longer occurs, and which because of this fact have been further simplified by the loss of the basidium." Whether or not this is the correct deduction the fact remains that the existence of autoecious forms, probably derived from heteroecious forms, is not out of line with what is known for a number of other rusts.

The acceptance of the co-existence of repeating and nonrepeating forms of a rust with what appears superficially to be the same type of aecial stage does not wholly resolve our difficulties, however, as Jackson points out. How are we to distinguish by name a repeating form of *Peridermium harknessii* from the Peridermium stage of the heteroecious form of that fungus? So far, no one appears to have sponsored a proposal on the question, perhaps because an acceptable one would involve much more than satisfying a need with respect to *Peridermium harknessii*.

If we concede that the evidence points to the existence of both long and short-cycle forms of *Peridermium harknessii*, why may we not expect to find similar divergences in some other tree rusts? We apparently have field indications of such a situation in *Peridermium filamentosum*, as indicated by publications of Hawksworth (5), Mielke (12), and myself (13). There is no question as to the presence of the ordinary heteroecious form of this rust in some parts of its range, and particularly in Arizona, but there are also field indications and experimental evidence for the presence of forms that do not appear to alternate between pines and *Castilleja* or other Scrophulariaceae.

Because a number of well-known tree rusts show every evidence of stable adherence to a normal heteroecious pattern in their life cycles, there has perhaps been a tendency among forest pathologists and mycologists to regard the group as a whole as in a more stable condition as regards life cycles than they probably actually are. However, a conspectus of life cycles in the rusts as a whole, such as provided by Jackson (6), reveals an astonishing amount of diversity, particularly through elimination of portions of the life cycle. There appears to be no reason why some diversity along these lines should not also be expected among the western tree rusts.

Other questions related to heteroecism in this group of rusts might be brought into our discussion, such as the significance of the occasional appearance of pycnia in aecial forms that are ordinarily autoecious. An example is the occurrence reported some years ago by Lake Gill (3) of pycnia on galls of the coast form of gall rust (*Peridermium* "cerebroides") for which heteroecism has not yet been demonstrated. Considering their manner of appearance and infrequence it seems probable that such pycnia are functionless and the significance of their occurrence lies only in the indication of the origin of the present autoecious form from an heteroecious progenitor. For the present, however, that hypothesis must remain in the realm of speculation.

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INFECTION REQUIREMENTS OF RUST FUNGI

Robert V. Bega

Because of their obligate relationship to their host, studies of the infection cycle of rust fungi must be broadened to include the period from production and dissemination of the given spore stage to penetration and the subsequent establishment of a food relationship. One important reason for including production and dissemination is that in studying the physiologic processes of the rusts the most direct and clearest information is obtained from that small segment of the life-cycle which proceeds independently of the host--this is that brief period from spore production to penetration. During this brief period the fungus is much more subject to influences of its environment than at any other time in its life cycle. Temperature, humidity, and nutritional conditions of the host are probably the chief of these environmental factors.

Studies of the uredinales in general have received as much attention as any other fungus group. Arthur (1) gave a general account of the rusts up to 1929 covering in particular their biology and this, together with DeBary's works (5), still remains the most thorough treatment. Regardless of the amount of research that has been conducted before and since the times of DeBary and Arthur there still remains a great need for further study, even of the seemingly simple processes of spore germination. To study the physiological processes involved in that portion of the infection cycle from the establishment of a food relationship with the host to the development of the subsequent spore stage we will--and this is especially true in the tree rusts--have to resort either to detached portions of the host or to tissue culture (Bega 2). However, until we acquire additional knowledge of the physiology of the host protoplast we are still limited as to the number of individual factors to which the phenomenon of obligate parasitic and pathogenic relationship can be attributed. So again we are returned to that brief period of the life cycle from spore production to penetration to give us direct information on rust physiology.

Rather than present you with a lengthy review of the literature on studies of the different rust infection cycles, I will present some of the research that is being conducted at Berkeley, California, on one of our most important tree rusts--white pine blister rust. The research is centered around that one important spore stage--the sporidium--which, as we know, is the stage that is airborne from the Ribes host and causes the pine infection. The ability of this spore stage to cause infection and thereby complete the life cycle is dependent largely on favorable microclimatic conditions prevailing during the time between production on ribes and penetration of pine needles. The primary limiting factors for pine infection have been generally defined as temperature and moisture. However, since the sporidium is a somewhat delicate, thin-walled organ, a third factor, time, is highly important and must be considered whether one is studying production from teliospores, dissemination by air currents, or germination and penetration of pine needles.

Various environmental conditions were imposed on the teliospores and sporidium stages of the fungus to determine their effect on germination and longevity. These conditions were broken down into individual factors wherever possible and experimentation carried on under controlled conditions. This was deemed necessary to answer the many questions which arise during field observations. Temperature, humidity, pH, substrate, and time were the factors studied most intensively.

Of particular importance in spread of the disease from ribes to white pines is, of course, the numerical threshold of infection--the number of sporidia which under favorable conditions is necessary to establish infection. The best quantitative method of measuring teliospore germination was based on the ability of a telial column to cast sporidia. Individual columns of known size, age, host, and formation temperature were germinated on water agar in petri dishes and each sporidium produced per column was counted. By using a rotating drum hygrothermograph the capacity and the period of maximum sporidium production were determined (Bega 3).

A representative telial column 1330µ x 105µ, 10 days old, from *R. aureum* kept at 16°C produced 4,930 sporidia. The column started casting sporidia 8½ hours after subjection to 100% humidity and complete exhaustion of the column took 70 hours. This work has shown that teliospore germination and subsequent casting of sporidia is not an instantaneous phenomenon, rather the rate of sporidia casting continues at a given high level for a considerable time period.

Sporidia of *C. ribicola* are formed under conditions of high humidity and proceed to germinate immediately. Although great numbers of sporidia may be produced from a single heavily infected plant, their immediate germination would tend to lessen the number capable of causing infection. However, laboratory studies have shown that sporidia are capable of overcoming this exhaustion by the process of indirect germination. This process is a type of perpetuation resulting in the production of secondary, tertiary, etc. sporidia. Each successive generation is formed at the expense of the preceding one. By a special technique the vegetative production of sporidia has been carried through six generations. Before continuing, two terms used throughout this paper should be defined: Direct germination is used to mean the germination of sporidia by germ tubes and indirect germination is used to mean the production of secondary, tertiary, etc. sporidia. The results presented in this paper will point to the conclusion that indirect germination is a means of vegetative perpetuation and an aid in dispersal and longevity of sporidia and that a spordium, with its ability to germinate either directly or indirectly, can act as an organ of infection or as an organ of sporulation.

During the course of study on germination response of sporidia to various environmental conditions several factors such as type of germination (direct or indirect), vigor of germination (here considered to be a measure of the length of germ tubes), the time interval involved, and the kind and condition of the substrate on which the spores were placed--all had a marked effect on the end result (Bega 4).

In the pH studies germination per se occurred over a range from pH 3.0 to 11.0. Superficially this would mean that sporidia germinate equally well over a wide range of pH.

Equal germination over this wide range is not true as shown by the length of germ tubes measured at these various time intervals and pH units. Here the optimum was obtained at pH 4.0 after 12 and 24 hours and at pH 5.0 after only 3 hours.

Indirect germination was favored by an alkaline substrate whereas direct germination was favored by an acid substrate.

In the time-temperature-pH studies only two units of pH were used because of the results presented above--these two units were pH 4.0 to favor direct germination and pH 6.8 to favor indirect and still include direct germination. Eight different temperatures were studied, 0.5-1°, 5°, 13°, 16°, 20°, 22°, 24°, and 28°C.

At pH 6.8 sporidia were found to germinate from 0.5-1° to 24°C after both 6 and 24 hours. The optimum after 6 hours was at 16°, but after 24 hours the optimum was a range extending from 5° to 20°. At pH 4.0 sporidia germinated from 0.5-1° to 24° after 6 hours and from 0.5-1° to 28° after 24 hours. The optimum after 6 hours was again at 16°. However, after 24 hours it was a range from 5° to 24°C.

Studies on vigor of germination brought out the need for consideration of the time factor--after 6 hours at pH 6.8 and 16°C germ tubes measured only 11.0 microns. However, at the same time and temperature, but at pH 4.0 germ tubes measured a very significant 41.5 microns. At higher temperatures sporidia exhibited greater vigor at pH 4.0 after only 6 hours than at pH 6.8 after 24 hours. Under field conditions the factor of time plays a much more important role than under controlled conditions as regards duration of optimum meteorological situations for production, germination, dispersal, and penetration.

Direct germination was favored at all temperature tested at pH 4.0. Interestingly enough, an increase in temperature resulted in an increase in direct germination except at 16°C where there was a sharp drop, then a steady rise again from 20 to 24°C. At pH 6.8 direct germination was 72% at 5°, dropped to 31% at 16°C, and rose again to 54% at 20°C.

Germination of sporidia on the surface of needles was studied with respect to species of conifer as well as to type and vigor of germination at various temperatures. On needles of Pinus lambertiana sporidia germinated from 0.5-1° to 28°C with no significant difference noted in germination per se between 5° and 24°C. The principal difference was, again, in vigor of germination. On white pine needles vigor was manifest not only by the length of germ tubes, but by the fact that 2-3 germ tubes per spore predominated and appeared to exhibit equal vigor. Very few secondary sporidia were formed on the white pine needles at any temperature. The reason for this may lie in the theory presented here that vigor of germination is a measure of germ tube growth during direct germination and not of indirect germination.

Whatever stimulus the spores are receiving from the host is being utilized in growth of the germ tubes. It may well be that here lies support for DeBary's (5) statement that indirect germination is the result of the spore not being able to find a suitable host.

Germination of sporidia on needles of six species of white pine showed no significant difference in type or vigor of germination. Variation in susceptibility to the rust of different white pine species is evidently not due to a variation in the suitability of the needle surface for germination of sporidia. On white fir, Douglas-fir, and ponderosa pine needles only one germ tube per spore was found to predominate and on white fir indirect germination was 20% of the total germination.

The predominance of direct germination on needles can be somewhat correlated with the results found in the pH tests. Experiments now in progress show that a film of water on the surface of sugar pine needles is acidic and increases in acidity with both washing of the needles with water and with allowing the film to remain on the needle for given periods of time--for example, the initial pH of a film of water on the needles was found to be 5.9 and after washing the needles in three changes of distilled water and then allowing a film to remain on the needles for one hour, the pH was found to be 4.0.

Another very interesting phenomenon was found in the type of germination on a water agar surface adjacent to sugar pine needles and at some distance (50 mm.) away from the needles. Adjacent to the needles sporidia germination was direct--50 mm. from the needles yet in the same petri dish the type of germination was predominantly indirect. Whether this is due to a gaseous or diffusible substance is now under investigation.

The role of indirect germination in nature as regards when and where they are formed is as yet undetermined. It has been shown that secondary and tertiary sporidia form quite abundantly in drops of rain water and conceivably, therefore, could be formed in flight. Pathogenicity of secondary and tertiary sporidia, however, has been proven.

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SOME ANATOMICAL ASPECTS OF DWARF MISTLETOE PARASITISM

John R. Parmeter, Jr.

Job Kuijt recently completed an extensive anatomical study of host-parasite relationships in dwarf mistletoe infection. Much of this as yet unpublished work is of special interest to forest pathologists. This discussion includes a brief consideration of a portion of Kuijt's work with a few comments on its significance to forest pathologists.

Kuijt recognized two basic types of mistletoe infection: (1) localized infection in which mistletoe shoot production is restricted to limited swollen areas (typical cankers), and (2) diffuse infection in which shoot production occurs for some distance along numerous branches without marked swellings. The localized type occurs with all species of dwarf mistletoes. The diffuse type occurs commonly only in certain host-parasite associations including Arceuthobium americanum on lodgepole, ponderosa and Jeffrey pines, A. douglasii on Douglas fir, and A. pusillum on white spruce. On these hosts, large witches brooms, called "isophasic" brooms, result from the diffuse type of infection. Occasionally in such associations as A. campylopodum on ponderosa, sugar, or digger pine, brooms bearing branches showing the diffuse infection pattern are found originating from typical, swollen cankers. An explanation for the occurrence of these types of symptoms and for the nature of localized versus diffuse infection is provided by the work of Kuijt.

Shea, Scharpf, and others have demonstrated that in typical, localized infections, the endophytic system extends only a few centimeters beyond the margin of the canker indicating a very limited capacity for invasion. The occurrence of shoots over several feet of branch in isophasic brooms clearly indicates that the endophytic system is much more extensive. Kuijt found that this extensive endophytic system was not the result of accelerated invasion, but rather it was the result of a peculiar and heretofore undescribed anatomical relationship between the host and the pathogen.

Dissection of the branches of isophasic brooms of douglas fir and lodgepole pine showed that the terminal buds on infected branches were invaded by the cortical strands to within a few cells of the host shoot apex. Since the terminal bud contains all the tissues of the next internode, or "segment" as a year's growth is called by Kuijt, the cortical strands in effect invade the segment when it is only a few millimeters long. When elongation of the host branch occurs, the cortical strands elongate with it. Thus by invading each year only a few millimeters of tissue in the bud, the endophytic system is able to become established over several feet of branch and to keep pace with branch growth. In most of the species associations in which this type of infection occurs, it can be recognized readily by the regular pattern of shoot emergence.

The pattern of shoot emergence varies somewhat with the species of mistletoe and with its associated host, but certain general features of emergence are common to all normal diffuse infections. Essentially, the emergence of shoots follows a definite order with respect to the age of the segment. No shoots appear on the youngest segment, but shoot buds may appear at the node or "girdle" at the base of the segment. Immature shoots with flower initials appear at the base of the second segment. At the bases of older segments, shoots in all stages of development may be found. After 2-3 years, depending on the species, shoots may begin to appear along the segment, as well as at the girdles. This definite sequence in the appearance of shoots along the branch serves to identify all but extremely rare and unusual cases of diffuse infection.

The fact that both localized and diffuse infections of mistletoe species may occur on the same host poses an interesting problem: How do the two types originate and what factors make one type common in some mistletoe-host associations and rare or absent in others? Kuijt has met this problem partially. In the case of *A. campylopodum* on some pines, diffuse infection arises from the invasion and reactivation of dwarf shoots in the area of infection. These shoots may then develop into diffusely infected branches. It is assumed that typical cankers without diffusely infected branches occur when no dwarf shoots are invaded or when the host species has no dwarf shoots. Invasion of dwarf shoots, however, does not explain the origin of diffuse infection in many host species.

According to Kuijt, dwarf shoots do not occur in members of the genera *Abies*, *Picea*, or *Pseudotsuga*. Diffuse infections are, however, common on *Pseudotsuga* and on *Picea glauca*. Thus another means of establishing infection of the buds must occur in these genera. Diffuse infection of *Abies* species is unknown, on the other hand, indicating that the means of diffuse infection of *Pseudotsuga* and *Picea* does not occur in *Abies*.

A number of possible explanations for the observations might be put forth. They are of necessity hypothetical since little information is available to substantiate or to eliminate such hypotheses. One possibility that may have some merit rests on the supposition that mistletoe seeds deposited on or close to terminal buds may germinate and invade such buds, thus establishing diffuse infections. This means of bud infection would require that penetration occur before host elongation. This in turn would suggest that the normal period for penetration and the normal period of host elongation might govern the likelihood of bud invasion.

A. campylopodum can produce diffuse infections by invading dwarf shoots, but on hosts without dwarf shoots diffuse infection is unknown. It seems quite possible that *A. campylopodum* does not produce diffuse infection on *Abies*, *Picea*, and similar genera without dwarf shoots because host penetration and tissue invasion does not occur until after host elongation. *A. douglasii*, *A. pusillum*, and *A. americanum*, on the other hand, might commonly produce diffuse infections because penetration and tissue invasion commonly precede host elongation. This hypothesis might explain the fact that *A. americanum* produces diffuse infections on both lodgepole and ponderosa pines, whereas *A. campylopodum* apparently produces diffuse infections on neither (except by dwarf shoot invasion). Alternative explanations are available.

It is possible that the 3 American mistletoe species commonly producing diffuse infections are capable of invading several inches of new growth and thus capable of invading the bud regardless of host elongation. Since all mistletoes produce localized infections, however, and since such rapid tissue invasion has never been demonstrated, it seems more likely that accelerated invasion does not occur. It is also possible that the _A. campylopodum_ lacks the ability to invade buds or to elongate with host elongation on some hosts. This explanation is, however, contradicted by the occurrence of diffuse infections on hosts where dwarf shoots allow bud invasion. The most logical explanation still seems to be that _A. campylopodum_ in nature is denied access to terminal buds and that this denial results from the removal of terminal buds by host elongation before tissue invasion by the mistletoe has occurred.

This presentation has included only a small portion of Job Kuijt's recent work. Much more of the new and interesting information contained in his thesis could have been presented except for the limitations of time, since much of his work, while botanical in viewpoint, bears directly on pathology and suggests a number of fertile fields for research on dwarf mistletoes.

The purpose of this presentation has been to promote interest and discussion of one of the questions posed by Kuijt's work. The possible hypotheses that might explain the phenomenon of localized versus diffuse infection have by no means been exhausted, and I do not wish to imply that the views expressed here are more than the application of imagination to the purpose of discussion.

Kuijt, Job. Morphological Aspects of Parasitism in the Dwarf Mistletoes, "Arceuthobium". Doctoral Dissertation. Univ. of Calif. 139 pp. 1958.

A REVIEW OF THE PHYSIOLOGY OF THE MISTLETOES[1]

Frank G. Hawksworth

In this review I have included information on the physiology of any members of the Loranthaceae. While no review of the physiology of the mistletoe family has been made, the physiology of certain species or genera has been summarized. Von Tubeuf (1923) discusses the physiology of _Viscum album_ in his voluminous "Monographie der Mistel." The rather meager amount of physiological information on _Arceuthobium_ has been reviewed by Gill (1935) and Kuijt (1955). It should be emphasized that the physiology of the mistletoes and their relationships with their hosts, even for the most-studied species, is poorly understood. While certain aspects of mistletoe physiology have received considerable attention, others have scarcely been touched and this irregularity is, of course, reflected in this review. _Viscum album_ has been by far the most intensively studied mistletoe from the standpoint of physiology and probably more has been written on this one species than on all other mistletoes combined. The reason for this is that it is the most common European species and also because there is considerable interest in it as a pharmaceutical agent. Most of the work on physiology of the mistletoes has been done by pharmacologists. For example, over 200 articles on the pharmaceutical aspects of _Viscum album_ have appeared.

In the 1800's and earlier, _Viscum album_ extracts or powders seemed to be used for treatment of nearly any disorder, although it is now used to a very limited extent in modern medicine. Perhaps it was most widely recommended for treatment of epilepsy and arthritis, but more recent work has centered about its ability in lowering blood pressure and also the possibility of its use in cancer therapy. The high esteem once held for _Viscum album_ is shown by the title of this article written in London in 1720: "A dissertation concerning mistletoe: A most wonderful specific remedy for the cure of convulsive distempers. Calculated for the benefit of the poor as well as the rich and heartily recommended for the common good of mankind." (Colbatch 1720).

There has been relatively little work on the pharmaceutical properties of _Phoradendron_ or the other mistletoes.

THE MISTLETOE FAMILY

The Loranthaceae contains some 30 to 60 genera and 1,000 to 2,000 species. The wide variation in estimates points out the unsettled taxonomic state of the family. At least 14 other higher plant families have parasitic members although the total number of parasitic species in these other families combined is probably fewer than that of the mistletoes.

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[1] This report is by no means a complete review of the subject, but representative articles illustrating the types of work which has been done are discussed.

Parasitism

Essentially all species of the Loranthaceae are parasitic. The only genus in which parasitism has not been demonstrated is Gaiadendron of south and central America. A few genera of the Loranthaceae are root parasites and these are quite different from the typical mistletoes as they begin life as independent soil plants and later become attached to the roots of the host trees.

Yarwood (1956) in recent review of the physiology of obligate parasitism states that the dodders are the only parasitic higher plants that have grown in vitro. Loo (1946) was able to maintain dodder shoots for at least 5 months on a medium made up of Hoagland's mineral nutrient solution, 4 percent sucrose and 0.1 gran/liter yeast extract.

Tubeuf (1912) germinated Viscum album seeds on nutrient agar in sterile flasks; the seeds remained alive for periods up to 4 years, but presumably survived on nutrient contained in the seed and not the agar medium.

Most writers before 1900 or so regarded the relationship between the European mistletoes and their hosts as a form of symbiosis rather than parasitism (Hartig 1874, Bohn 1865, Bonnier 1891) but the more recent authors take the oppostie view (Pitra 1861, Tubeuf 1923). However, the question is more of a matter of degree since there is little doubt that there is translocation of metabolites from the mistletoes to their hosts. This has been demonstrated repeatedly by experiments in which all the host leaves of an infected tree are removed and noting how long the mistletoe leaves can sustain the host (Heinricher 1913, Molisch 1920, Winkler 1913). Although de-leaved plants with mistletoe usually live longer than those without it, the mistletoes are not able to maintain the host indefinitely and the maximum such period reported is about 4 years (Tubeuf 1923). Weir (1916) reported a similar experiment with Arceuthobium americanum on lodgepole pine. He removed all needles from infected and uninfected trees, and all those with mistletoe were still living after 2 years while all uninfected trees were dead.

Van Poeteren (1865) grafted 3 Viscum album plants on a leafless Sorbus aucuparia stock and noticed that, although no leaves were developed by the Sorbus, the parasites grew vigorously and the host stem thickened for 2 years before it died.

Translocation from mistletoe to host is also indicated by observation of Phoradendron on junipers (Phillips 1907, Wagener 1957). In these cases the host plants died following killing of mistletoes by cold. The junipers had lost so much of their foliage that they were being sustained by the mistletoe.

Launay (1950) studied the relative rates of translocation from the host to Viscum album and vice versa by the use of dyes. He concluded that the dyes passed much more readily from the host to the parasite than in the opposite direction, but gave no quantitative information on the rates of spread in each direction.

Effects on Host

The many effects of mistletoes on their hosts are well known (growth reduction, mortality, etc) so these won't be discussed, but there are a few papers on physiological effects which will be noted. Koernicke (1937) noted that Papaya trees infected by Loranthus retained their leaves in the fall for about one month longer than uninfected trees. O'Kelley (1953) reports a similar situation with Phoradendron flavescens on sugar maple in North Carolina, only the period here was 1 to 2 weeks. He also noted that (1) the chlorophyll content of maple leaves on mistletoe-infected branches was about 50 percent greater than for leaves on uninfected branches and (2) that maple buds break dormancy, flower, and leaf out about 1 week earlier on infected than on uninfected branches of this same tree.

In 1955, Nicholson reports for Loranthus on Eucalyptus that a substance is transferred from the parasite to the host that prevents the growth of epicormic shoots on the branch below the mistletoe. I suspect that a chemical influence may also be present in Arceuthobium as infections on a branch some distance from the bole are able to cause stimulation of the growth rate of the infected branch.

One last effect will be noted and this is a report from Hungary (Minev 1951) that no mildew on oaks was found on trees infected by Loranthus europaeus although it occurred on trees without mistletoe.

Germination and Establishment

Germination

As with previous topics, germination in the mistletoes has been most intensively studied for Viscum album.

Wiesner (1879) discovered that light was necessary for germination of Viscum album. Since that time several other mistletoes have been studied and it has generally been found that germination is favored by light. A fairly complete summary of the effects of light on the germination of Loranthaceae was made by Crocker (1936).

Wiesner (1893) states that for Viscum album the minimum intensity for germination was 4 percent of maximum Vienna sunlight (presumably about 400 foot candles) and the optimum was about one-half maximum sunlight (presumably about 5,000 foot candles). Tubeuf (1923) reports that germination was progressively less with increasing time in darkness and 5 weeks or more of darkness completely inhibited germination.

Heinricher (1915) reports that Arceuthobium oxycedri seeds showed 7 percent germination after 3 months in the dark and, hence, retain their viability in the dark much longer than do Viscum album seeds.

Percent germination for Phoradendron flavescens was about 5 times greater in the light than in the dark (Gardner 1921), while that for the Australian Amyema migueli was about twice as great (Coleman 1949).

Wiesner (1897) notes that in nature *Viscum album* seeds undergo a 6-month rest period before germinating, but that several tropical mistletoes germinated within 2 to 5 days. A high proportion of *Arceuthobium vaginatum* seeds in Colorado this summer germinated within 5 days after being expelled from the fruits.

Responses of Radicles

The tropisms of germinating *Viscum album* seeds have been studied by several investigators (Dutrochet 1822, 1837, Pitra 1861, Wiesner 1879) and it was found that they are strongly negatively phototropic. There is also a negatively geotropic response, but this is relatively weak and evident only under low illumination (Wiesner 1879). A thermotropic response in this species has also been claimed (Schnasse 1851).

A similar situation prevails for other species of *Viscum* (Wiesner 1894, Tubeuf 1908). However, McLuckie (1923) reports no geotropism in *Loranthus celastroides*, but that they are strongly negatively phototropic. He also demonstrated that the phototropic response mechanism is located in the tip of the radicle.

Heinricher (1917) reports both negative phototropism and negative geotropism for the radicles of *Arceuthobium oxycedri*.

Establishment

There is little direct evidence on just how the mistletoes penetrate the host tissues. It seems that both mechanical and chemical means are involved and the situation described for an Australian *Loranthus* by McLuckie (1923) might be rather general. He states that penetration of the epidermal layer of the host was principally by mechanical force, but that subsequent development of the haustoria in the host is primarily dependent on chemical action.

The formation of the hold-fast of *Viscum album* has been studied by Thoday (1951) who found that close contact and firm pressure with the exclusion of air are required for its formation. On a smooth surface, such as glass, no hold-fast is formed (Tubeuf 1923). Thoday (1951) also studied the enzymatic action of the initial haustoria of *Viscum album* on filter paper, cambric, and cork. He obtained no conclusive evidence of solvent action on cellulose, but he found definite indications of disintegration of cork. Thoday concluded that the haustoria of the mistletoe had a solvent action on the pectic middle lamella of cork. Thoday (1951) lists 3 factors which enable the haustoria of *Viscum album* to invade the phloem tissues of its host: (1) the solvent action of enzymes secreted by the tip, especially pectase attacking the middle lamella, (2) tissue tensions in the host phloem which tend, as cambial activity proceeds, to widen a gap once formed, and (3) growth in thickness of the strand itself.

According to Gaumann (1950), *Viscum album* on pear represents the only instance in plant pathology in which premunization of the host may occur through a local infection, such as is common in animal pathology. The mistletoe is relatively rare on pear and some varieties are immune due to the defense reactions of the tree (Heinricher 1917a, 1929). However, Paine (1950) was unable to confirm Gaumann's hypothesis. Further work on the relationships between Viscum album and pear trees is reported by Scholl (1957).

PHYSIOLOGY - WATER RELATIONS

Studies of water relations of the mistletoes have been primarily of 2 types, (1) comparative transpiration rates of the parasite and host, and (2) comparative osmotic concentration studies of the parasite and host. The water relations of parasitic plants (including the Loranthaceae) has recently been reviewed by Hartel (1956).

Transpiration

Hartel (1937) showed that in the case of Viscum album on birch that the transpiration rate of the parasite was about 6 times that of the host during July and August. Transpiration by the mistletoe in winter was about one-tenth its rate during the summer.

Vareshi and Pannier (1953) report a study on the transpiration rates of 2 Venzuelan Phoradendrons and their hosts. The transpiration rates for the mistletoes were consistently higher than the hosts in both the wet and dry seasons. The high transpiration rates of the mistletoes was considered to be very detrimental to the host plants, particularly during the dry season.

Wood (1924) found a similar relationship between an Australian Loranthus and its host Acacia. During a 24-hour period the mistletoe transpired 3½ times as much water per unit leaf area as did its host; in some hourly measurements the rate of water loss for the Loranthus was 8 to 9 times that of the host.

Kamerling (1914a, 1914b) reports studies on the comparative rates of drying of twigs of Viscum album and 2 tropical mistletoes and their hosts.

Osmotic Concentration

This phase of mistletoe study has received considerable attention, particularly by Harris and his coworkers (1916, 1918a, 1918b, 1930b, 1930a, 1930b, 1934). MacDougal and Cannon (1910) seem to be the first to state that, in general, parasitic plants require a higher osmotic concentration than their hosts. This hypothesis was confirmed for Viscum album by Arens (1911), Senn (1913), and Hartel (1937). On the average these workers found that the osmotic concentration (based on plasmolytic measurements of tissue in potassium nitrate) of the mistletoe was about 2½ times that of the host.

Harris' osmotic concentration measurements were based on freezing point depressions. Harris & Lawrence (1916) studied 7 Jamaican mistletoes on 19 hosts and found that the osmotic concentration of the mistletoe leaves was generally, but not invariably, higher than that of the host leaves. They also studied secondary parasitism in which one mistletoe was parasitic upon another and it was found that the osmotic concentration was lowest in the primary host, higher in the primary parasite, and highest in the secondary parasite.

Later, Harris (1918, 1930a) studied mistletoes in the Arizona desert and found the same relationship as in Jamaica -- i.e. osmotic concentration generally higher in the parasite than in the host.

Harris, et al. (1930b) suggest that the unusually high osmotic concentration of creosote bush might account for the scarcity of Phoradendron on it. The only instances seen for mistletoe on creosote bush were near a pumping station where soil moisture conditions were unusually favorable. In this case the mistletoe was able to parasitize creosote bush even though the osmotic concentration of the host was higher than that in the mistletoe.

A book by Harris (1934) contains several thousand osmotic measurements of various plant saps including over 300 paired determinations of mistletoes and their hosts. This book merely lists the basic data and no summaries were made. Some of his data on Phoradendron are summarized in Table 1. Phoradendron macrophyllum was from Arizona, but the other two species are from the Southeast part of the United States. Information on the osmotic pressure of the dwarfmistletoes is given in Table 2.

Harris and Valentine (1920) have also shown that tissue fluids of the mistletoes generally have a higher specific electrical conductivity and a higher chloride content than that of the hosts.

Table 1. Comparison of osmotic pressure of three *Phoradendrons* and their hosts (Harris 1934).

Mistletoe	Host		Mistletoe		Difference
	Basis	Osmotic pressure	Basis	Osmotic pressure	
	(no.)	(atm.)	(no.)	(atm.)	(atm.)
P. macrophyllum	68	21.6	80	25.2	+3.6
P. flavescens	21	15.8	34	21.5	+5.7
P. macrotomum	32	17.0	57	24.5	+7.5

Table 2. Comparative osmotic pressure of dwarfmistletoes and their hosts.

Species and host	Locality	Reference	Basis	Osmotic pressure
Arceuthobium douglasii	Utah	Korstian 1924a	?	19.7
on Douglas-fir	"	" "	?	11.8
Arceuthobium douglasii	Utah	Harris 1934	1	19.7
on Douglas-fir	"	" "	1	21.7
Arceuthobium americanum	Utah	Korstian 1924a	?	18.3
on lodgepole pine	"	" "	?	17.0
Arceuthobium cyanocarpum	Colorado	Harris 1934	2	18.0
on *Pinus flexilis*	"	" "	2	17.6
Arceuthobium vaginatum	Utah	Harris 1934	1	23.7
on *Pinus ponderosa*	"	" "	1	20.1
Arceuthobium vaginatum	Arizona	Korstian 1924a	?	17.6
on *Pinus ponderosa*	"	" "		17.1

PHYSIOLOGY - ASH ANALYSES

Comparative studies of ash analyses of Viscum album and its hosts have been relatively popular but little is known for other mistletoes. The earliest found was that by Will and Fresnius in 1844. In most cases twigs of the host and mistletoe were used. Although there is some variation in results by the different workers, the proportion of the various elements is about the same. The proportion of potassium, phosphorus, sulfur, and magnesium is higher in the parasite than the host, but the converse is true for calcium.

A comparison of the amount of various elements in the ash of Viscum album and its host is shown in Tables 3 and 4. Calcium was the most abundant element in the host, but potassium was the predominant element in the mistletoe.

Nicoloff (1923b) measured the ash constituents of Loranthus europaeus on oak and found about the same relationship between the mistletoe and the host as for the Viscum album.

Herbert (1931) in Australia studied an instance of triple parasitism involving 3 species of mistletoe and found that there was consistently more potassium and phosphorus and less silicon and calcium in each parasite than in the preceding host.

For Viscum album there was no consistent relationship between the amount of silicon, sodium, chlorine, manganese, or iron in the mistletoe and the host. It is perhaps significant that these elements are either not required by higher plants or needed only in minute quantities.

Table 3. Ash analyses of Viscum album and its host plants. (Combined results of Erdmann 1855, Will and Fresnius 1844, Nicoloff 1923, Wolf 1923, Grandeau and Bouton 1877, Reinsch 1861, and Councler 1889).

Element	Approximate composition of ash - percent Host plants	 Viscum album
Calcium	67	24
Potassium	9	31
Phosphorus	5	17
Magnesium	5	9
Sulfur	2	4
Manganese	1	1
Sodium	3	4
Silicon	4	3
Others	4	7
Total	100	100

Table 4. Comparison of ash analyses of *Viscum album* and its hosts.

Element	Ratio: $\frac{\text{Mistletoe Ash}}{\text{Host Ash}}$	
	Average	Range
Potassium	3.5	2.1 - 6.8
Phosphorus	3.3	1.7 - 5.5
Sulfur	1.8	0.8 - 3.6
Magnesium	1.7	1.0 - 3.0
Calcium	0.35	0.1 - 0.6

Jadin and Astruc (1912b) found that the arsenic content of the leaves of Viscum album was surprisingly constant while that of its host varied markedly. The ratio of arsenic content between host and mistletoe ranged from 1/5 to 2, but the amount in the mistletoe remained about the same. Jadin and Astruc (1912a) give information on the amount of manganese in Viscum album and its host plants and Hoffman (1943) gives similar data for uranium.

Tubeuf (1923) reports that the proportion of calcium in the ash of Viscum album growing on apple was practically the same whether the trees were growing on "lime-rich" or "lime-poor" soils. However, no mention was made of the calcium content of the trees on the two soil types. Laurent (1900) noted that while Viscum album is not confined to calcareous soils, it is found most abundantly in areas where the soil contains over 1 percent calcium.

Korstian (1924b) in his article on the growth of ponderosa pine in central Idaho states that dwarfmistletoe is not found in the eastern parts of the Payette National Forest, but the parasite is common on the basaltic soils of the western division of this Forest and the nearby Weiser National Forest. He concludes that "there is a suggestion here of an interesting causal relationship between soil type and the local distribution of mistletoe, although the significance and constancy have not been determined."

Photosynthesis

As most of the mistletoes are green plants, the presence of chlorophyll and the ability to manufacture carbohydrates has long been assumed. Luck (1851) demonstrated starch synthesis in Viscum album leaves and in 1861, Reinsch isolated chlorophyll from the same species. In 1943, Freeland studied Phoradendron flavescens and showed that both chlorophylls a and b are present. He also found that photosynthesis occurs and he considered this as the first experimental demonstration of the process in the mistletoes.

Heinricher (1923) noted chloroplast-like bodies in the haustoria of Arceuthobium oxycedri and made the questionable assumption that they were green-colored leucoplasts rather than chloroplasts. In any case the photosynthetic activity of the haustoria is presumably limited because of the scarcity of light (Gill 1935).

BIOCHEMISTRY

As will be evident from the following discussion, the biochemistry of the mistletoes is little known. Most of the articles cited are reports on one or a few compounds and in most cases only qualitative information is given. The most comprehensive accounts are those on Viscum album by Wester (1921), Einleger (1924) and a series of papers by Obata (1941-1944). For this presentation, biochemistry will be discussed in 5 categories:

1. Carbohydrates
2. Plant Acids
3. Nitrogen and nitrogen metabolism
4. Phosphorus and phosphorus metabolism
5. Secondary plant products

Carbohydrates

Sugars

The only quantitative report found on the sugar content of any mistletoes was that for the Javanese *Dendrophthoe pentandra* (Schoorl 1929). Here glucose was essentially the only sugar and this totaled about 6 percent of the fresh weight of the fruits. Glucose was also found in *Viscum album* (Einleger 1923). Free fructose has not been listed, but sucrose was detected in *Viscum album* and *Loranthus europaeus* (Beguin 1931, Einleger 1923). Desantis and Lynn (1937) report 4.5 percent reducing sugars in *Phoradendron flavescens* but these were not identified.

The ascorbic acid (vitamin C) content of *Viscum album* berries has been reported as 750 mg. per 100 grams fresh weight (Rikovski and Besaric 1949). This is equal to about 15 times the vitamin C content of oranges.

Sugars which occur in combined forms reported for various mistletoes are galactose, arabinose, and rhamnose.

Starch

Starch is of very frequent occurrence in the mistletoes and nearly every report indicates substantial quantities of it. In general, the amount of starch in the mistletoes is greater than in adjacent host tissues. There is disagreement as to how the greater starch concentration in the parasite develops as Brittlebank (1924) suggested that this is due to an accumulation of carbohydrates from the host, but Kerr (1924) believes that this is due to a higher rate of carbohydrate metabolism of the mistletoe. In any case, the common occurrence of starch in the mistletoes seems to indicate that their carbohydrate supply is plentiful.

Sugar Alcohols

Sugar alcohols were first reported by Tanret (1907) who isolated "inositol" and "racemic inositol" from *Viscum album* berries. An intensive study of sugar alcohols in *Viscum album* and its hosts was reported by Plouvier (1953). He isolated pinitol (D-inositol) from the parasite on 14 species of dicotyledonos trees, but, as he found the compound in only 1 of the host trees (Black locust), he assumed that pinitol was formed by the mistletoe. Quebrachitol (L-inositol) was detected in *Viscum album* on 3 species of maple and on *Fraxinus*. Quebrachitol was abundant in the three maples so it may have passed from the host to the parasite, but none was found in *Fraxinus* so here it was assumed to have been produced by the mistletoe. For quercitol on oak and mannitol on 3 species of ash, the amount of the compound in the mistletoe and in the host was about the same. However, Plouvier detected no sorbitol in *Viscum album* growing on *Crataegus* although this compound was present in the host.

Glycosides

Plouvier (1953) also examined the glycosides of *Viscum album* and seven host species. He found a number of glycosides in the host trees, but in only one case was the compound also present in the mistletoe. This was syringoside, which occurred in *Fraxinus* and also to a limited extent in the stems, but not the leaves, of the mistletoe parasitic upon it. Plouvier concluded from this that the absorption tissues of the parasite are not impermeable to these glycosides, but that their general scarcity in the mistletoe is due to their immediate utilization.

A yellow glycoside, quercitrin, has been isolated from the leaves of two tropical species of *Loranthus* by Wester (1921). McNair (1941) notes that no cyanogenetic glucosides have been found in the Loranthaceae or any other parasitic higher plants.

Plant Acids

No studies of the plant acids of the mistletoes were seen, but some mention is made of the calcium crystals of oxalic and malic acids. A single record of calcium malate was found (in *Arceuthobium oxycedri* -- Livon 1912), but there are many references on calcium oxalate in various mistletoes. Detailed studies on the structure and forms of calcium oxalate crystals found in *Viscum album* are given by Gerard (1882) and Walter-Levy and Strauss (1954).

Nitrogen and Nitrogen Metabolism

The total nitrogen in the leaves of *Viscum album* and *Loranthus europaeus* was determined by Nicoloff (1923a, 1923b). *Viscum album* had about 6 times as much nitrogen as its host and the *Loranthus* about twice as much.

Lutz (1908, 1912a, 1912b) measured the amount of nitrate and total nitrogen in several chlorophyll-bearing and chlorophyll-less parasitic higher plants. He concluded that parasitic plants which contain chlorophyll (in this case *Viscum album* and *Arceuthobium oxycedri*) have low nitrate levels, but high total nitrogen, while the reverse was true for the chlorophyll-less parasitic plants.

Obata (1941a) studied the nitrogenous compounds in a Japanese form of *Viscum album* and found arginine but no free amino acids.

There have been several European reports on the protein content of *Viscum album* and these seem to justify the widespread use of this species as winter livestock feed. Grandeau and Bouton (1877) report maximum protein values (dry weight basis) of 20.4 percent in the stems and 25.7 percent in the leaves. Reports of protein in *Phoradendron* leaves range from 9.8 percent for an unidentified species in California (Anon. 1915) to 15.1 percent for the eastern *P. flavescens* (Desantis and Lynn 1937).

Cutter (1955) conducted an anatomical study of a number of parasitic phanerogams including two mistletoes: *Phoradendron flavescens* and an

African species *Loranthus globiferus*. She found evidence suggesting that nitrogen may be a limiting factor in the physiology of these parasites. This is based in part on the fact that mechanical tissue (stonecells, thick-walled parenchyma cells, lignified cell walls) is considerably more common in parasitic and saprophytic plants than in autotrophic plants. Burkholder and McVeigh (1940) studied the nitrogen metabolism of the corn plant and found that nitrogen deficiency was associated with xeromorphic characters such as thick cell walls, sclerenchymatous tissue, etc. These authors indicate that when a considerable amount of available nitrogen is present, the carbohydrates are used up in protein sythesis and hence are not available for thickening and lignification of cell walls. On this basis Cutter (1955) suggests that the prevalence of mechanical tissues in parasitic plants indicates that their carbohydrate supply is adequate and that nitrogen may be limiting. Perhaps more significant is Burkholder and McVeigh's (1940) finding that in corn plants the apical regions developed in direct proportion to the nitrogen supply. Cutter found that both of the mistletoes studied had unusually small apices and she considered this as further evidence of the importance of nitrogen.

Alkaloids

The first report of alkoloids in the mistletoes was that by LePrince (1907) who found tyramine ($C_8H_{11}N$) in *Viscum album*. This same alkaloid was found in *Phoradendron flavescens*, *P. villosum*, and *P. californicum*, but not in *P. juniperinum*, *P. bolleanum*, *Arceuthobium campylopodum* or *A. vaginatum* (Crawford and Watanabe 1916). Other workers report no alkaloids in *Phoradendron flavescens* (Desantis and Lynn 1937). Such discrepancies are discussed by McNair (1941) who suggests that they may be explained by different concentrations of electrolytes, particularly nitrates, in the host trees. He supposes that alkaloids may be formed only under high nitrate concentrations. Information on alkaloids in tropical mistletoes is given by Trautner (1952), Wehmer (1935), and Chatin (1897).

Miscellaneous Nitrogenous Substances

Choline ($C_5H_{15}NO_2$) was found in the leaves and fruits of *Viscum album* and *Loranthus europaeus* (Einleger 1924) and has also been reported in *Phoradendron flavescens* (Desantis and Lynn 1937). Choline is one of the substances which cause lowering of the blood pressure. Recently histamine ($C_5H_9N_3$), which also lowers blood pressure, has been found in *Viscum album* (Sajner and Veris 1957).

Phosphorus and Phosphorus Metabolism

The proportionately high phosphorus content of the ash of *Viscum album* (over 3 times that of the host) has already been mentioned.

The phosphorus metabolism of *Viscum album* was studied by Michel-Durand (1934) who measured the amount of the different forms of phosphorus at 6 dates from May to September. He found that lipid phosphorus remained about the same during the period, phytic and mineral phosphorus decreased markedly as the season progressed and organic phosphorus increased reciprocally with the decrease in phytic and mineral phosphorus. Michel-Durand concluded that the high phosphorus levels of Viscum album make it a choice plant for the study of phosphorus metabolism.

Secondary Plant Products

Lipids

Fatty acids have been studied primarily in Viscum album and palmitic is the principal fatty acid in this species and in Loranthus europaeus (Einleger 1923). Seven other fatty acids have been found in Viscum album: myristic, stearic, arachidic, cerotic, oleic, linoleic, and linolenic. (Braunhauser 1926, Einleger 1924, Obata 1941a). Einleger (1923) notes a paraffin $C_{30}H_{62}$ and a wax alcohol ("Loranthylalcohol") $C_{24}H_{50}O$ in Loranthus europaeus. This wax alcohol has also been isolated from Viscum album as has been ceryl alcohol and cetyl alcohol (Braunhauser 1926, Einleger 1924).

Essential Oils

Oleanoleic acid ($C_{30}H_{48}O_3$) is reported to comprise 1 to 2 percent of Viscum album leaves (Winterstein and Hamerlee 1931, Obata 1941). Other essential oils found in Viscum album are beta-amyrin and lupeol (Bauer and Gerloff 1936, Obata 1941a, Barton and Jones 1944, Meyer and Jeger 1948).

Anstee et al. (1952) record betulic acid in Nuytsia floribunda, a terrestrial member of the Loranthaceae from Australia.

Tannins

Tannins seem to be common in the Loranthaceae but little quantitative information on the subject is available. Desantis and Lynn report 3.9 percent tannin in Phoradendron flavescens leaves. Although in most cases the type of tannin is not identified apparently both gallotannins ("blue tannin") and phlobotannins ("green tannin") are found in the mistletoe family.

There have been several reports of tannin in Arceuthobium (Datta 1954, Peirce 1905, Thoday and Johnson 1930).

Rubber

The Loranthaceae is one of several families which contain rubber-bearing species. In general, the amount of rubber is very small although in one instance mistletoe-rubber has been used commercially. This apparently short-lived operation existed in Venzuela in the early 1900's and produced about 100 tons of rubber annually from several species of mistletoe (Warburg 1905).

There is little information on the amount of rubber in the mistletoes, but that of Viscum album (whole plant) is about 1.5 percent (Fernandez 1947).

Carotenoids

There is little information on the carotenoids of the mistletoes. Wester (1921) reports a "considerable amount" of xanthophyll in *Viscum album*. Strain (1935) found beta-carotene but no alpha-carotene in the leaves of *Phorandendron villosum* in California.

Viscin

A mucilagenous substance called viscin occurs in the fruits of most, if not all, species of mistletoe. This viscin serves as an adhesive to attach the seed to the host and also presumably aids germination in some species by providing better moisture conditions.

Detailed studies of the viscin of *Viscum album* have been made by Tomann (1926) and Mangenot et al. (1948). They report two layers: an inner pectic-viscin layer and an outer cellulose-viscin layer. Tomann believed that this was an adaptation to the dissemination of this species by birds as in the passage of the seeds through the birds only the outer cellulose-viscin layer is digested and the inner pectic-viscin layer surrounding the seed remains essentially intact.

PHYSIOLOGY - ANTIBIOTIC ACTIVITY

As is customary in modern plant studies, tests on the anti-biotic activity of the mistletoes have been made. The results indicate that aqueous extracts of *Viscum album* are ineffective *in vitro* to *Staphylococcus aureus* or *Escherichia coli* (Osborne 1943). Aqueous extracts of the same mistletoe stimulated the growth of a yeast and a species of *Aspergillus* in culture tests (Hueber 1938).

SUMMARY AND CONCLUSIONS

Some of this foregoing information may give us clues to the physiology of the parasitism of the mistletoes, but much of it refers to one or a few compounds and such information cannot be evaluated until the physiology of the mistletoes and their hosts is much better understood.

The work by Harris and his coworkers shows conclusively that the osmotic concentration of the mistletoes is generally higher than that of the hosts. Although practically nothing is known of the osmotic concentration of the dwarfmistletoes and their hosts, I suspect that this may be an important factor in the distribution of *Arceuthobium*. At least in the case of dwarfmistletoe on ponderosa pine in the Southwest, I feel that some of the irregularities in distribution can be logically explained on the basis of comparative osmotic concentrations of the parasite and its host.

The information on ash analyses show that the mistletoes are very selective; for example, they contain over 3 times as much phosphorus and potassium as the host tree but only about 1/3 as much calcium. The fact that the mistletoes are selective indicates to me that the possibilities of chemical control are good. The significance of the low calcium levels in the mistletoes is not known,[2] but it is of interest that even with these low concentrations that calcium oxalate crystals are commonly found. This would seem to suggest that even the small amounts of calcium present are in excess of the needs of the parasite.

As the mistletoes have not yet been grown <u>in vitro</u> the limiting factors in their physiology have not been determined. However, some speculation along this line might be warranted on the basis of the scanty information available.

Some workers (Lunay 1950) have suggested that the water economy of the mistletoes is the limiting factor in their physiology and cite as evidence the common occurrence of xerophytic features in the leaves of many species. While the water use of the mistletoe is of course restricted to what the host can supply, that the parasite can effectively compete for water with that portion of the host distal to the point of attachment, is evidenced by the progressive decline and frequent death of this part of the host. Although xerophytic features are common in the mistletoes, the few studies made show that their transpiration rates are high and in most cases higher than the hosts. So perhaps water economy is not the limiting factor in the physiology of the mistletoes.

Another factor which has been suggested as limiting is the carbohydrate supply. However, the abundant accumulation of starch in the mistletoes, even in those forms such as <u>Arceuthobium</u> which are presumably able to manufacture only a small portion of their carbohydrates, would seem to indicate that this is not the case.

Anatomical evidence cited by Cutter (1955) also suggests that the carbohydrate supply of these plants is adequate, but that nitrogen may be limiting. This is based on the common occurrence of mechanical tissues in the mistletoes (which is interpreted as indicating high carbohydrate levels). Also, Cutter found that the mistletoes had unusually small shoot apices and, at least for the corn plant, this is correlated with nitrogen deficiency. The high nitrogen content of <u>Viscum album</u> (over 6 times that of the host) further suggests that nitrogen may be of unusual importance in the physiology of the mistletoes.

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[2] Dr. J. R. Parmeter suggested that this might be associated with the reduction of roots in the mistletoes. In the autotrophic plants, calcium deficiency is evidenced first in the root system.

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SOME STUDIES OF MYCORRHIZAE ON WESTERN PINES BASED ON FIELD PLANTATIONS

Ernest Wright

Introduction

Perhaps the title of this paper would be more exact if it were entitled, "Some Inconclusive Studies of Mycorrhizae on Western Pines" because the more I study this problem the more inadequate I feel my efforts have been. No subject has so completely captured the attention of foresters and botanists alike as the development of mycorrhizae on the roots of pines and other forest species. Those of you who are acquainted with the literature will agree that references to mycorrhizae are extremely voluminous. In fact there are several texts dealing only with this subject. In these reports, there has been little or no mention made of the influence of the size of mycorrhizal seedlings as compared to those without mycorrhizae as related to field survival. This is a seemly vital omission since seedlings of the same age with mycorrhizae generally have a larger caliper and are better developed than those without mycorrhizae. They have, therefore, a somewhat better chance of survival because of their superior size.

The symbiosis theory is now more firmly established than in the days of Frank. There are, however, still prominent supporters of Hartig's theory that mycorrhizae are fungi parasitic on the host roots. In later years even Frank thought that mycorrhizae are finally consumed by the higher plants.

The data in the present paper are not concerned with either the identity or the function of mycorrhizae but rather with the occurrence and appearance of mycorrhizae based on the survival and development of seedlings in field plantations. No studies are reported here on endotrophic mycorrhizae, and only ectotrophic or external mycorrhizae have been considered. The pine seedlings examined have shown mainly two kinds of actotrophic mycorrhizae: black and white mycorrhizae. Occasional gray mycorrhizae occur on one- and two-year-old seedlings, but no brightly colored ones have been observed.

Methods and Procedures

The method which has been adopted for the study of mycorrhizae in the field is based on microscopic examination of the roots of representative seedlings before they are planted in the field and after they have grown for different periods of time as transplants. In some instances this may have the disadvantage of destroying the transplants for future study. Furthermore, definite identification of the mycorrhizal fungi is difficult by this method unless it can be supported by cultural isolations, which are usually unsuccessful.

After the seedlings are lifted from the soil for examination, the roots are washed carefully to clean them up for observation under a binocular microscope of 25 to 60 power magnification and an occasional examination under a high-power microscope of 1000 or more magnification. Lateral roots are first cut from the main root and examined individually for mycorrhizae. At the same time the depth at which the laterals occur and their relative length are recorded. The seedlings examined are selected at random from a number of plants growing under similar conditions and are considered as representative for each particular test. Usually only five seedlings were thus critically examined in each test reported, supported by occasional less thorough examinations.

The data recorded for the seedlings examined are top height, the extent and spread of the roots, and ratio of the roots to the tops on an oven dry weight basis. The presence of ectotrophic mycorrhizae on the lateral roots, their depth, type, and number are determined. The determination of abundance of mycorrhizae presents a problem. When they are single or digitlike such as black mycorrhizae generally are, the problem is not very complicated. However, when coralloid or clustered mycorrhizae are encountered, the problem becomes quite complicated. For example, figure 1 shows typical black mycorrhizae with numerous strands of mycelium extending in all directions. Such mycorrhizae can be accurately counted under a binocular microscope. In figure 2 simple white mycorrhizae are shown which also are easily counted. In figure 3, however, mycorrhizae are of the coralloid-type, some of which have a definite Hartig net while others do not have. How are these to be counted? Are they all to be counted as mycorrhizae, or only those coralloid formations which have the so-called Hartig net? In this study it has been assumed that the coralloid formations without mycelium have not developed full mycorrhizal capacity yet and are, therefore, not counted.

There is also a problem in counting mycorrhizae in clusters. Is each projecting short root enveloped to be counted as a mycorrhizae, or are only the mycorrhizal clusters to be counted? The latter procedure has been chosen. Also, in the data which will be presented the gray mycorrhizae, have for the time being, been classed with the white mycorrhizae because of their similarity in appearance.

Field Tests on Survival of Mycorrhizal and Nonmycorrhizal Stock

Table 1 shows the mortality of equal size but smaller than normal mycorrhizal and nonmycorrhizal stock of 2-0 ponderosa pine. In this South Lava Butte plantation on the Deschutes National Forest of Oregon, there were 1,000 seedlings planted in 10 rows of 100 seedlings with mycorrhizae alternating with 100 nonmycorrhizal stock. At the end of the first growing season there was a significantly better survival of the mycorrhizal stock. However, in the East Lava Butte plantation there was no significant difference in survival of mycorrhizal and nonmycorrhizal seedlings due to competition with bunchgrass (Idaho fescue). Significant differences between field plantations, therefore, are best obtained when the planting site is not complicated by factors other than the presence or lack of mycorrhizae. At least that has been my experience.

Table 2 data present the mortality of field plantations of mycorrhizal and nonmycorrhizal stock of unequal size. Here the mycorrhizal stock was originally considerably larger than the seedlings without mycorrhizae. There was a significant difference favoring the survival of the mycorrhizal stock. However, as has been stated, this is not considered a fair comparison because of differences in size and caliper of the mycorrhizal stock. It is an interesting comparison, however, since this plantation has been observed for a period of seven years, and the original advantage in size of the seedlings with mycorrhizae still persisted.

These are considered valid tests since the seedlings were all planted by Forest Service field crews and were not given any special attention at any time. The type and kind of mycorrhizae present on the stock before planting was determined by examination of representative seedlings as they were taken from the nursery seedbeds. White mycorrhizae were found to predominate, but no record is available on the proportion of black mycorrhizae to the white mycorrhizae. On the basis of a relatively few examinations made in the field at the end of the first growing season, it was found that the white mycorrhizae still predominated.

The Effect of Shade on Mycorrhizae Formations

Additional data which have been accumulated since 1957 while working for the Oregon Forest Lands Research Center at Corvallis will now be presented. These tests are based upon seedlings taken from several field plots also in central Oregon in the vicinity of Bend. The data presented are averaged counts. In these tests the stock was not transplanted, but originated from direct seeding in the field protected by fencing. These studies were initiated to determine whether there is any consistent difference in the kind and the occurrence of mycorrhizae on the roots of shaded pine seedlings as compared to unshaded plants. All observations were made on two-year-old seedlings of ponderosa and lodgepole pine.

Table 3 shows that white mycorrhizae predominated over the black mycorrhizae, especially on seedlings in the shaded plots. For unshaded seedlings black mycorrhizae increased proportionally, but white mycorrhizae were still more numerous. In table 4 the 2-0 ponderosa pine seedlings from Kiwa Springs in partially shaded plots showed that black mycorrhizae dominated about 5:1 over white mycorrhizae. Generally black mycorrhizae occurred at a relatively shallow depth, about 80 mm, but there were usually a few of the black kind also at greater depths than the white mycorrhizae. This was not a consistent occurrence however. In table 5 averages are given for two-year-old ponderosa and lodgepole pine dug in March at the Tumalo Reservoir site. White mycorrhizae dominated for both species in both full and partial shade, although it can be said that the domination was less distinct in partial shade. It can also be stated that the depth of the mycorrhizae was in general greater on the partially shaded seedlings. The root length of the seedlings in the partially shaded plots was somewhat longer than on those seedlings in the fully shaded plots. The data from seedlings taken from the Sand Springs plot are presented in table 6.

Table 7 summarizes the data for all soils and all plots and shows a consistent trend throughout. An unavoidable feature that further complicates the study of mycorrhizae is that the roots of unshaded seedlings (#11) are generally much differently developed than are those of shaded seedlings (#12). How then can one evaluate the importance of mycorrhizae when the seedlings have variations in root development as well? This is shown in figures 4 and 5. In other words, is the type of root system or the mycorrhizae the more important in the development and survival of the seedling?

Tentative Conclusions

It would be rash indeed to draw definite conclusions from the data presented. However, it can be stated tentatively, for ponderosa and lodgepole pine seedlings, that white mycorrhizae usually predominate over black mycorrhizae when the seedlings are grown in full or partial shade. When they grow unshaded, black mycorrhizae become more numerous and may even occasionally predominate over white mycorrhizae. As to the function and importance of the two types of mycorrhizae, little can be said at this time. Perhaps there is no difference. Further studies are needed to determine this, and these should include controlled pure culture inoculation tests.

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Mortality* of Small 2-0 Ponderosa Pine, 1952

After	Mycorrhizae			Remarks
	Few	Abundant	Significance	
Months	%**	%**		
1½	18.2	7.0	HS*	South Lava Butte,
2½	31.0	17.4	HS	cut-over,
5	64.2	47.2	S	good site.
1½	31.2	23.8	NS	East Lava Butte,
5	70.8	68.2	NS	bunchgrass, poor site.

*HS, Highly significant; S, Significant; NS, Not significant.
**Based on 1000 machine-planted stock, each location.

Mortality of Unequal Size 2-0 Ponderosa Pine
1951 - 1957

After	Mycorrhizae				Remarks
	Few		Abundant		
	Seedling caliper	Mortality*	Seedling caliper	Mortality*	
Years	Mm	%	Mm	%	
½	2	17	4	4	Lava Butte, cut-over,
7	24	44	40	10	good site.

*Based on 500 hand-planted seedlings in alternate rows of 50 each.

Tumalo Reservoir Plot* - 1957

Seedlings	Root length	Top height	Mycorrhizae				Remarks
			Black		White		
			No.	Depth	No.	Depth	
Basis	Mm	Mm		Mm		Mm	
Ponderosa pine							
5	159	60	9	42	22	94	Shade
5	215	58	12	89	31	104	½ shade
Lodgepole pine							
5	137	40	1	80?	31	64	Shade
5	164	38	14	87	27	106	½ shade

*Sandy loam with clay loam subsoil.

Sand Springs Plot* - 1957

Seedlings	Root length	Top height	Mycorrhizae				Remarks
			Black		White		
			No.	Depth	No.	Depth	
Basis	Mm	Mm		Mm		Mm	
Ponderosa pine							
8	155	67	4	73	28	86	Shade
8	195	43	20	98	17	108	No shade
Lodgepole pine							
5	127	47	0	0	73	50	Shade
5	166	40	10	109	46	81	No shade

*Recent pumice soil, pH 6.1 - 6.6

Summit Stage Plot* - 1958

Seedlings	Root length	Top height	Mycorrhizae				Remarks
			Black		White		
			No.	Depth	No.	Depth	
Basis	Mm	Mm		Mm		Mm	
Ponderosa pine							
5	195	73	21	101	35	90	Shade
5	282	55	16	113	51	117	No shade
Lodgepole pine							
5	95	63	2	72	10	59	Shade
5	123	45	11	66	12	68	No shade

*Sandy loam to clay loam, pH 6.1 - 6.6

Kiwa Springs Plot* - 1957

Seedlings	Root length	Top height	Mycorrhizae				Remarks
			Black		White		
			No.	Depth	No.	Depth	
Basis	Mm	Mm		Mm		Mm	
Ponderosa pine							
5	163	51	16	96	4	95	No shade

*Sandy loam, pH 6.0 - 6.4

All Plots and All Soils - 1957 and 1958

Seedlings	Root length	Top height	Mycorrhizae				Remarks
			Black		White		
			No.	Depth	No.	Depth	
Basis	Mm	Mm		Mm		Mm	
Ponderosa pine							
18	168	67	34	50	85	90	Shade
5	215	58	12	89	31	104	½ shade
18	213	50	52	102	73	107	No shade
Lodgepole pine							
15	117	50	3	71	114	58	Shade
5	164	38	14	87	27	106	½ shade
10	144	42	21	87	58	74	No shade

SUMMARY CONSIDERATIONS ON THE SCOLYTIDAE OF THE GENUS DENDROCTONUS IN MEXICO

Julio Riquelme Inda

Of the Scolytid insects observed in the forests of Mexico, those of the genus Dendroctonus are considered the most harmful, principally because of their destructive action on trees of the genus Pinus, and also because they have propagated in extensive areas where pines grow.

In the first two or three years of this century a few Mexican naturalists undertook to study certain forest insects that had been noticed by reason of the trail of destruction they left in their wake. Many ocote pines (Pinus leiophylla and Pinus ayacahuite) attacked by said insects had been observed in the Cuautzingo woodlands in the District of Jonacatepec, State of Morelos.

It is clarified that four or five years prior to 1903 the Cuautzingo woods were free from plagues of any kind. Therefore, the infestation came to light unexpectedly when it was noticed that trees in various parts of the woods began to shrivel and dry up.

How the infestation originated and whence it came is not known to date. However, it may have been due to a natural emigration of the insects from regions already infected or perhaps the plague was carried by carved wood from infested areas. The fact is that thereafter, the forest owners, in an effort to preserve same, disposed that no animals were to be taken to pasture in the forests and that not even one branch was to be cut off the forest trees. To all purposes, the woods were closed grounds.

The procedure outlined above was sound on principle but, unfortunately, it was misunderstood and badly carried out. As a result of its enforcement, no dead trees or even dry branches were removed from the Cuautzingo forests for many years. The fallen trees rotted on the ground fostering the growth of myriad parasitic fungi, saprophytes, and innumerable destructive insects, wood- and bark-borers, the latter including scolytid insects of the genus Dendroctonus mostly.

Consequently, the conclusion is that the principal reason why the Dendroctonus plague preyed on the trees in the Cuautzingo forest was the neglect and abandonment enforced on the forest. Furthermore, as a result of the fact that Mexico did not have an efficient forest service to undertake to study and combat that type of plague, the Dendroctonus beetles spread unhampered to other regions of Mexico where various species of the genus Pinus grow.

At the beginning of this century, the Cuautzingo forest covered a very large area. It is located in a zone where the land is generally fertile although variable as to its physico-chemical constitution. The forest is about 2,000 meters over sea level. Due to steep slopes and many deep ravines, rain water easily furrows the ground, opens cracks and washes away the humus-covered surface layer that benefited the earth in the plains at the foot of the forest or was lost in the ravines.

The predominant species of trees in the Cuatzingo forest were two different species of Ocote pine: one called "Chinese ocote pine" (*Pinus Ieio-phylla*, Ch. & Sch.) and the other "White ocote pine" (*P. ayacahuite, Ehr.*). Observation disclosed that the attack on the former was far worse.

At present, the Cuatzingo forest has suffered great changes and the trees found in same have disappeared to a large extent. In addition to ocote pine, there used to grow oaks (*Quercus*), cedars (*Cedrela* and *Cupressus*), sabines (*Juniperus* and *Taxodium*), and also many wild weeds, some possessing useful properties. Certain portions of the Cuatzingo woodlands are now in the process of natural regeneration.

In the course of the years, the *Scolytidae Dendroctonus* have spread to other regions of Mexico where pines are found, such insects attacking pines preferentially.

After the first study of the *Dendroctonus* made by us at the turn of this century, we continued observing and investigating other forest insects in general, having received valuable assistance from Dr. A. D. Hopkins who was for many years one of the most competent forest insect specialists in the Enthomology Division of the Department of Agriculture in Washington (In charge of Forest Insect Investigations) and with whom we corresponded regularly. Dr. Hopkins helped us greatly in our work, particularly in the identification and classification of various species of insects destructive to Mexican forests. Among the specimens we sent him were various *Dendroctonus*, including the *D. Mexicanus* and the *D. valens*, some of the most dreaded species because of the damage caused to pines.

The species *D. Mexicanus*, Hopk., is probably the one that has caused the greatest destruction and currently is extended throughout the pine forests, with the exception of the State of Chiapas, where not this but other species of the same genus are known. The presence of this scolytid is constant in *Pinus leiophylla* and in *Pinus Montezumae*. However, this *Dendroctonus* as well as others causing secondary damage which will be mentioned hereinafter, are dangerous only when the soil and microclime conditions in general evidence a marked drop in humidity, according to our observations.

In effect, it was observed at Cuatzingo and it has been confirmed in other places subsequently, that a prolonged drought, concurrently with other causes at times, such as fires, for example, cause a shortage of sufficient humidity, which the Ocote pines had enjoyed at the Cuatzingo forest over a long period of time. The lack of humidity and the lack of sap in the trees brings about a disturbance of equilibrium in the annual physiological work and thus vegetation loses vigor, weakens and is rendered an easier prey to parasites.

Unquestionably, the peculiar nature of the soil is a factor of importance to the propagation of plagues; although the value of chemical properties must not be overlooked, the fact is that the physical properties of the soil are the ones that most especially determine the healthy and vigorous vegetation of wood plants or trees. But even in such grounds, when there is no forest cultivation and the trees are absolutely neglected, the ravage is far more serious because the insects, finding the vegetation stunted and feeble, attack more vigorously and destroy it more quickly.

The *Dendroctonus* currently observed in the Mexican forests are the following:

D. convexifrons, Hop.--In the pine woods of the States of Mexico and Michoacán.

D. Mexicanus, Hop.--In the Federal District and in the States of Durango, Hidalgo, Mexico, Michoacan, Morelos and Tlaxcala.

D. paralellocollis, Chap.--In the States of Chiapas, Durango, Mexico, Michoacan, Morelos, Tlaxcala and Veracruz.

D. valens, Lec.--In Lower California, Colima, Chiapas, Chihuahua, Federal District, Durango, Hidalgo, Mexico, Michoacan, Morelos, Puebla and Tlaxcala.

There are other species living on the Ocote pines in different spots in the Federal District and the State of Mexico, and in the sides of the Popocatepetl volcano. Such species are: *D. terebrans*, Oliv.; *D. simplex*, Lec.; *D. rufipennis*, Kirby.; *D. similis*, Dietz.; *D. approximatus*, Dietz; and *D. frontalis*, Zimm. These same species and the *D. Beaumanni*, were found in the cedars (*Cedrela* and *Cupressus*) in the Chapultepec Woods and in a Park in Tacubaya, of Mexico City, together with the genus *Gnatothrichus* and *Phloeosinus*, also Scolytids. The *D. piceaperda*, Hopk., was likewise found beneath the bark of trees in the Amecameca are in the State of Mexico.

The procedures used in Mexico to combat in certain cases the *Dendroctonus* and other bark-boring insects have consisted only in chopping down the attacked trees, peeling off the bark and burning it in the same place to prevent dispersion of the insects. Flame-throwers are directed against the surface of trees stripped of bark, at the same time.

Various insecticides have been tested to determine which may find application in different areas of the country containing pines affected by the above described parasites. However, the use of insecticides is difficult and costly. Application has been made of the following substances: arsenic and copper arsenic acetate in oil emulsions, in oil and soap emulsion, carbon bisulphide, tar, gasoline, etc., but they all turned out too expensive.

Fortunately, we have had in Mexico for several years, and some of its competent technicians still live in this country, a Forest Mission dependent on the United Nations Food and Agriculture Organization, which has made very interesting studies that may well be taken as basis for further studies subsequently undertaken by the Institute of Forest Research, soon to be inaugurated

Several Mexican technicians who have been part of the Mission, will probably guide the future activities of the Institute of Forest Research.

Dr. Fred Hartig, of the personnel of the Forest Mission of the FAO in Mexico, in his Report on Forest Enthomology, recommends for the fight against forest insects the use of a new fog-making apparatus employing products manufactured in an oil emulsion of BBC (benzol hexachloride) DDT and Lindanum, or else the use of a new product Merskche Forst Viton.

Dr. Hartig's report states that "in other countries excellent results have been obtained with the following mixtures: DDT in a 17% solution (15% with 2% HCH, or 12% with 5% HCM. This product is hexachlorocyclohexane) and also, cammexane in a 15% solution. Use has also been made, with good results, of Cerason ML, Gamma ML 15% and 2 with DDT 17%, 6 DDT 12% plus 5%, or 2% Gamma. DDT Gamma in a 9% solution has been tested, too."

Anyway, for large forest areas, the application of insecticides still presents difficulties and its cost is too high.

In our opinion, future research for control of the bark-boring insects, whose existence is concealed between the tree trunk and its bark, should be directed with a view to the natural enemies of those insects, i.e., by the method of biological control.

Such research will probably be undertaken by the Institute of Forest Research. The construction of its new building has just been completed in the Tree Nursery maintained by the Mexican Department of Agriculture in Coyoacan, Federal District, within Mexico City.

In view of the above described conditions, the Undersigned, currently Life President of the Mexican Forest Society, deems most advantageous to establish direct and constant contact with forest pathologists and entomologists in the United States and Canada, because the exchange of scientific information between said men and the Mexican forest specialists will result in a joint work of great mutual benefit.

Therefore, upon extending cordial greetings to the Gentlemen attending the Sixth Western International Forest Disease Work Conference, we would like to say that the furtherance of scientific and friendly relations with Mexico is most desirable for the good of the forest resources of the three countries and the progress of forest parasitology.

Needless to say, Mexico shall always welcome your visits to this country with great pleasure and interest, and both the Mexican Forest Society, a private association, and the Institute of Forest Research, an official organization, will be happy to assist you in every way to carry out the study and research of forest sicknesses and plagues in Mexican soil.

APPENDIX I

Active Projects, New

(Projects leaders' affiliations and addresses are given in membership list Appendix VI.)

A. Forest Disease Surveys - General

58-A-1. Taxonomic and biological studies of the Ascomycetes and Fungi Imperfecti. (A. Funk).
Objective: To isolate in culture, identify, and study the biology and pathogenicity of fungi associated with cankers, dieback, and related disorders.

58-A-2. Studies of native and introduced *Populus* sp. (W. J. Bloomberg).
Objective: To determine the susceptibility to disease of native and introduced species of poplar with primary emphasis on the fungus *Cytospora chrysosperma*.

B. Noninfectious Diseases

58-B-1. Drought damage to western white pine and associated tree species (Charles D. Leaphart).
Objective: To study the effects of summer drought on western white pine and associated tree species.

C. Cone, Seed, and Seedling Diseases

58-C-1. Effect of Storage on Seedling Vitality (Ernest Wright).
Objective: To determine how to improve storage of stock as related to field survival.

D. Root and Soil Diseases or Relationships

58-D-1. Eastern Oregon Regeneration (Ernest Wright).
Objective: To determine the role of mycorrhizae on the growth and survival of western pines in field plots.

58-D-2. Fungi-Bark Beetle Study (Ernest Wright and Don Allen).
Objective: To determine the relation of fungi and other microscopic organisms to the success of beetle infestations.

58-D-3. Soil Microbiology Study (Ernest Wright and William Lowry).
Objective: To determine the relation of micro-organisms in forest soil to root-rot and other losses.

E. Foliage Diseases

None.

F. Stem Diseases - Malformations, dwarfmistletoes, etc.

58-F-1. Silvicultural control of dwarfmistletoe in the Douglas-fir, lodgepole pine, and western larch types (Charles D. Leaphart). Objective: To study the biology of the dwarfmistletoes attacking Douglas-fir, lodgepole pine, and western larch so that sound guidelines for silvicultural control of the parasite can be recommended.

G. Stem Diseases - Stains and decays - None.

H. Stem Diseases - Rusts and Cankers

58-H-1. Gall rust of lodgepole pine (R. S. Peterson). Objectives: To determine the life history of lodgepole pine gall rust in the central Rocky Mountains. To determine the nature and development of damage in individual lodgepole pines and the extent of damage in selected stands.

58-H-2. Western tree rusts of the coleosporioides complex (W. W. Wagener). Objective: To supplement, revise and prepare for publication the extensive experimental results of the late George G. Hedgcock pertaining to this group of rusts.

58-H-3. Cronartium top-kill in ponderosa pine (John Hunt). Objective: (1) To identify the pathogen, (2) to determine rate and extent of damage. Results: (1) No spores of the fungus have been found in the area where damage is most severe. Elsewhere along the eastern slope of the Cascades, Cronartium comandrae has been identified as the cause of death in pole-size ponderosa pines. (2) Two 6-acre plots were established in 1958. On one plot, 45 out of 130 ponderosa pines 11" dbh and larger were infected; 29 of the 45 had dead tops. On the other plot, 19 of 77 trees were infected and 4 had dead tops. Progress of the disease will be noted annually.

I. Wilt and Blight Diseases

58-I-1. Dendroclimatological studies in the western white pine type (Charles D. Leaphart). Objective: (1) To determine when and how frequently drought (or dry cycles) occurred in the past several centuries within the western white pine type and, more specifically, if any cycle in the past was as dry or of as long duration as the one starting around 1917 and reaching a peak in 1929 and 1930. (2) To compare growth of trees of different age classes through the first years of their life and thus determine if the recent climate, as reflected by growth in the 70-year-old age class, was different from the climate that older trees underwent when they were growing to age 70. (3) To compare growth of trees in the 70-year-age class growing on sites with various available moisture storage capacities, to compare growth of healthy and diseased trees within diseased stands with growth of healthy stands both adjacent to diseased stands and outside the pole blight range, and to determine if growth on residual healthy trees in diseased stands has returned to normal.

J. Defects and Decays of Forest Products - Dead timber, slash, etc.

58-J-1. Deterioration of beetle-killed Engelmann spruce in Colorado (F. G. Hawksworth and T. E. Hinds).
Objective: To determine the rate of windfall and decay in standing trees in beetle-killed Engelmann spruce stands in relation to time since kill.

K. Miscellaneous Studies

58-K-1. Tests of systemic fungicides (G. M. Harvey).
Objective: To determine the effectiveness of systemic fungicides such as Acti-dione against such diseases as white pine blister rust and ponderosa pine needle blight.

APPENDIX II

Terminated Projects

(For publications see Appendix IV under author.)

53-D-7. Phytophthora root rot of coniferous trees in British Columbia (P. J. Salisbury). Publications - none.

53-F-1. Biological and chemical control of dwarfmistletoes (R. J. Bourchier).

Results: Six chemicals were tested for their suitability as control agents of dwarfmistletoes. The best result obtained was the killing of a high percentage of the aerial shoots, with light to moderate damage to the host. No killing of the endophytic system was obtained, as evidenced by re-sprouting of the mistletoe plants.

53-G-4. Decay of subalpine spruce on the Rocky Mountain Forest Reserves in Alberta (D. E. Etheridge).

53-G-5. Root and butt rot of subalpine spruce on the Rocky Mountain Forest Reserve in Alberta (D. E. Etheridge).

54-G-4. The influence of moisture and other factors on the activity of heartrot fungi in subalpine spruce (D. E. Etheridge).

Results: Subalpine spruce on the Rocky Mountain Forest Reserve was found to be decayed to the extent of 20 percent of the gross merchantable volume but varied in different areas from 1.4 to 41.9 percent. Much of the variation is attributed to site differences as follows: moist sites were 24.5 percent decayed and dry sites were 9.2 percent decayed. The optimum moisture content for the maximum development of butt-rotting fungi was determined to be higher than that for trunk-rotting fungi. Significantly, the moisture content of subalpine spruce heartwood is higher in overstory trees than in understory trees as well as being higher in the basal portions of trees than farther up.

55-G-4. Hyphal fusions and their value in identifying various species of Thelephoraceae (R. J. Bourchier).

Results: Hyphal fusions occurred between different isolates of 5 of the 6 species tested (Corticium vellereum, C. galactinum, Peniophora aspera, Stereum sanguinolentum, S. purpureum). Hyphal fusions did not occur between isolates of Peniophora gigantea. Potatoe-dextrose agar produced the greatest number of fusions, between isolates of Corticium vellereum at least. Temperature and pH variations had little effect on fusions taking place. The hyphal fusion technique is not amenable to development for use in identifying large numbers of cultures, but rather has limited or supplementary values only.

53-J-2. Deterioration of logging residue on the British Columbia coast (H. W. Eades and J. W. Roff).

Results: The rate of deterioration of residue increased rapidly to a maximum between the second and third years following logging and decreased annually thereafter. During the first three years losses amounted to over one-half the net volume. Sitka spruce was more decay-resistant while amabilis fir was less resistant--particularly at the outset--than western hemlock residue.

In western hemlock decay was mainly of the brown rot type, in Sitka spruce white rot was more prevalent while in amabilis fir both types were approximately equal in importance.

Deterioration of residue was affected by retention of moisture by bark or proximity to ground, also it was more severe in pieces infested with ambrosia beetle or which contained decays from the standing tree.

APPENDIX III
New and Modified Techniques

1. Random plot selection in disease survey (D. R. Miller).

To accelerate the statewide disease survey in California and to correlate these results more closely with those of other resource surveys, a new sampling procedure was devised and used in 1958. Randomly located plots based on a specific number of trees are now being used rather than permanent plots of prescribed acreage.

The randomly established plot consists of 25 trees over 11 inches DBH. These trees are taken on a strip $\frac{1}{2}$ chain (33 feet) wide and up to 50 chains (5/8 mile) in length. The strip runs 10 chains in the direction selected; then, after an offset of one chain to the left the direction is reversed and the strip continues for 20 chains. If the 25 trees have not yet been found, a 2-chain offset is made to the left. Again the direction is reversed (this portion of the strip is run in the original direction and parallel to the other two strip segments) and the strip continues up to 20 more chains. If 50 chains of strip are traversed without getting the 25 trees, the plot is discarded and a new one is drawn to replace it.

The starting point of the plot must be at least 2 and not more than 22 chains from and at right angles to the road. The location and position of the initial point is determined by the procedure described in item 6 below. The method provides a 20-chain ($\frac{1}{4}$ mile) strip on either side of the road that may be sampled. When the strip crosses a road, a 4-chain offset is made on which no data are taken to eliminate any influence or bias that might be caused by the road. The data will be summarized by subregions.

The steps used in selecting the plot locations are:

1. The commercial timber type in the State is divided into seven subregions.

2. The townships supporting commercial timber type in each subregion are numbered consecutively.

3. Aluminum tags about the size of a quarter bearing the numbers for all timbered townships of the subregion are placed in a container, thoroughly shaken and then one tag is drawn.

4. Similar tags numbered from 1 to 36, representing the sections in a township, are placed in another container and one of these is selected in a similar manner.

5. The plot-location point within a section is obtained by using tags numbered from 1 to 80. The first draw gives the distance eastward from the northwest corner. The second draw determines the distance southward from the same point.

6. The plot is then moved from the location determined (in item 5) to the nearest road. The road must be passable for the vehicle being used by the disease survey crews. Next the distance from some determinable feature common to both the ground and map (such as a road junction, stream crossing, section line marker, etc.) is measured. The point on the road to which the plot is moved is known as the "initial point."

7. The distance from the road, and the side of the road on which the plot must start, is next determined. Tags numbered from 2 to 22 and from 102 to 122 are used. Tags of the "hundred" series place the plot across the road from the location of the original plot site.

8. The last determination to be made is the azimuth or direction of the plot strip. This is done by drawing tags numbered from 1 to 360.

If the plot falls outside known type, it is discarded and another plot drawn from the "township through the complete drawing process." The above steps and eliminations are performed in the office. Upon examination in the field, any plot that does not have a sufficient number of trees is discarded and a new location selected as outlined.

In addition to the "readily accessible" or "road zone" plots a small group of plots (about 5 percent of the number scheduled as road zone plots) is drawn to sample disease conditions on the timber growing in the "back country." Thus the entire timbered area is sampled even though the sample is small for the area outside the "road zone."

By following this standard, random procedure each year, the data are cumulative. The scheduled survey is expected to answer many of our questions in 4 or 5 years and to have statistically reliable data in 10 years.

All pest and disease data are taken in code and when transferred to punch cards can be summarized on the International Business Machines.

2. Expanded polystyrene (styrofoam) method of studying dew deposit. (M. G. Lloyd)

Expanded polystyrene (styrofoam) blocks can be used to obtain a measure of dew deposit. The material is non-hygroscopic and has radiational characteristics similar to leaf surfaces.

Blocks of styrofoam weighted before and after exposure for a night will give information on amount of dew deposited. A block of styrofoam mounted with one end on a fulcrum and the other balanced and geared to a pen riding on a chart mounted on a clock-driven drum will give a measure of duration as well as amount of dew deposited.

Seven recording instruments, developed by the Northern Rocky Mountain Experiment Station to record change in weight of fuel moisture sticks, were modified to record duration and amount of dew by replacing the fuel moisture sticks with styrofoam blocks $1\frac{1}{2}$ x 12 x 24 inches.

Observations were taken of moisture deposited as dew under a variety of topographic and vegetative cover conditions on the Priest River Experimental Forest of northern Idaho from July through September, 1958. Strong gusty winds blew the blocks from their supports, otherwise the instruments gave an excellent record of moisture deposited as dew. Approximately one-hundredth of an inch of moisture per square inch of surface gave full scale deflection of the pens. Dew deposits at one foot above the ground adjacent to the main meteorological station ranged from amounts equal to .015 inches of precipitation on clear quiet nights following rainy periods to zero on windy cloudy nights.

3. A modified spore trap of the vaselined slide type (John C. Hopkins).

A spore trap, employing a vaseline smeared slide as the adhesive surface, was modified by provision of a collecting system for retention of water droplets drained from the slide.

To collect spores of Atropellis piniphila, an aluminum plate, slightly larger than the standard microscope slide size, was attached to the tree in a vertical position with heavy gauge wire and placed so as to lie about 10 mm. from the surface of the apothecia. A vaseline coated slide was then attached, by means of a "bull dog" clip.

Spore release occurred during or after rain had fallen but erratic results soon became manifest. These were traced to the removal by water droplets on the vaselined surface of most of the spores in their path. Shields from rain could not be devised because of the necessary proximity of slide and apothecium and also because of the importance of exposing the apothecia to the elements. Accordingly, the slide trap was modified by bending an additional basal piece into the form of a trough which sloped gently. Below this trough, and at the side down towards which the trough sloped, a lateral extension was made and looped back over the base of the trap. A test tube was inserted into the loop, while a "bull dog" clip, placed over the free end and the base, secured it in position. The open end of the tube then lay immediately below the end of the trough.

After deposition of water droplets on the vaselined surface of the slide, water from a wash bottle was used to transfer them down the trough and into the test tube, carrying any spores with them. Later, the slide, after removal from the trap, was heated under a thin film of water to facilitate removal of any further spores. Examination of slides indicated that this treatment resulted in virtually all the spores being transferred from the vaseline to the water. Counts were then made on the combined suspensions by means of a haemocytometer.

APPENDIX IV

Publications

1. Anonymous. What's wrong with my trees? Calif. For. & Range Expt. Sta. Misc. Paper No. 26. Oct. 1958.

2. Andrews, S. R. Dwarfmistletoe of ponderosa pine in the Southwest. U.S.D.A., Forest Service, Forest Pest Leaflet 19. 4 pp. 1957.

3. Bourchier, R. J. The effects of temperature, pH, and medium on hyphal fusions in the Thelephoraceae. Can. Dept. Agr., For. Biol. Div., Calgary, Alberta. (Mimeographed.) Dec. 1955.

4. ______. Variation in cultural conditions and its effect on hyphal fusions in *Corticium vellereum*. Mycologia 49(1): 20-28. 1957.

5. ______. Chemical control of dwarfmistletoe on lodgepole pine in Alberta. *In* Can. Dept. Agr., For. Biol. Div., Bi-monthly Prog. Rept. 10(1): 4. 1954.

6. ______. Chemical control of dwarfmistletoe on lodgepole pine in Alberta. Can. Dept. Agr., For. Biol. Div., Calgary, Alberta. (Mimeographed.) January 1956.

7. ______. Red belt, Atropellis canker, and tree mortality of lodgepole pine in Alberta. *In* Can. Dept. Agr., For. Biol. Div., Bi-Monthly Prog. Rept. 13(2): 2-3. 1957.

8. Davidson, R. W., and T. E. Hinds. Unusual fungi associated with decay in some forest trees in Colorado. Phytopathology 48: 216-218. 1958.

9. Eades, H. W. Color tests for the differentiation of heartwood and sapwood in western hemlock. For. Prod. Jour. March 1958.

10. Engelhardt, N. T. Pathological deterioration of wind-damaged white spruce and alpine fir in the Crescent Spur area, B. C. Can. Dept. Agr., For. Biol. Div., Victoria. (Processed.) 1957.

11. Etheridge, D. E. Differentiation of white- and brown-rot fungi by an oxidase reaction. Nature 179(4566): 921-922. 1957.

12. ______. Moisture and temperature relations of heartwood fungi in subalpine spruce. Can. Jour. Bot. 35: 935-944. 1957.

13. ______. The effect of variations in decay of moisture content and rate of growth in subalpine spruce. Can. Jour. Bot. 36: 187-206. 1958.

14. Etheridge, D. E. Decay in subalpine spruce on the Rocky Mountain Forest Reserve in Alberta. Can. Jour. Bot. 34: 805-818. 1958.

15. _______. Decay losses in subalpine spruce on the Rocky Mountain Forest Reserve in Alberta. For. Chron. 34(2): 116-131. 1958.

16. _______. Moisture and temperature relations of heartwood fungi in subalpine spruce. Can. Jour. Bot. 35: 935-944. 1957.

17. _______. The effect on variations in decay of moisture content and rate of growth in subalpine spruce. Can. Jour. Bot. 36: 187-201. 1958.

18. _______ and J. C. Laut. Fungi associated with living and dead branches of pole-sized aspen. In Can. Dept. Agr., For. Biol. Div., Bi-Monthly Prog. Rept. 14(4): 2-3. 1958.

19. Foster, R. E. Proposed standards of measurement and procedure relating to investigations of decay. Can. Dept. Agr., For. Biol. Div., Victoria. (Processed.) 1958.

20. _______. Forest disease investigations. In Ann. Rept. of the For. Serv. for the year ended Dec. 31, 1957, Prov. of Brit. Col., Victoria. 1958.

21. _______. An estimate of total loss from decay in natural forests of British Columbia. Can. Dept. Agr., For. Biol. Div., Victoria. (Processed.) 1957.

22. _______, J. E. Browne, and A. T. Foster. Studies in forest pathology. XIX. Decay of western hemlock and amabilis fir in the Kitimat region of British Columbia. Can. Dept. Agr., For. Biol. Div., Pub. 1029. Ottawa. 1958.

23. Gill, L. S. Dwarfmistletoe of lodgepole pine. U.S.D.A., Forest Service, Forest Pest Leaflet 18. 5 pp. 1957.

24. Graham, D. P. Results of some silvicultural tests in pole blight diseased white pine stands. Jour. For. 56: 284-287. 1958.

25. _______. Results of pole blight damage surveys in the western white pine type. Jour. For. 56: 652-655. 1958.

26. Harvey, George M., and Leon I. Cohen. The extent of blister rust mycelia beyond bark discolorations on sugar pine. Pac. N. W. For. & Range Expt. Sta. Res. Note 159. March 1958.

27. Hawksworth, F. G. Survey of lodgepole pine dwarfmistletoe on the Roosevelt, Medicine Bow, and Bighorn National Forests. Rocky Mtn. For. & Range Expt. Sta. Paper 35. 13 pp. 1958.

28. Hawksworth, F. G. Rate of spread and intensification of dwarfmistletle in young lodgepole pine stands. Jour. For. 56: 404-407. 1958.

29. Hopkins, J. C. Studies on the Atropellis canker disease of lodgepole pine in Alberta. Can. Dept. Agr., For. Biol. Div., Calgary, Alberta. (Mimeographed.) 1957.

30. Hunt, John, and T. W. Childs. Ponderosa pine needle blight in eastern Oregon during 1955 and 1956. Pac. N. W. For. & Range Expt. Sta. Res. Note 147. May 1957.

31. ________ and Edward J. Dimock II. Port-Orford-cedar--a poor risk for reforestation. Pac. N. W. For. & Range Expt. Sta. Res. Note 139. April 1957.

32. ________ and Ernest Wright. Needle cast of Sitka spruce in Oregon. Plant Disease Reporter. July 15, 1957.

33. Kimmey, J. W. The heart rots of redwood. U.S.D.A., Forest Service. Forest Pest Leaflet 25. 7 pp., illus. 1958.

34. ________. Application of indicator cull factors to white and red fir stands in the Sierra Nevada. U. S. Forest Service, Calif. For. & Range Expt. Sta. For. Res. Note 127. 5 pp., illus. 1957.

35. Leaphart, C. D. Pole blight--how it may influence white pine management in light of current knowledge. Jour. For. 56: 746-751. 1958.

36. ________. Root characteristics of western white pine and associated tree species in a stand affected with pole blight of white pine. U. S. Forest Service, Intermountain For. & Range Expt. Sta. Res. Paper 52. 10 pp. 1958.

37. Molnar, A. C. Province of British Columbia, Forest Disease Survey. In Ann. Rept. of the For. In. and Dis. Surv., Can. Dept. Agr., For. Biol. Div., Ottawa. 1958.

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39. Nordin, V. J. Basal fire scars and the occurrence of decay in lodgepole pine. For. Chron. 34(3): 257-265. 1958.

40. Offord, H. R. Phytocides in Silviculture. Proc. 58th Ann. Meeting of Soc. Amer. For. October 1958.

41. ________. Dwarfmistletoe on conifers. Tenth Annual Calif. Weed Conf. pp 18-22. January 1958.

42. Offord, H. R., Clarence R. Quick and Virgil D. Moss. Blister Rust Control Aided by Use of Chemicals for Killing Ribes. Jour. For. 56: 12-18. 1958.

43. Parker, A. K. Decay associated with logging injury to spruce and balsam in the Prince George region of British Columbia. Can. Dept. Agr., For. Biol. Div., Victoria. (Processed.) 1958.

44. Paul, G., and D. E. Etheridge. Decay of aspen and balsam poplar in the Lesser Slave Lake region of Alberta. Alta. Dept. Lands and For., For. and Wild Life Div., Edmonton, and Can. Dept. Agr., For. Biol. Div., Calgary. (Mimeographed.) 1958.

45. Porter, W. A. Biological studies of western red cedar needle blight caused by *Keithia thujina* Durand. Can. Dept. Agr., For. Biol. Div., Victoria. (Processed.) 1957.

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47. ______. Host fungus index for the Pacific Northwest. II. Fungi. Wash. Agr. Expt. Sta. Circ. 336. 237 pp. Nov. 1958.

48. Shearer, R. C., and J. L. Mielke. An annotated list of the diseases of western larch. U. S. Forest Service, Intermountain For. and Range Expt. Sta. Res. Note 53. 6 pp. 1958.

49. Thomas, G. P. Studies in forest pathology. XVIII. The occurence of the Indian paint fungus, *Echinodontium tinctorium* E. & E., in British Columbia. Can. Dept. Agr., For. Biol. Div. Pub. 1041. Ottawa. 1958.

50. ______ and H. M. Craig. Deterioration by fungi of killed Douglas-fir in Interior British Columbia. Can. Dept. Agr., For. Biol. Div., Victoria. (Processed.) 1958.

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54. Wallis, G. W. *Poria weirii* root rot of Douglas-fir. Can. Dept. Agr., For. Biol. Div., Victoria. (Processed.) 1957.

55. Woods, F. W., O. L Copeland, Jr., and Carl E. Ostrom. Soil management for forest trees. U.S.D.A. Yearbook of Agr. 1957: 710-715.

56. Wright, Ernest. Influence of temperature and moisture on damping-off of American and Siberian elm, black locust and desert willow. Phytopath 47: 658-662. 1957.

57. _______. Cytospora cankers of cottonwood. Plant Dis. Reporter 41(10): 2 pp. 1957.

58. _______. Cytospora canker of Rocky Mountain Douglas-fir. Plant Dis. Reporter 41(9): 3 pp. 1957.

59. _______. Importance of mycorrhizae to ponderosa pine seedlings. For. Sci. 3(3): 275-280. 1957.

60. _______ and Robert F. Tarrant. Occurrence of mycorrhizae after logging and slash-burning in the Douglas-fir type. Pac. N. W. For. & Range Expt. Sta. Res. Note 160. 8 pp. 1958.

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APPENDIX V

Minutes of the Business Meeting

Chairman Kimmey called the meeting to order at 1:30 P.M., December 5. Moved, seconded and approved to dispense with reading of last year's minutes. The Treasurer submitted the following report:

	Receipts	Expenses
Registrations - 35 at $3.	$ 105.00	
Banquet - 47 paid at $4.	188.00	$ 251.83
Luncheon - 37 paid	55.05	53.87
Rent Conference Room		70.00
Rent Tape Recorder		3.00
Receipt Books and Name Tags		2.00
	$ 348.05	$ 380.70
Deficit paid in Canadian funds from $40.30 U.S. funds	32.65	
	$ 380.70	
Balance on hand in treasury (5th Proc., p. 116)		$ 40.30
Deficit on 6th Meeting	$ 32.65	
Exchange on U.S. Funds 4% x $32.65	1.31	
Balance in treasury		$ 6.34

Moved and seconded that Treasurer's report be accepted. Motion carried.

<u>D. C. Buckland Memorial Committee</u>. J. E. Bier reported on status of memorial action and described difficulties of binding in gift book form the odd sizes of the Buckland publications. Moved, seconded and carried that committee proceed with the job of binding.

<u>Decay Standards Committee</u>. R. E. Foster reported work of committee completed and presented a copy of final report. "Proposed Standards of Measurement and Procedure Relating to Investigation of Decay" by R. E. Foster, 20 pp. Multilith, Forest Biology Laboratory, Victoria, B.C., Canada, February, 1958. Moved, seconded and carried that this committee be dissolved with appreciation for its accomplishments.

<u>Dwarfmistletoe Research Committee</u>. H. R. Offord reported as follows:

COMMITTEE REPORT ON STATUS AND NEEDS OF RESEARCH ON DWARFMISTLETOE, 1958

J. E. Bier, K. R. Shea, H. R. Offord (Chairman)

Highlights of 1958 Research

1. Intensification and spread

   a. Larch, Douglas-fir, and lodgepole pine dwarfmistletoe did not seriously affect reproduction less than 10 years old. The youngest infected trees found were 7 years old. Rate of spread in lodgepole pine in Idaho and Montana was calculated to be a little faster than in Colorado and Wyoming as reported by Hawksworth in Journal of Forestry 56: 404-407, 1957. Germinating seeds were found as far as 40 feet from the nearest source tree. (Leaphart, Int.)

   b. Distribution of dwarfmistletoe in both overstory and understory was observed to be very patchy in Oregon and Washington. Large acreages were found where the parasite was abundant in the overstory while most of the understory was free. (Childs, PNW.)

   c. Dwarfmistletoe occurrence on the first year's statewide randomly located disease survey plots showed dwarfmistletoe infected trees on 59 out of 125 plots. Most frequent occurrence was on red fir, where 76 (or 42 percent) of the 181 red fir trees on plots were infected. Extending similar comments to other species: 13.9 percent of white fir were infected, 13.9 percent of ponderosa pine, 8.1 percent of sugar pine, 10 percent of lodgepole. (Miller and Bynum, Cal.)

2. Biological and chemical control

   a. An undescribed twig disease was found in Colorado. The disease causes necrotic areas in the outer bark of dwarfmistletoe infected twigs. The parasite shoots are killed but the vigor of the branch is apparently not affected. In one area, 85 percent of the mistletoe plants were diseased. A similar disease but less intense was found on _A. vaginatum_ on ponderosa pine and _A. campylopodum_ f. _cyanocarpum_ on limber pine. The suspected causal fungus has been isolated but not identified. (Hawksworth, RM.)

   b. Chemical control tests on _A. americanum_ on lodgepole pine were made with Acti-dione and its derivatives and maleic hydrazide. By mid-October sprays of Acti-dione had killed over 80 percent of the sprayed shoots. The effect on the endophytic system is unknown. Pine foliage was damaged. Sprays of maleic hydrazide had no apparent effects on the parasite but the higher concentrations (2 percent) killed the host foliage. (Hawksworth, RM.)

c. 1957 tests of chemicals on *A. campylopodum* f. *campylopodum* on Jeffrey pine showed no obviously useful selectivity in toxicity in either the series of foliage sprays or in the series of stem sprays and stem injections. Chloro IPC continues to be one of the more promising phytocides. In 1958 Acti-dione in oil diluent and in thick emulsion was applied to dwarfmistletoe infections on Jeffrey, ponderosa, and white fir. No reportable data from 1958 tests as yet. (Bega and Offord, Cal.)

d. A new disease of dwarfmistletoe shoots has been discovered. While little work has yet been done, pathogenicity has been established and the fungus has been tentatively assigned to the genus *Colletotrichum* as delimited by von Arx. Preliminary observations suggest that the disease may have promise as a biological control. (J. R. Parmeter, Univ. of Calif.)

3. Life history, taxonomy, and morphology

a. Studies of seed ballistics indicate that the initial velocity of *A. vaginatum* seeds as they leave the exocarp is about 45 ft. per second. This species apparently has a higher vertical angle of discharge than *A. americanum* which averages about 40° above the horizontal. (Hawksworth, RM.)

b. The seed dispersal period of *A. vaginatum* in Colorado was similar to that found in Arizona. The peak discharge of *A. americanum* in Colorado was about 2 weeks later than for *A. vaginatum*. (Hawksworth, RM.)

c. Inoculations with *A. vaginatum* at the Fort Valley Experimental Forest show that over 90 percent of the dwarfmistletoe plants produce their first shoots in 3 to 5 years. Very few make it in 2, and one plant has taken 8 years. (Andrews and Hawksworth, RM.)

d. Job Kuijt's thesis on the "Morphological aspects of parasitism in dwarfmistletoe" was completed and is on file at the University of California. Important information from this work as summarized by Parmeter is as follows:

I - All species of mistletoe produce localized swellings restricted to a definite portion of the branch. Some species, however, produce also isophasic brooms in which little swelling is observed, but proliferation of branches is extreme. The same mistletoe on the same host may produce both types. Isophasic brooming occurs with these combinations: *A. americanum* x *Pinus contorta*, *A. douglassii* x *Pseudotsuga taxifolia*, *A. pusillum* x *Picea glauca*, *A. minutissimum* x *Pinus excelsa*.

II - In isophasic brooms the endophytic system invades the buds each year and subsequent host elongation is accompanied by parasite elongation and/or division. In this way the parasite is able to keep up with host growth and thus yearly invade the new bud.

III - Shoot production follows a definite sequence in isophasic brooms. This sequence varies somewhat with species, but essentially it gives a different stage of development on each year's growth, the youngest having only buds, the next year flowering shoots, etc.

IV - Mistletoe infection may result in:

a - sexuality being overridden by vegetative growth
b - loss of apical dominance
c - intensification of negative geotropism
d - disturbed periodicity

These phenomena thought to result from interference with host auxin transport.

V - In addition the physiology and pathogenesis of mistletoe is discussed. The morphological association of host and parasite during penetration, growth, and fruiting are discussed in detail.

e. Field evidence indicates that there are at least two forms of dwarfmistletoe in true firs of California: a form that attacks only red fir and one that attacks only white fir. (J. R. Parmeter and R. F. Scharpf, Univ. of Calif.)

4. Host-parasite relationships

a. Studies at Centralia, Washington, on endophytic system and on the translocation of radioactive material between host and parasite have been previously reported. Translocation studies are being continued as inoculated pines develop satisfactory infections. (Keith Shea, Weyerhaeuser.)

b. Anatomical studies of phloem and xylem tissue of Arceuthobium spp. and their several coniferous hosts in California showed (1) that contact between parasite and host is direct in xylem area but indefinite in the phloem and (2) that different species of dwarfmistletoe show different levels of adaptation and parasitism to the host. (K. Esau and L. Srivastava, Univ. of Calif., Davis.)

Needed Research and Studies Not Yet Reported On

1. Intensification and spread

a. Studies will be initiated to explain the occurrence of clean reproduction in the immediate vicinity of infected overstories. (Childs, PNW.)

b. Research to answer these questions in lodgepole pine is needed: What is the actual rate of spread in reproduction after it has been exposed to 10, 20, or 30 years of infection from the overstory? How does including the first 10 years (where little or no infection occurs) affect the calculated rate of spread? How does stand history affect dwarfmistletoe intensity? (Leaphart, Int.)

  c. Pruning techniques and schedules. Research has established what a prunable infection is but we should know what constitutes a prunable tree. Latent infections, economics of pruning, and effects of pruning on growth need to be examined. (Keith Shea, Weyerhaeuser.)

  d. Economics of silvicultural control in relation to the intensity or level of infection. Some stands appear so heavily infected that there seems no alternative to clear cutting. (Keith Shea, Weyerhaeuser.)

  e. Applied research to determine silvicultural methods for control of dwarfmistletoe and at the same time reproduce a new stand of lodgepole pine in stands where much of the advanced reproduction is infected. (Kimmey, Int.)

2. Biological and chemical control

  a. Parasitic organisms noted in several forest types throughout the Western States will be observed and further tested for possible field use in biological control of dwarfmistletoe. (Hawksworth, RM; Parmeter, Univ. of Calif.; Mielke, Int.; Waters, Montana Univ.)

  b. For chemical control of mistletoes: antibiotics and promising new phytocides should be tested; rapid methods of screening chemicals for mistletoe control should be developed and transport of systemics from soil, stem, and foliage applications need further study. (RM, Int., Cal., Weyerhaeuser, Montana State.)

3. Life history, taxonomy, and morphology

  a. Laboratory tests to determine the factors affecting germination of dwarfmistletoe seeds are planned. (Hawksworth, RM; Parmeter, Univ. of Calif.; Waters, Montana State.)

  b. Life history studies are planned involving the fate of naturally dispersed seeds (germination, predation, percent survival at different times after discharge, proportion that results in infection, etc.). (Hawksworth, RM; Parmeter, Univ. of Calif.; Waters, Montana State; Keith Shea, Weyerhaeuser.)

  c. Inoculation studies with A. americanum will be started to determine the age of tissues susceptible to infection and the length of the latency period. (Hawksworth, RM.)

4. Host-parasite relationships

a. Studies are planned on the ability of dwarfmistletoe to go from one host to another--a question that must be answered in connection with certain proposed management practices. (Childs, PNW; Parmeter, Univ. of Calif.)

b. It is planned to test the relative susceptibility of Colorado and Black Hills ponderosa pine to infection by *A. vaginatum*. (Hawksworth, RM.)

c. Studies of the endophytic system of pedigreed infections of *A. vaginatum* will be started. (Eslyn, RM.)

d. Research on the resistance of selected ponderosa pines to infection by *A. vaginatum* will be undertaken. (Eslyn, RM.)

e. Detailed studies on the effect of *A. vaginatum* on growth and mortality of ponderosa pine will be started. (Andrews, RM.)

f. Continuation of anatomical studies on the vascular systems of host and parasite. (K. Esau and L. Srivastava, Univ. of Calif., Davis.)

g. Attention is called to the problem of water transport in host and parasite and to the moisture content of tree or tree parts affected. (J. Bier, Univ. B.C.)

Other Discussions of Afternoon Session. V. J. Nordin reviewed highlights of the several panels of the technical program. J. E. Bier outlined the program of the International Botanical Congress 1959 meeting at Montreal commenting on the plant science sections of particular interest to pathologists. H. S. McNabb outlined the new procedures to be followed in obtaining back copies and future annual addenda of the Boyce Index. Orders should be placed through Iowa State College Library.

Election of Officers. H. R. Offord was elected Chairman of the 7th Conference and R. E. Foster was elected Secretary. In line with tradition both officers were chosen rapidly and by unanimous vote.

Seventh Conference Meeting. The Conference voted to accept the invitation of Dr. C. G. Shaw to hold next year's meeting at Pullman, Washington on or about December 1, 1959.

The group extended formal thanks to the 1958 officers, to the local arrangements committee at Vancouver and Victoria, and to Dr. J. E. Bier for his hospitality on the afternoon of December 4.

The Conference adjourned at 3:45 P.M., December 5.